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A new westward migration route in an Asian passerine bird

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1 **Title:** Uncovering a new westward migration route in an Asian passerine bird

2

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15 **Summary**

16 The evolution of migration routes in birds remains poorly understood as changes in migration
17 strategies are rarely observed on contemporary time scales.¹⁻³ The Richard's Pipit *Anthus*
18 *richardi*, a migratory songbird breeding in Siberian grasslands and wintering in Southeast Asia,
19 has only recently become a regular autumn and winter visitor to Western Europe. Here, we
20 examine whether this change in occurrence merely reflects an increase in the number of
21 vagrants, that is, "lost" individuals that likely do not manage to return to their breeding grounds,
22 or represents a new migratory strategy.⁴⁻⁶ We show that Richard's Pipits in southwestern
23 Europe are true migrants: the same marked individuals return to Southern France in subsequent
24 winters and geo-localization tracking revealed that they originate from the western edge of the
25 known breeding range. They make an astonishing 6,000 km journey from Central Asia across
26 Eurasia, a very unusual longitudinal westward route among Siberian migratory birds.^{7,8}
27 Climatic niche modeling using citizen-science bird data suggests that the winter niche
28 suitability has increased in southwestern Europe, which may have led to increased winter
29 survival and eventual successful return journey and reproduction of individuals that initially
30 reached Europe as autumn vagrants. This illustrates that vagrancy may have an underestimated
31 role in the emergence of new migratory routes and adaptation to global change in migratory
32 birds.^{9,10} Whatever the underlying drivers and mechanisms, it constitutes one of the few
33 documented contemporary changes in migration route, and the first longitudinal shift, in a long-
34 distance migratory bird.

35

36 **Keywords**

37 Climate change, seasonal migration, geolocators, vagrancy, molt, Richard's Pipit

38 **Results and Discussion**

39

40 **Evidence for a new migration route**

41 Like many other Siberian birds that normally winter in southern Asia, Richard's Pipits have
42 long been known to reach Western Europe in small numbers in autumn.¹¹⁻¹³ The occurrence of
43 such "accidental" or "lost" birds outside their normal distribution range, which are mostly
44 juvenile birds that will never return to their breeding grounds, is often referred to as vagrancy.¹⁴
45 However, the pattern of Richard's Pipit occurrence has recently changed in southwestern
46 Europe (Figure 1). In France for example, the number of records increased from three to six
47 birds annually between 1981 and 1993 to a maximum of 144 birds in 2018 (Figure 2A) and this
48 increase is apparent in several localities in southern France that have been consistently
49 monitored since the 1950s or 1980s; the maximum flock size also increased during the same
50 1981-2019 period (Figure S1). The number of sightings of other Siberian vagrant species in
51 France has increased to a much lesser extent (average regression coefficient over time, 3.47 in
52 Richard's Pipit vs. 0.05 ± 0.057 for other vagrants; Figure 2B, Table S1), excluding that this
53 increase simply reflect a simultaneous increase in identification skills and observation
54 pressure.^{4,15} The first overwintering in Europe has been documented in 1991 in southern
55 France,¹⁶ after which overwintering and staging was reported from an increasing number of
56 sites (Figure S1). The species has now become a regular winter visitor to Southern and Western
57 France, as well as to Spain, Portugal and Italy.¹⁷

58 Two non-exclusive hypotheses can explain this recent increase: the number of vagrants
59 reaching Europe has increased or Richard's Pipit has established a new migration route, in
60 accordance with the "pseudo-vagrancy" hypothesis of Gilroy and Lees (2003).⁴⁻⁶ To
61 disentangle these explanations, we studied the species during three wintering periods along the
62 Mediterranean coast of France and Spain (Figure 1). Because the vast majority of vagrant
63 passerines are birds in their first post-natal migration, we specifically looked for the presence
64 of adults (birds more than one year old). Moreover, since most migratory passerines are faithful
65 to their migratory routes and wintering areas,^{18,19} we marked individuals to test if they were
66 returning the next winter. Both the presence of adults and of returning individuals would
67 support the migration hypothesis over the vagrancy hypothesis. Among 81 birds examined in
68 the hand in southern France and northeastern Spain, 28 (34.6 %) were found to be adults: a high
69 proportion similar to that observed in regular wintering species in Southern Europe (e.g.
70 European Robin *Erithacus rubecula*²⁰) and supporting the migration hypothesis. In addition,
71 from the 68 individuals that were color-ringed during the first two seasons, 11 were re-sighted

72 or re-trapped the following winters (four of them over two consecutive seasons; Table S2),
73 providing further empirical support to the migration hypothesis.

74 To determine whether birds that winter in France originate from the known breeding
75 area or from a previously undetected breeding population, we equipped seven individuals with
76 Global-Location-Sensors (GLS) during winter 2019/2020 (Table S2). The following winter, we
77 re-captured three of these individuals (recapture is needed for data retrieval with GLS). All
78 three birds spent the summer at the western edge of the known breeding range in a small area
79 of the Novosibirsk Oblast in Russia (Figure 3) where light data indicates that at least one
80 individual engaged in breeding behavior (Figure 3F), supporting the hypothesis that these birds
81 were regular migrants rather than vagrants. During the spring migration, the three individuals
82 used three different stopover locations for more than 24 hours; the second-year individual first
83 headed north and stopped in Sweden before redirecting eastward to reach a likely breeding site
84 where it lingered until the GLS stopped (Figure 3E). These three individuals thus traveled 5750,
85 7045, and 7320 km during their spring migration between Southern France and Siberia along a
86 migratory route that crosses countries where the species is rarely sighted.

87 To determine whether regular migrants are also present in other parts of the western
88 non-breeding range (Figure 1), we tested for the presence of adult birds in these locations using
89 pictures from citizen-science databases to estimate the age-ratio. On good quality pictures, first-
90 generation wing coverts (grown in the nest) can easily be distinguished from second-generation
91 feathers (see Figure S2), allowing safe ageing of birds with first-generation coverts as young
92 bird (i.e. less than one-year-old). However, some young birds molt all wing coverts during the
93 autumn, resulting in an *adult-type* plumage in winter that cannot be separated from adults
94 without in-hand examination. To estimate the proportions of the different molt stages among
95 young birds, we examined in-hand and aged 78 birds caught in France and Northeastern Spain,
96 to classify them into three molt phenotypes (*full-juvenile*, *extended-molt*, and *adult-type*, see
97 Figure S2), all of which can be determined based on pictures. Of 50 young birds examined, six
98 were of the *full-juvenile* type (12%), 39 belonged to the *extended-molt* type (78%), and five to
99 the *adult-type* (10%; see Figure S2 for details). Within 33 *adult-type* birds (which of course
100 include all adults), five (15 %) were found to be young birds upon in-hand examination. Molt
101 phenotype thus provides an imprecise but meaningful information on age. We then scored
102 pictures of 331 individuals across Europe and North Africa to estimate age-ratio variation. In
103 Northern Europe, *adult-type* birds are rare (10% in autumn, 15.2% in winter) and their number
104 is not significantly different from the number of *adult-type* birds expected if all birds were
105 young birds (7 *adult-type* birds out of 46 scored individuals versus 5 *adult-type* birds among 50

106 in-hand aged juveniles; Fisher's exact test p -value = 0.55). In southwestern Europe and North
107 Africa, however, *adult-type* birds are more common (48.5% in autumn, 59% in winter, Figure
108 S3), significantly more common than expected if all birds were young (winter period: 57 *adult-*
109 *type* out of 97; Chi-square test = 54.1, p -value < 0.001). The proportions of *adult-type* molt
110 phenotypes in citizen-science pictures thus demonstrate the regular occurrence of adult birds,
111 and hence likely regular migrants and wintering individuals, in the Iberian Peninsula, North
112 Africa (Morocco), western France, and Italy.

113

114 **Can vagrancy promote the emergence of new migratory routes?**

115 The change in status of Richard's Pipit from vagrant to regular migrant in southwestern Europe
116 opens up the question of the role of vagrancy in the establishment of new migration routes.
117 Large angle misorientation, also known as reverse migration¹¹ or mirror-image migration,²¹ has
118 been proposed to explain the occurrence of Siberian vagrants in Europe, particularly for
119 populations breeding in the western part of their distribution^{15,22,23} (but see²⁴). Such errors in
120 migratory orientation have usually dramatic consequences on fitness,²⁵ especially in passerines
121 where the energy cost of long migratory flights is very high,²⁶ and vagrants are therefore usually
122 thought to perish.^{14,27} The ability of vagrants to establish new migration routes may thus depend
123 crucially on the wintering conditions they encounter in the areas where they end up (i.e.,
124 overwinter survival) and on their ability to perform a successful return journey and transmit
125 their migration route to their offspring (via genetic inheritance as migration direction is
126 genetically determined in songbirds, e.g.²⁸⁻³⁰).

127 In Richard's Pipit, the main wintering grounds are in Southern and Southeast Asia
128 (Figure 1).¹³ Thus, the most parsimonious hypothesis is that the species' ancestral wintering
129 grounds are in Asia and that the European wintering range represents a derived state that was
130 recently established, or at least recently increased. To investigate the factors that may have
131 favored the observed change in migration strategy, we examined the wintering niche conditions
132 in the ancestral and derived ranges. When citizen-science occurrences data were plotted in a
133 two-dimensional space defined by PCA axes on climatic and habitat variables (Figure 4A),^{13,31}
134 we found that the niche of the European wintering range is broadly similar but not identical to
135 the niche used in Asia: niches overlapped with a Schoener's D value of 0.31 (D = 0: no overlap,
136 D = 1: complete overlap) and 68.8% of the European niche was included within the Asian niche.
137 We also performed two niche distribution models, one calibrated in Europe and one calibrated
138 in Asia, then projected them under current conditions (Figure 4B, S4). The projection of the
139 Asian calibrated model under current conditions over Europe mainly predict wintering in

140 western Iberian Peninsula and North Africa (Figure 4B), confirming that the species encounter
141 slightly different (but still overlapping) climatic conditions in southern France and northeastern
142 Spain compared to the ancestral wintering areas in Asia. To test for recent changes in European
143 wintering conditions, we projected a European calibrated model over two periods in 1961-1990
144 and 1990-2018, and found an extension in suitable wintering areas (mostly due to increasing
145 temperature; see Figure S5) between these periods, especially in northern Spain, southern and
146 western France and Italy (Figure 4C). Vagrant Richard's Pipits migrating west from Asia may
147 thus have found suitable environmental conditions to survive the winter in large areas of North
148 Africa and Iberian Peninsula (see ¹²), after which environmental changes (here climate change)
149 might have increase wintering opportunities for Richard's Pipit in southern Europe.

150 If these results suggest that the emergence of new migratory routes can ensue from the
151 survival and successful return migration of vagrants to Europe, to what extent natural selection
152 may explain the emergence and spread of this new wintering range remains to be investigated.
153 In particular, although proximate mechanisms of vagrancy remain largely unknown to date, it
154 should be verified that vagrancy is to some degree hardwired (otherwise this new migratory
155 orientation could not be transmitted to young) and that some forms of reproductive isolation
156 exist between individuals migrating west and east (otherwise panmixia would prevent the
157 stability of migration to Europe).^{5,6} We suppose that a migratory divide could exist in this
158 species with individuals at the western margin of the species' range, which should constitute a
159 distinct population, all having a westerly migratory route,^{32,33} but this would need to be tested
160 by deploying data loggers in breeding populations.

161 Ancient literature suggests that this species may have been observed with some
162 regularity in few European localities during the 19th century.^{34,35} Although we showed that
163 Richard's Pipit numbers have undoubtedly increased in recent decades, particularly in
164 southwestern Europe and probably due to changing temperatures, we cannot rule out the
165 hypothesis that a westward migratory route had existed for a long time and that we observed an
166 increased use of this route in recent decades.

167

168 **Concluding remarks**

169 In this study, we show that the occurrence of Richard's Pipit in southwestern Europe is, at least
170 in part, due to a population performing a regular seasonal migration, and cannot solely be
171 explained by disoriented vagrant individuals. While the role of vagrancy in colonization of new
172 breeding range has been documented in several species,³⁶⁻³⁹ our results support the idea that
173 vagrancy may also promote the establishment of new migratory routes.⁴ This idea was also

174 proposed to explain one of the few known contemporary changes^{2,3} in migration route in
175 passerines: the change from southwestern to northwestern orientation in central European
176 Blackcap *Sylvia atricapilla*,^{1,5,6} selected as a response to changing environment that increased
177 overwinter survival.^{40,41} Increased overwinter survival, helped by climate change, may also
178 explain recent increases in autumn and winter numbers of other Siberian species in Europe (e.g.
179 Yellow-browed Warbler *Phylloscopus inornatus*, Siberian Chiffchaff *Phylloscopus collybita*
180 *tristis*, Olive-backed Pipit *Anthus hodgsoni*) that may also be currently establishing new
181 secondary migration routes to Europe. The lack of records of these species during the spring
182 migration was perceived as undermining the “pseudo-vagrancy” theory⁴ but we have shown
183 here that such spring return migration can be particularly under-detected. The Richard’s Pipit
184 might thus be the most prominent example of a phenomenon that could change current
185 paradigms on the flexibility and constraints of avian migration. Indeed, there is no passerine
186 species confirmed to undertake such longitudinal migration to European wintering grounds and
187 most similar routes concern species with East African wintering grounds that probably spread
188 eastwards from an ancestral breeding range in Europe to breed in the Eastern Palearctic but
189 return to winter in same locations.^{7,8} Such examples of apparent failure to discover new, less
190 energetically demanding, wintering areas explain why migration orientation is usually
191 perceived as highly constrained in passerines.^{25,28} Our results suggest that we need to temper
192 this view and that vagrancy due to misorientation during migration is more than a mere natural
193 curiosity without much scientific interest.

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211

212 **Author contributions**

213 P-A.C., S.L. and P.D. designed the study. C.d.F., P.D-V., F.J. and P.D. performed the fieldwork.
214 J.R. M.G., P.D-V. and P.D. collected occurrences and environmental data. M.G. and P.D. ran
215 the analyses. P.D. wrote the first version of the paper and all authors contributed substantially
216 to the revisions.

217

218 **Declaration of interests**

219 The authors declare no competing interests.

220 **Figure titles and legends**

221 **Figure 1. Distribution ranges and migratory movements of Richard's Pipit**

222 Breeding, migrating and ancestral non-breeding ranges are taken from ⁴². Suspected new non-
223 breeding areas are defined from occurrences collected from the Global Biodiversity Information
224 Facility (GBIF) for countries that regularly host the species in winter.^{13,17,43} Locations of the
225 monitored sites are indicated by blue dots in the zoomed panel, with the size representing the
226 mean annual numbers of birds caught per season. The yellow arrow illustrates the suspected
227 new migratory route that birds should undertake to reach Southern Europe. Note that there is
228 no clear evidence that central Asian populations migrate through or west of the Himalayas to
229 reach ancestral non-breeding areas and could instead head a south/south-west direction thereby
230 avoiding the Gobi Desert, the Tibetan Plateau, and the Himalayas.^{13,44} Illustration © Per
231 Alström. Related to Table S2.

232

233 **Figure 2. Trends in Richard's Pipit occurrences in France during the last decades**

234 (A) Barplot representing the temporal evolution of the number of Richard's Pipits observed in
235 France between 1981 and 2019. (B) Graphic comparing the trends in the number of Richard's
236 Pipits (red line) versus other vagrant species of eastern origin (black line) regularly observed in
237 France over the same period (1981-2019). Other vagrant species were used as a proxy for the
238 evolution of the observer effort. Regression lines and coefficients are shown. For vagrant
239 species, the coefficient represents the mean value for all vagrant species. Related to Figure S1,
240 Table S1.

241

242 **Figure 3. Migration routes, stopovers and breeding sites of three GLS-tracked Richard's**
243 **Pipits**

244 Individuals are identified by their GLS numbers: BW367 (A-B), BW376 in (C-D) and BW372
245 (E). Panel (F) indicates the light intensity (log-transformed) recorded by GLS BW372 in May-
246 June. Blue dots indicate the wintering location in Southern France (Labruguière for BW376
247 and BW372, Lespignan for BW367) where the GLS were deployed. Pink dots indicate the
248 estimated breeding location from the retrieved GLS ($55.35\text{ N} \pm 0.8\text{ SD}$, $77.53\text{ E} \pm 1.3\text{ SD}$, 54.45
249 $\text{N} \pm 0.4$, $79.82\text{ E} \pm 0.6$, and $56.74\text{ N} \pm 0.3$, $79.54\text{ E} \pm 0.9$ for the three birds, respectively), at
250 the limit of the known breeding distribution represented by the pink polygon.⁴² The change of
251 pattern in light intensity data (F) suggests that this individual was likely incubating and thus
252 engaged in breeding behavior. Other dots (with error bars corresponding to standard errors of
253 longitude and latitude estimates) indicate stopover sites, where the bird stayed more than 24 h.

254 The sizes of these dots are proportional to the duration of the stopover. For each individual, the
255 migration phenology is indicated alongside the map where colored bars indicate stopovers and
256 white spaces between them represent movement periods between the stopovers. The equinox
257 period (22 September \pm 14 days) is indicated for the autumn migration (panels B-D), since birds
258 undertook most of their autumn migrations during this period, latitudinal positions have large
259 errors.

260

261 **Figure 4. Wintering niches comparisons and niche-based distribution modelling**

262 (A) Niche comparison between wintering areas in Europe and North Africa (dark blue) and
263 Southeast Asia (light blue). The convex hulls indicate the prevalence (25%, 50%, 75%, and
264 100% of locations included) of the environmental conditions. Small dots indicate GBIF
265 occurrences and black-circled dots represent the centroids of these occurrences. The correlation
266 circle (inset) indicates the loading of environmental variables onto the first two PCA axes: PRW
267 (precipitation during winter months), TW (temperature of winter months), AR (aridity), OH
268 (open-habitats) and CH (closed-habitats). The first axis (PC1, 39.6% of total variance)
269 differentiated the environmental spaces between wintering ranges with warmer and less-humid
270 winters in Asia than in Europe. The second axis (PC2, 26.4%) is associated with the opening
271 of habitats, with the Asian niche of the species being characterized by more closed habitats than
272 in Europe. (B) Map representing the projection over Europe and North Africa under current
273 conditions of the niche-model calibrated with Asian occurrences. Colors from white to green
274 represent an increasing scale of suitability. The coastal plain in northwest Morocco and to a
275 lesser degree the Portugal coast and the coastal plain area between Alger and Tunis (in Algeria
276 and Tunisia) corresponds to the environmental conditions experienced by Richard's Pipit on
277 their ancestral wintering areas. (C) Map representing the change of suitability based on the
278 projection over two periods (1961-1990 and 1990-2018) of a niche-model calibrated with
279 European occurrences. Dark green represents gain of suitable areas between these periods.
280 Related to Figure S4, S5.

281 **STAR Methods**

282

283

284 **Resource availability**

285 **Lead contact**

286 Further information and requests for resources should be directed to and will be fulfilled by
287 the Lead Contact, Paul Dufour (paul.dufour80@gmail.com).

288

289 **Material availability**

290 This study did not generate new unique reagents.

291

292 **Data and code availability statement**

293 Raw geolocator data have been archived on Movebank.org (study ID: 1720094461).
294 Occurrences data are from published or downloadable online sources (e.g. Global Biodiversity
295 Information Facility). Environmental data used in this paper are freely available and
296 downloadable from the web, the R code for running niche modeling analyses is available on
297 Zenodo: <https://doi.org/10.5281/zenodo.5500364>.

298

299 **Experimental model and subject details**

300 We captured, measured, and tagged Richard's Pipits *Anthus richardi* during the non-breeding
301 period in different localities of France and Spain (see Table S2). Birds were handled with
302 permission from MNHN-CRBPO (reference program #989) for France and SEO-BirdLife
303 (reference program #SF/0106/2019 and #SF/0103/2020) for Spain.

304

305 **Methods details**

306 *Estimating trends in Richard's Pipit occurrence*

307 To check whether the number of Richard's Pipits occurring in Europe actually increased over
308 the last few decades, we studied the trend in occurrence numbers in France between 1981 and
309 2019. We focused on France because the country hosted the first documented wintering record
310 for Europe¹⁶ and because data have been meticulously collected over a period of about 30 years.
311 The French Birds Rarities Committee collected data between 1981 and 2005 when the species
312 was still rare to scarce. From the 1990s onwards, numbers of occurrences started to increase
313 and data on the species were collected by another committee between 2005 and 2010, after
314 which the citizen-science databases took over. To avoid double-counting, we used the

315 maximum number of individuals simultaneously recorded on a given locality and on a given
316 year.

317 To test whether the species increasing trend is entirely driven by an increase in observer
318 effort, we compared linear regression coefficients of number of individuals over time for
319 Richard's Pipit and other vagrants of eastern origin. As these data have always been collected
320 using the same methodology by the French Birds Rarities Committee, we assumed no reporting
321 bias over time and we considered these data as an approximation of observer effort. We
322 excluded the rarest species from the dataset (less than 5 records over the 1981-2019 period; the
323 list of species and numbers of individuals can be found in Table S1). We repeated these analyses
324 for the Mediterranean region of southern France (defined as departments bordering the
325 Mediterranean Sea) as this region hosted the first and most of the wintering sites and includes
326 several localities where observation pressure had remained strong over this period.

327 In addition, to test whether the trend can be explained by the establishment of a new
328 migration route, we collected flock size data in France over the same period since an increase
329 in group size can only result from actual increase in number rather than increase in probability
330 of detection of the species. To avoid double-counting, we considered, per season and on a given
331 year, the maximal flock size recorded in sites known to host the species during winter and each
332 flock size record in other sites.

333 Finally, we reported the number of sites frequented by the species in winter between
334 1981 and 2019. By gridding the whole France territory in cells of 10 x 10 kilometers, we
335 evaluated the number of new grid cells frequented each year between 1981 and 2019. We
336 studied this trend for the winter period (December-February) and the migration period
337 (September-November and March-May).

338

339 *Ringling campaigns*

340 We caught Richard's Pipits over the course of three wintering periods between 2018 and 2021
341 on several locations along the Mediterranean coast of France and Spain (see Figure 1 and details
342 in Table S2). Since capture success of the capture sessions was strongly dependent on weather,
343 the effort of capture was heterogeneous between sites and between wintering seasons. Birds
344 were attracted with conspecific call playback and caught using vertical monofilament mist nets
345 or (in Spain only) spring traps, mainly at dawn or dusk. Due to a very variable attraction success
346 of call playback, capture rates were also very variable and null on several sessions. All captured
347 birds were measured, ringed with a metal (left leg) and a Darvic band (engraved with a unique
348 alphanumeric code; right leg), photographed, and a feather sample (one greater covert) was

349 taken before birds were released after ca. 5 min of handling. There is no known reliable way to
350 determine the sex in this species from in-hand examinations and we thus have no information
351 on the sex of the birds we caught.

352

353 *Birds ageing and molt scoring*

354 First-generation feathers can be easily recognized from field observations or photographs as
355 they show a characteristic thin whitish edge (Figure S2). In contrast, second-generation coverts
356 are indistinguishable from adult (i.e. at least two-year old birds) feathers and the only way to
357 separate young birds (i.e. less than one-year-old) with advanced molt (i.e. having molted most
358 of their wing coverts) from older birds is to examine the shape and color of their primary coverts
359 (Figure S2).¹³ As a consequence, it is necessary to handle young birds with advanced molt to
360 age them accurately. Birds that were caught were thus separated into adult and young birds and
361 we measured the molt extent in the latter age class. Since birds were caught mostly between
362 November and February, they had already achieved their autumn molt. We assessed the molt
363 extent within feathers that are apparent when a bird is perched (i.e. with the wing closed). We
364 thus counted the number of molted feathers in median secondary coverts (from 0 to 8), in greater
365 secondary coverts (from 0 to 10) and in tertials (from 0 to 3) on the right wing. The molt score
366 varied from 0 (no molted feathers) to 21 (completely molted; adult birds logically had a score
367 of 21; Figure S2).

368 Based on the molt patterns observed during captures, we consider that a young bird with
369 a molt score above 18 cannot be safely distinguished from an adult bird from field observations
370 or photographs. We thus defined an *adult-type* phenotype for this type of individuals and
371 identified, in total, three phenotypes that we called *full-juvenile*, *extensive* and *adult-type* molt
372 phenotypes. The first molt phenotype called *full-juvenile* corresponds to young birds that have
373 not molted after fledging (score of 0-1). The *extended post-juvenile* molt phenotype concerns
374 birds that have replaced part of their first-generation medium coverts (from 0 to 8), tertiarials
375 (from 0 to 3), and up to eight greater coverts (score of 6-18). The *adult-type* molt phenotype
376 grouped adults and young birds having replaced most of their first-generation covert feathers
377 and which may retain a maximum of one first-generation tertial and some first-generation
378 greater coverts (score of 19-21; Figure S2).

379

380 *Assessing the geographical distribution of molt phenotypes from pictures*

381 We collected georeferenced pictures on citizen-science databases and Internet picture
382 repositories across different European and North African countries that regularly host the

383 species in autumn and/or during the wintering period. After February, young birds that have
384 not finished molting in the autumn can resume their molt and become similar to adult birds,
385 hence we only collected data associated with pictures obtained between 08 (2013) and 02
386 (2019). We selected good quality pictures of perched birds showing the secondary coverts and
387 tertials correctly. When several photos were available for a single location where several birds
388 were reported, we allocated photos to different individuals by comparing photos (individual
389 birds usually differ in details of molt or plumage); when in doubt, only one picture was selected
390 from the available sample. We thus obtained 349 pictures from 331 individuals (presumably all
391 different from the birds we caught ourselves) from 17 European and North African countries.
392 Details on picture collections and websites consulted are available in Table S3. We assigned
393 each bird to one of the three molt phenotypes identified during captures based on its molt score.

394 For the winter period, we assessed whether the proportions of molt phenotypes in
395 northwestern Europe (Norway, Sweden, Denmark, Germany, the Netherlands, the United-
396 Kingdom, Ireland, Switzerland and Western France) and southwestern Europe (Southern
397 France, Italy, Catalonia, Spain, Portugal, Morocco) are different from the expected proportions
398 under the full vagrancy hypothesis (i.e. under the hypothesis that only young birds are seen in
399 Europe) by performing a Fisher' exact or Chi-square test on contingency tables summarizing
400 observations (the choice of the test depending on the number of observations per category). We
401 thus compared the proportions of molt phenotypes from the 50 young birds examined in the
402 hand with the proportions of molt phenotypes estimated from pictures in Northwestern and
403 Southwestern Europe. A significant test would indicate that the proportions of molt phenotypes
404 differ from those observed in a sample of juvenile birds. If only vagrant birds were involved,
405 we would expect that all or most are juveniles.

406

407 *Tracking the breeding range of Richard's Pipits with archival light loggers*

408 During the 2019-2020 winter period, we deployed seven INTIGEO P65C2-7 Global-Location-
409 Sensors (GLS) in Southern France (Migrate Technology, 0.74 g; Covid-19 lockdown stopped
410 the fieldwork season in early 2020). GLS are small electronic devices that record time and light
411 intensity, enabling the calculation of the approximate position of the logger given the duration
412 of the day and the time of solar noon, both depending on latitude and longitude for a given
413 calendar day.⁴⁵ Due to the small body size of the Richard's Pipit, there were no other technology
414 available at the time to track the movements of the species during the annual cycle. Since GLS
415 do not remotely transmit positions, they have to be retrieved to download the data and birds
416 must thus be captured again. Due to the equivalent day length everywhere on Earth at the

417 autumnal and spring equinoxes, latitudinal positions within 15 days on each side of the two
418 equinox dates cannot be estimated accurately.⁴⁶ The error of GLS locations during migration is
419 known to vary up to 200 km⁴⁶ but the precision increases (in the order of a few dozen
420 kilometers) when the bird stays several days at the same location⁴⁷. Using the same technique
421 as explained above, we equipped four adults and three young birds with leg-loop harnesses
422 made from rubber bands to attach the loggers. The device and fitting material represented less
423 than 3% of a bird's weight (average weight: 31.9 ± 2.2 g, $n=78$; *unpublished data*). We retrieved
424 three devices the next winter, containing data from at least one complete migration per bird
425 (Table S2). Return rates of GLS-equipped birds did not differ obviously from those that have
426 been colored-ringed during winter 2018-2019 and re-sighted during winter 2018-2019 (42% of
427 returning GLS-equipped bird and 33% of returning color-ringed individuals, but note small
428 sample sizes).

429 We followed the method described in Lisovski et al. (2020)⁴⁸ to analyze the light data
430 recorded by GLS devices. We first looked for changes in light intensity pattern that could
431 provide evidence for an incubating behavior (i.e., for a bird hidden in the vegetation). Then, we
432 used the *TwGeos* R package⁴⁹ to define twilights with the *preprocessLight* function, using a
433 threshold of 2.5 lux. We manually removed obviously erroneous twilights and applied an
434 additional automated screening using the *twilightEdit* function (settings were window = 4,
435 outlier.mins = 45 and stationary.mins = 25). We then used the *FLightR* package⁵⁰ to determine
436 migration timing. Since, the package requires calibration periods during which the bird is
437 stationary in a known location, we ran the model a first time using the month of March as
438 calibration period and with a particle filter of 10^4 particles (color-ringed birds were observed
439 throughout March on their wintering site, *pers. obs*). We refined the calibration period using
440 the *plot_lon_lat* function (plot of latitude and longitude in horizontal layout). We defined the
441 *FLightR* search grid between 35° S and 65° N latitude and 0° W and 100° E longitude and ran
442 the particle filter with the recommended 10^6 particles. We estimated the breeding location,
443 migration timing, potential stationary periods and their locations using the
444 *stationary.migration.summary* function by defining a minimum duration of stationary period of
445 24 hours and testing different values of minimum probability of movement (*prob.cutoff*). We
446 estimated the migratory route and the distance travelled via the shortest route (i.e. a great circle
447 route; *distHaversine* function in the *geosphere* R package)⁵¹ between these different stationary
448 locations.

449

450 *Wintering niche comparison*

451 To compare environmental niches of birds wintering in their ancestral Asian areas and birds
452 wintering in Europe, we collected occurrences of Richard's Pipit from the Global Biodiversity
453 Information Facility (<https://www.gbif.org/>). We selected occurrence data for the wintering
454 period alone (from December to February) and from countries known to host the species
455 regularly during this period (Europe and North Africa: France, Spain, Portugal, Italy, Morocco;
456 Asia: Taiwan, Thailand, Hong-Kong, China, India, Myanmar, Vietnam, Laos, Cambodia, Sri
457 Lanka; see ¹³). We retained verified and georeferenced occurrences, resulting in 1,268
458 occurrences for Europe and North Africa and 6, 717 occurrences for Asia, derived from citizen
459 science databases widely used by the ornithological community (mostly eBird.org,
460 iNaturalist.org, observation.org and the various Biovision national reporting systems). For
461 Europe, these databased are usually well curated by validation committees that operate at local
462 (regional) or national scales. Data were then thinned prior to analyses to reduce the effect of
463 biased species occurrence collections, using the *spThin* R package⁵² with a thinning parameter
464 of 0.5 kilometers, leaving a total of 1,638 occurrences.

465 Since environmental conditions seem to play a key role in the selection of species'
466 wintering grounds, particularly for finding the resources necessary for winter survival,³¹ we
467 collected several climatic and habitat variables related to the species preference.¹³ We
468 downloaded the temperature and precipitations of the winter months (between December and
469 February), an aridity index (the ratio of the mean annual precipitation on the mean annual
470 potential evapo-transpiration) and a discrete variable characterizing open and closed habitats.
471 The climatic data were collected from the CHELSA database v1.2 (<http://chelsa-climate.org>)
472 at a resolution of 30 arc seconds, with monthly mean temperature and precipitation averaged
473 over the period 1979– 2013.⁵³ The aridity index was collected from the CGIAR-CSI Database
474 (<http://www.cgiar-csi.org>) at a resolution of 30 arc seconds for the period 1970–2000⁵⁴ and
475 habitat variable from the Global Land Cover Map (GlobCover)⁵⁵. The habitat variable was
476 coded as “open” and “closed” habitats based on GlobCover categories; crop and mosaic habitats
477 with more than 50% of cropland or grassland were considered as open habitats whereas mosaic
478 habitats with less than 50% of cropland or grassland and more than 50% of forest or scrubland
479 were considered as closed habitats. We checked that variables were not collinear (correlation
480 coefficients < 0.50) using occurrences in both European and Asian regions, resulting in five
481 variables to represent environmental variation among regions: PRW (precipitation during
482 winter months), TW (temperature of winter months), AR (aridity), OH (open-habitats) and CH
483 (close-habitats).

484 Environmental niche variation was evaluated using principal component analysis (PCA)
485 implemented in the *ade4* R package.⁵⁶ We assessed the variation between the European-North
486 African and Asian wintering ranges by comparing the coordinates of occurrences in a two-
487 dimensional environmental space (PC1 x PC2). We evaluated the niche overlap between the
488 Asian and the European niches using Schoener's D.⁵⁷ We also evaluated the percentage of
489 inclusion of the European niche within the Asian niche by measuring the intersection between
490 each convex hull defined by 100% of occurrences.

491 To investigate if vagrant birds may have found suitable wintering conditions in Europe,
492 we performed niche distribution models with the *BIOMOD* R package^{58,59} implemented in the
493 *biomod2* R package. For each region, an ensemble of projections from four statistical models
494 was obtained, including random forest (RF), generalized linear models (GLM), generalized
495 additive models (GAM) and general boosting method (GBM).⁶⁰ Models were calibrated for the
496 baseline period using 70% of observations randomly sampled from the initial data and evaluated
497 against the remaining 30% data using the true skill statistic (TSS)⁶¹ and the area under the curve
498 (ROC).⁶² For each model, the relative importance of each environmental variable was assessed
499 by calculating the Pearson's correlation between the standard predictions (i.e. fitted values) and
500 the predictions after randomly permuting the values of the variable. The ensemble forecasting
501 was then built by assigning weight to each individual model depending on its quality (TSS) and
502 taking the weighted sum of occurrence probabilities. Both calibrated models were projected
503 under current conditions over Europe – North Africa and Asia.

504 To evaluate changes in suitability across Europe over the period 1960-2018, we also
505 performed niche distribution models using the same methodology with environmental variables
506 available for this time period. We thus downloaded the temperature and precipitation of the
507 winter months (between December and February) from the CHELSA database v1.2 (<http://chelsa-climate.org>) at a resolution of 30 arc seconds, with monthly mean temperature and
508 precipitation averaged for the 1961-2018 period.⁵³ The aridity index (CGIAR-CSI Database)
509 and habitat variable from the Global Land Cover Map (GlobCover)⁵⁵ were not available for the
510 entire study period. Therefore, we calculated the De Martonne index⁶³ as an aridity index, from
511 monthly precipitation and annual temperature data for the 1961-2018 period. But we finally
512 found high collinearity (correlation coefficients > 0.50) with precipitations data. The calibrated
513 model based on two environmental variables (PRW and TW) was projected over Europe under
514 conditions of the 1961-1990 and the 1990-2018 periods.
515

516 **References**

- 517 1. Berthold, P., Helbig, A.J., Mohr, G., and Querner, U. (1992). Rapid microevolution of
518 migratory behaviour in a wild bird species. *Nature* 360, 668–670.
- 519 2. Winkler, D.W., Gandoy, F.A., Areta, J.I., Iliff, M.J., Rakhimberdiev, E., Kardynal,
520 K.J., and Hobson, K.A. (2017). Long-Distance Range Expansion and Rapid
521 Adjustment of Migration in a Newly Established Population of Barn Swallows
522 Breeding in Argentina. *Curr. Biol.* 27, 1080–1084.
- 523 3. Areta, J.I., Salvador, S.A., Gandoy, F.A., Bridge, E.S., Gorleri, F.C., Pegan, T.M.,
524 Gulson-Castillo, E.R., Hobson, K.A., and Winkler, D.W. (2021). Rapid adjustments of
525 migration and life history in hemisphere-switching cliff swallows. *Curr. Biol.* 31, 2914-
526 2919.e2.
- 527 4. Gilroy, J., and Lees, A. (2003). Vagrancy theories: Are autumn vagrants really reverse
528 migrants? *Br. Birds* 96, 427–438.
- 529 5. Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., Bowen,
530 G.J., Berthold, P., and Farnsworth, K. (2005). Assortative Mating as a Mechanism for
531 Rapid Evolution of a Migratory Divide. *Science*. 310, 502–504.
- 532 6. Rolshausen, G., Segelbacher, G., Hobson, K.A., and Schaefer, H.M. (2009).
533 Contemporary Evolution of Reproductive Isolation and Phenotypic Divergence in
534 Sympatry along a Migratory Divide. *Curr. Biol.* 19, 2097–2101.
- 535 7. Bairlein, F., Norris, D.R., Nagel, R., Bulte, M., Voigt, C.C., Fox, J.W., Hussell, D.J.T.,
536 and Schmaljohann, H. (2012). Cross-hemisphere migration of a 25 g songbird. *Biol.*
537 *Lett.* 8, 505–507.
- 538 8. Sokolovskis, K., Bianco, G., Willemoes, M., Solovyeva, D., Bensch, S., and Åkesson,
539 S. (2018). Ten grams and 13,000km on the wing - route choice in willow warblers
540 *Phylloscopus trochilus yakutensis* migrating from Far East Russia to East Africa. *Mov.*
541 *Ecol.* 6, 1–10.
- 542 9. Sutherland, W.J. (1998). Evidence for Flexibility and Constraint in Migration Systems.
543 *J. Avian Biol.* 29, 441.
- 544 10. Zurell, D., Graham, C.H., Gallien, L., Thuiller, W., and Zimmermann, N.E. (2018).
545 Long-distance migratory birds threatened by multiple independent risks from global
546 change. *Nat. Clim. Chang.* 8, 992–996.
- 547 11. Rabøl, J. (1969). Reversed migration as the cause of westward vagrancy by four
548 *Phylloscopus* warblers. *Br. Birds* 62, 89–92.
- 549 12. Cramp, S., and Simmons, K.E.L. (1983). *The Birds of the Western Palearctic Volume*

- 550 III. (Oxford University Press).
- 551 13. Alstrom, P., and Mild, K. (2003). Pipits and Wagtails of Europe, Asia and North-
552 America Helm, ed.
- 553 14. Alerstam, T. (1990). Ecological causes and consequences of bird orientation.
554 *Experientia* 46, 405–415.
- 555 15. Jiguet, F., and Barbet-Massin, M. (2013). Climate change and rates of vagrancy of
556 Siberian bird species to Europe. *Ibis*. 155, 194–198.
- 557 16. Dulau, S. (1997). Nouveau cas d'hivernage du Pipit de Richard *Anthus richardi* dans le
558 sud de la France. *Ornithos* 4, 90–91.
- 559 17. Biondi, M., and Grussu, M. (2004). Record numbers of wintering Richard's Pipit in the
560 Western Palearctic. *Br. Birds* 97, 194–195.
- 561 18. Stanley, C.Q., MacPherson, M., Fraser, K.C., McKinnon, E.A., and Stutchbury, B.J.M.
562 (2012). Repeat Tracking of Individual Songbirds Reveals Consistent Migration Timing
563 but Flexibility in Route. *PLoS One* 7, e40688.
- 564 19. van Wijk, R.E., Bauer, S., and Schaub, M. (2016). Repeatability of individual
565 migration routes, wintering sites, and timing in a long-distance migrant bird. *Ecol.*
566 *Evol.* 6, 8679–8685.
- 567 20. Catry, P., Campos, A., Almada, V., and Cresswell, W. (2004). Winter segregation of
568 migrant European robins *Erithacus rubecula* in relation to sex, age and size. *J. Avian*
569 *Biol.* 35, 204–209.
- 570 21. DeSante, D.F. (1983). Annual Variability in the Abundance of Migrant Landbirds on
571 Southeast Farallon Island, California. *Auk* 100, 826–852.
- 572 22. Thorup, K. (2004). Reverse migration as a cause of vagrancy. *Bird Study* 51, 228–238.
- 573 23. Thorup, K. (1998). Vagrancy of Yellow-browed Warbler *Phylloscopus inornatus* and
574 Pallas's Warbler *Ph. proregulus* in north-west Europe: Misorientation on great circles?
575 *Ringing Migr.* 19, 7–12.
- 576 24. Lees, A., and Van der Werf, E.. (2011). First record of Blyth's Pipit *Anthus*
577 *godlewskii* for Micronesia. *Bull. Br. Ornithol. Club* 131, 212–217.
- 578 25. Delmore, K.E., and Irwin, D.E. (2014). Hybrid songbirds employ intermediate routes
579 in a migratory divide. *Ecol. Lett.* 17, 1211–1218.
- 580 26. Alerstam, T., Hedenstrom, A., and Akesson, S. (2003). Long-distance migration:
581 evolution and determinants. *Oikos* 103, 247–260.
- 582 27. Ralph, C.J. (1978). Disorientation and Possible Fate of Young Passerine Coastal
583 Migrants. *Bird-Banding* 49, 237.

- 584 28. Helbig, A. (1991). Inheritance of migratory direction in a bird species: a cross-breeding
585 experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). *Behav. Ecol.*
586 *Sociobiol.* 28.
- 587 29. Lundberg, M., Liedvogel, M., Larson, K., Sigeman, H., Grahn, M., Wright, A.,
588 Åkesson, S., and Bensch, S. (2017). Genetic differences between willow warbler
589 migratory phenotypes are few and cluster in large haplotype blocks. *Evol. Lett.* 1, 155–
590 168.
- 591 30. Delmore, K.E., Toews, D.P.L., Germain, R.R., Owens, G.L., and Irwin, D.E. (2016).
592 The Genetics of Seasonal Migration and Plumage Color. *Curr. Biol.* 26, 2167–2173.
- 593 31. Thorup, K., Tøttrup, A.P., Willemoes, M., Klaassen, R.H.G., Strandberg, R., Vega,
594 M.L., Dasari, H.P., Araújo, M.B., Wikelski, M., and Rahbek, C. (2017). Resource
595 tracking within and across continents in long-distance bird migrants. *Sci. Adv.* 3,
596 e1601360.
- 597 32. Irwin, D.E., and Irwin, J.H. (2005). Birds of Two Worlds: The Ecology and Evolution
598 of Migration. In, J. H. University, ed., pp. 27–40.
- 599 33. Møller, A.P., Garamszegi, L.Z., Peralta-Sanchez, J.M., and Soler, J.J. (2011).
600 Migratory divides and their consequences for dispersal, population size and parasite-
601 host interactions. *J. Evol. Biol.* 24, 1744–1755.
- 602 34. Campayo, L. (1863). *Histoire naturelle du département des Pyrénées-Orientales.*
- 603 35. Gätke, H. (1895). Heligoland as an Ornithological Observatory. The result of fifty
604 years' experience.
- 605 36. Holt, E.G. (1933). Definite Breeding of the Glossy Ibis in Louisiana. *Auk* 50, 351–352.
- 606 37. Veit, R.R., and Lewis, M.A. (1996). Dispersal, Population Growth, and the Allee
607 Effect: Dynamics of the House Finch Invasion of Eastern North America. *Am. Nat.*
608 148, 255–274.
- 609 38. Massa, C., Doyle, M., and Callicó Fortunato, R. (2014). On how Cattle Egret
610 (*Bubulcus ibis*) spread to the Americas: meteorological tools to assess probable
611 colonization trajectories. *Int. J. Biometeorol.* 58, 1879–1891.
- 612 39. Dufour, P., Pons, J.-M., Collinson, J.M., Gernigon, J., Ignacio Dies, J., Sourrouille, P.,
613 and Crochet, P.-A. (2017). Multilocus barcoding confirms the occurrence of Elegant
614 Terns in Western Europe. *J. Ornithol.* 158, 351–361.
- 615 40. Plummer, K.E., Siriwardena, G.M., Conway, G.J., Risely, K., and Toms, M.P. (2015).
616 Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird
617 species? *Glob. Chang. Biol.* 21, 4353–4363.

- 618 41. Van Doren, B.M., Conway, G.J., Phillips, R.J., Evans, G.C., Roberts, G.C.M.,
619 Liedvogel, M., and Sheldon, B.C. (2021). Human activity shapes the wintering ecology
620 of a migratory bird. *Glob. Chang. Biol.*, 1–13.
- 621 42. BirdLife International (2020). IUCN Red List for birds.
- 622 43. Biondi, M., Corso, A., and Grussu, M. (2004). Nuovi dati sullo svernamento e la
623 fenologia del Calandro maggiore *Anthus richardi* in Italia (1995-2004). *Gli Uccelli*
624 *d'Italia* 29, 39–47.
- 625 44. Delany, S., Williams, C., Sulston, C., Norton, J., and Garbutt, D. Passerine Migration
626 across the Himalayas. In *Bird Migration Across the Himalayas* (Cambridge University
627 Press).
- 628 45. Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner-Nievergelt, F., Kristensen,
629 M.W., and Hahn, S. (2012). Geolocation by light: accuracy and precision affected by
630 environmental factors. *Methods Ecol. Evol.* 3, 603–612.
- 631 46. Phillips, R.A., Silk, J.R.D., Phalan, B., Catry, P., and Croxall, J.P. (2004). Seasonal
632 sexual segregation in two *Thalassarche* albatross species: competitive exclusion,
633 reproductive role specialization or foraging niche divergence? *Proc. R. Soc. London.*
634 *Ser. B Biol. Sci.* 271, 1283–1291.
- 635 47. Rakhimberdiev, E., Senner, N.R., Verhoeven, M.A., Winkler, D.W., Bouten, W., and
636 Piersma, T. (2016). Comparing inferences of solar geolocation data against high-
637 precision GPS data: annual movements of a double-tagged black-tailed godwit. *J.*
638 *Avian Biol.* 47, 589–596.
- 639 48. Lisovski, S., Bauer, S., Briedis, M., Davidson, S.C., Dhanjal-Adams, K.L., Hallworth,
640 M.T., Karagicheva, J., Meier, C.M., Merkel, B., Ouwehand, J., et al. (2020). Light-
641 level geolocator analyses: A user's guide. *J. Anim. Ecol.* 89, 221–236.
- 642 49. Lisovski, S., Sumner, M.D., and Wotherspoon, S.J. (2015). TwGeos: Basic data
643 processing for light based geolocation archival tags. R package.
- 644 50. Rakhimberdiev, E., Saveliev, A., Piersma, T., and Karagicheva, J. (2017). FLIGHTR: an
645 R package for reconstructing animal paths from solar geolocation loggers. *Methods*
646 *Ecol. Evol.* 8, 1482–1487.
- 647 51. Hijmans, R., Williams, E., and Vennes, C. (2015). Geosphere: spherical trigonometry.
648 R package.
- 649 52. Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., and Anderson, R.P.
650 (2015). spThin: an R package for spatial thinning of species occurrence records for use
651 in ecological niche models. *Ecography.* 38, 541–545.

- 652 53. Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W.,
653 Zimmermann, N.E., Linder, H.P., and Kessler, M. (2017). Climatologies at high
654 resolution for the earth's land surface areas. *Sci. Data* 4, 170122.
- 655 54. Zomer, R.J., Trabucco, A., Bossio, D.A., and Verchot, L. V. (2008). Climate change
656 mitigation: A spatial analysis of global land suitability for clean development
657 mechanism afforestation and reforestation. *Agric. Ecosyst. Environ.* 126, 67–80.
- 658 55. Arino, O., Ramos Perez, J.J., Kalogirou, V., Bontemps, S., Defourny, P., and Van
659 Bogaert, E. (2012). Global Land Cover Map for 2009 (GlobCover 2009). Eur. Sp.
660 Agency Univ. Cathol. Louvain.
- 661 56. Chessel, D., Dufour, A.-B., and Thioulouse, J. (2004). The ade4 package.R package.
- 662 57. Schoener, T.W. (1970). Nonsynchronous Spatial Overlap of Lizards in Patchy
663 Habitats. *Ecology* 51, 408–418.
- 664 58. Thuiller, W., Lafourcade, B., Engler, R., and Araújo, M.B. (2009). BIOMOD - a
665 platform for ensemble forecasting of species distributions. *Ecography* 32, 369–373.
- 666 59. Thuiller, W. (2003). BIOMOD - optimizing predictions of species distributions and
667 projecting potential future shifts under global change. *Glob. Chang. Biol.* 9, 1353–
668 1362.
- 669 60. Araujo, M., and New, M. (2007). Ensemble forecasting of species distributions. *Trends*
670 *Ecol. Evol.* 22, 42–47.
- 671 61. Allouche, O., Tsoar, A., and Kadmon, R. (2006). Assessing the accuracy of species
672 distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.*
673 43, 1223–1232.
- 674 62. Swets, J. (1988). Measuring the accuracy of diagnostic systems. *Science* (80-.). 240,
675 1285–1293.
- 676 63. De Martonne, E. (1926). Aréisme et indice d'aridité in *Bulletin de l'Association de*
677 *Géographes Français*.
- 678

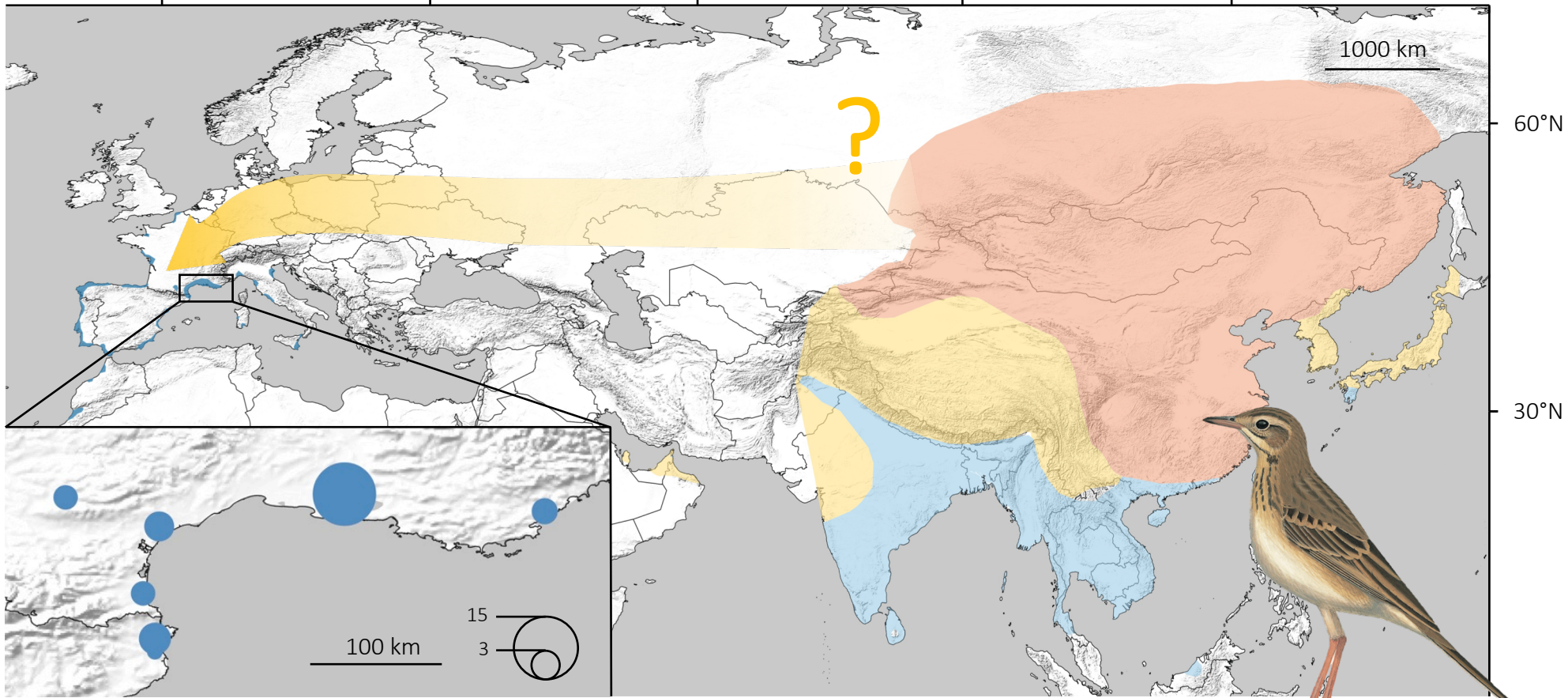
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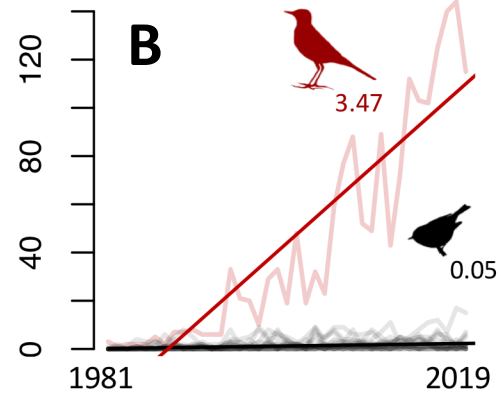
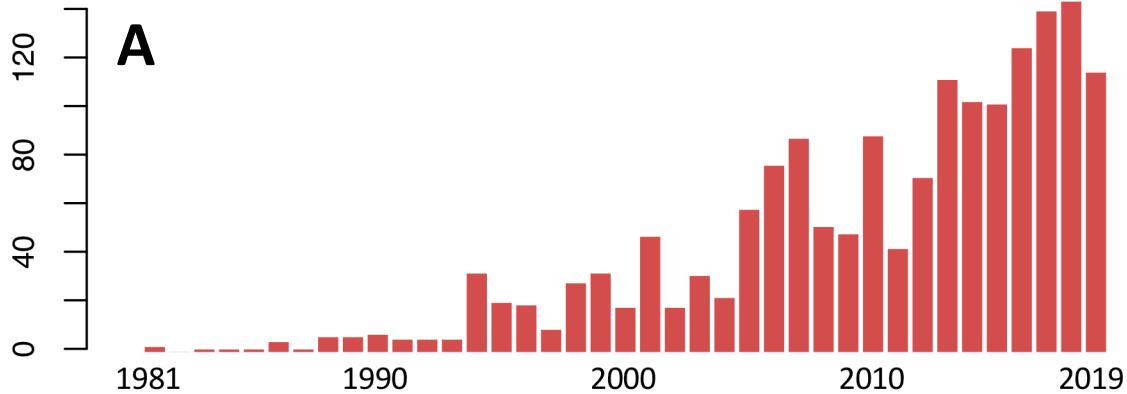
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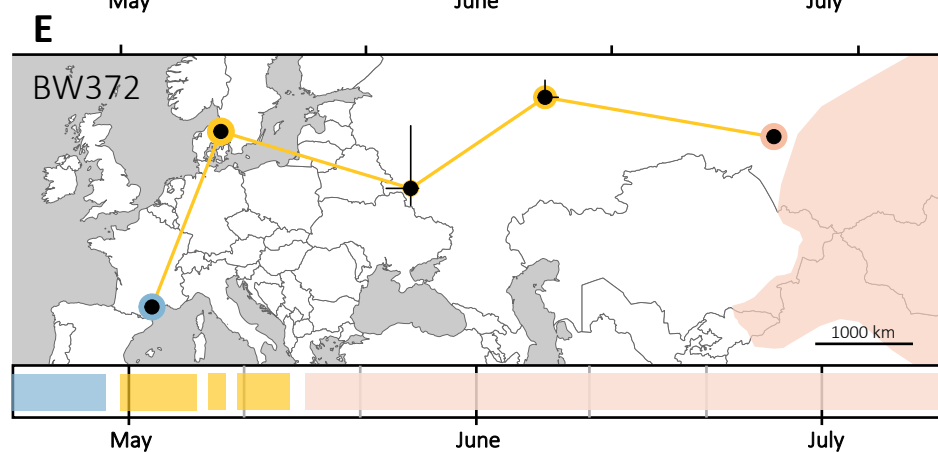
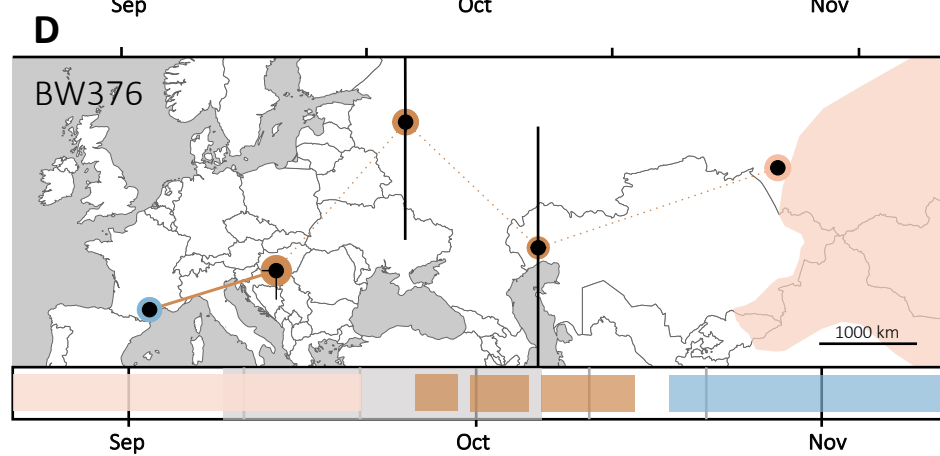
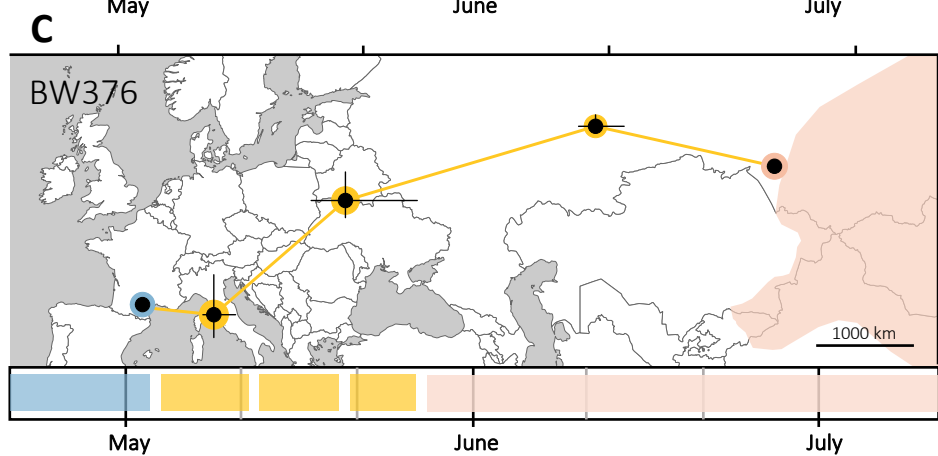
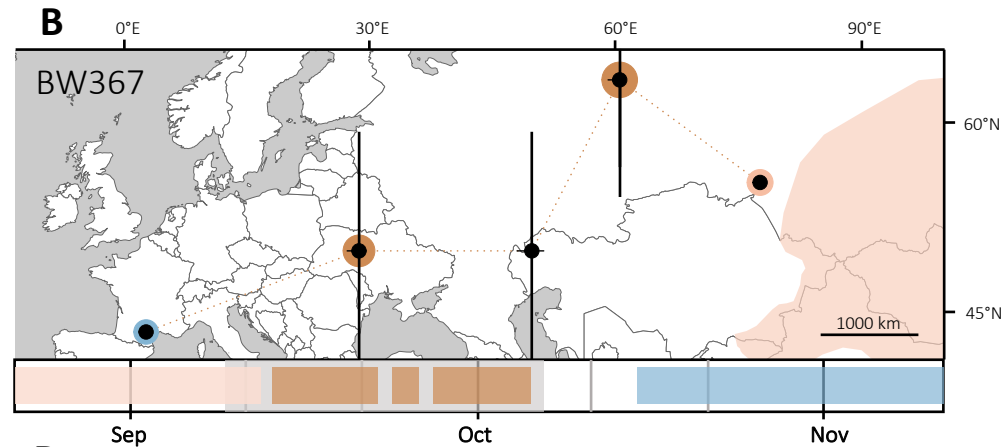
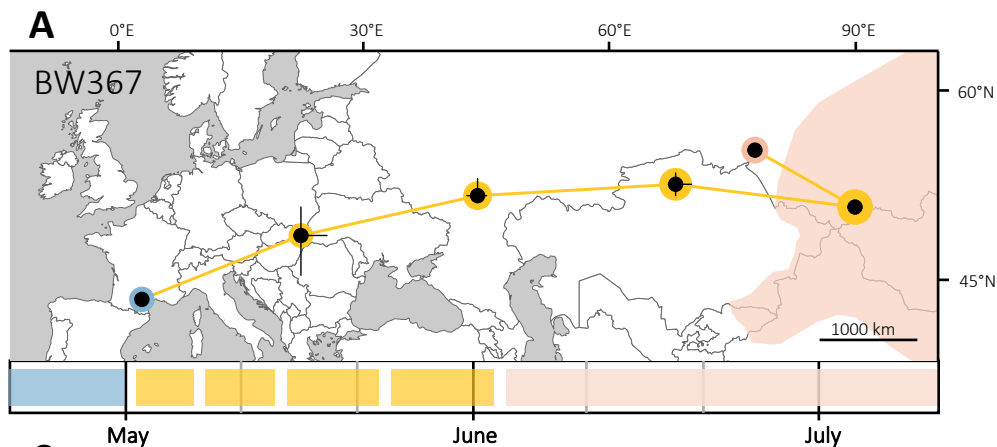
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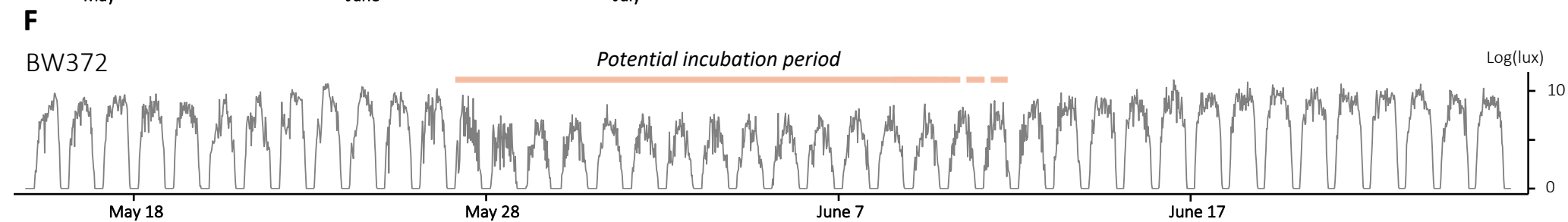
western non-breeding areas

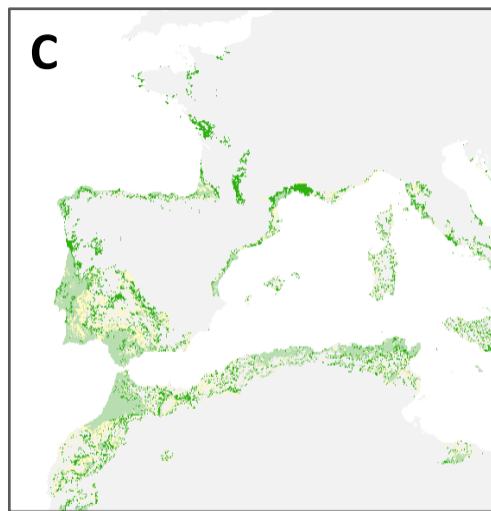
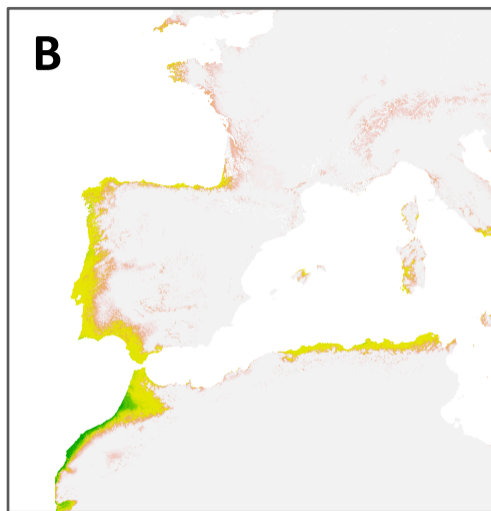
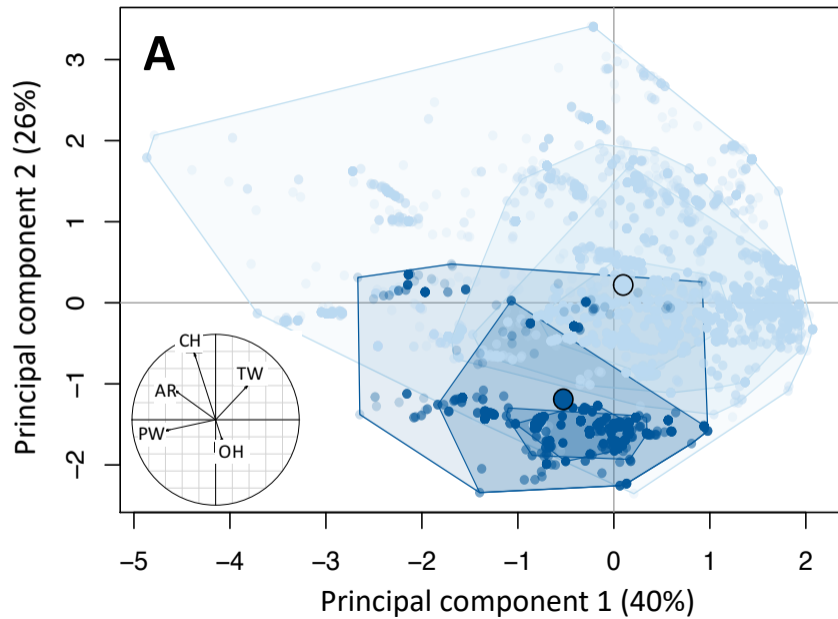
western autumnal migration route





- breeding location
- non-breeding location
- stopovers and spring migration
- stopovers and autumn migration
- breeding range
- equinox period

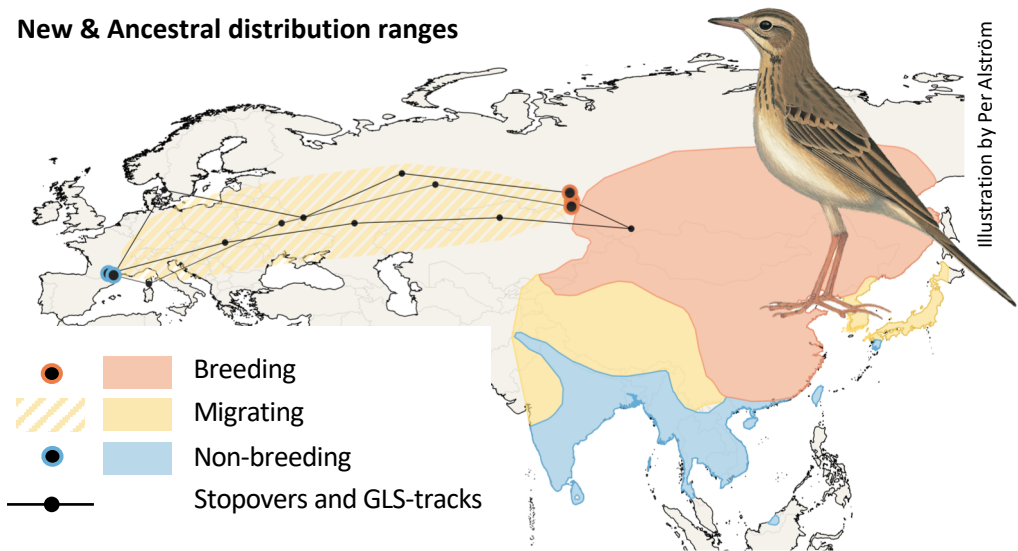




absence presence
lost gain

0 .2 .4 .6 .8 1

New & Ancestral distribution ranges



Increasing occurrences and spreading suitable wintering niche in Europe

