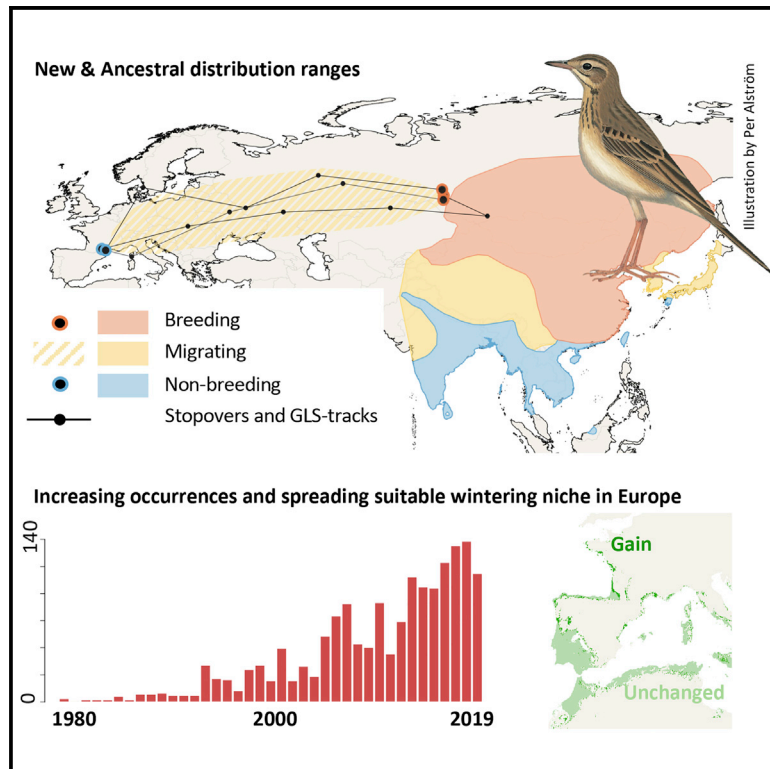# Current Biology

A new westward migration route in an Asian passerine bird

Graphical abstract

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In brief

Richard's Pipit is an Asian migratory passerine that normally winters in Southeast Asia. Dufour et al. find that the species is now a regular migrant to Europe. Vagrancy probably allowed the colonization of this new wintering area, helped by an increase of wintering niche suitability due to climate change.

Highlights

- Richard's Pipit normally breeds in Siberia and winters in southern Asia

- The species has recently increased in Europe from occasional to regular visitor

- Birds undertake a rare westward seasonal migration across Eurasia to southern Europe

- Vagrancy and climate change likely promoted the establishment of this migration route

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A new westward migration route in an Asian passerine bird

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https://doi.org/10.1016/j.cub.2021.09.086

SUMMARY

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

RESULTS AND DISCUSSION

Evidence for a new migration route

Like many other Siberian birds that normally winter in southern Asia, Richard's Pipits have long been known to reach western Europe in small numbers in autumn.[11–13] The occurrence of such "accidental" or "lost" birds outside their normal distribution range, which are mostly juvenile birds that will never return to their breeding grounds, is often referred to as vagrancy.[14] However, the pattern of Richard's Pipit occurrence has recently changed in southwestern Europe (Figure 1). In France, for example, the number of records increased from three to six birds annually between 1981 and 1993 to a maximum of 144 birds in 2018 (Figure 2A), and this increase is apparent in several localities in southern France that have been consistently monitored since the 1950s or 1980s; the maximum flock size also increased during the same 1981–2019 period (Figure S1). The number of sightings of other Siberian vagrant species in France has increased to a much lesser extent (average regression coefficient over time, 3.47 in Richard's Pipit versus 0.05 ± 0.057 for other vagrants; Figure 2B; Table S1), excluding that this increase

simply reflects a simultaneous increase in identification skills and observation pressure.[4,15] The first overwintering in Europe was documented in 1991 in southern France,[16] after which overwintering and staging were reported from an increasing number of sites (Figure S1). The species has now become a regular winter visitor to southern and western France, as well as to Spain, Portugal, and Italy.[17]

Two non-exclusive hypotheses can explain this recent increase: the number of vagrants reaching Europe has increased or Richard's Pipit has established a new migration route, in accordance with the "pseudo-vagrancy" hypothesis of Gilroy and Lees.[4–6] To disentangle these explanations, we studied the species during three wintering periods along the Mediterranean coast of France and Spain (Figure 1). Because the vast majority of vagrant passerines are birds in their first postnatal migration, we specifically looked for the presence of adults (birds more than 1 year old). Moreover, since most migratory passerines are faithful to their migratory routes and wintering areas,[21,22] we marked individuals to test if they were returning the next winter. Both the presence of adults and of returning individuals would support the migration hypothesis over the vagrancy hypothesis.
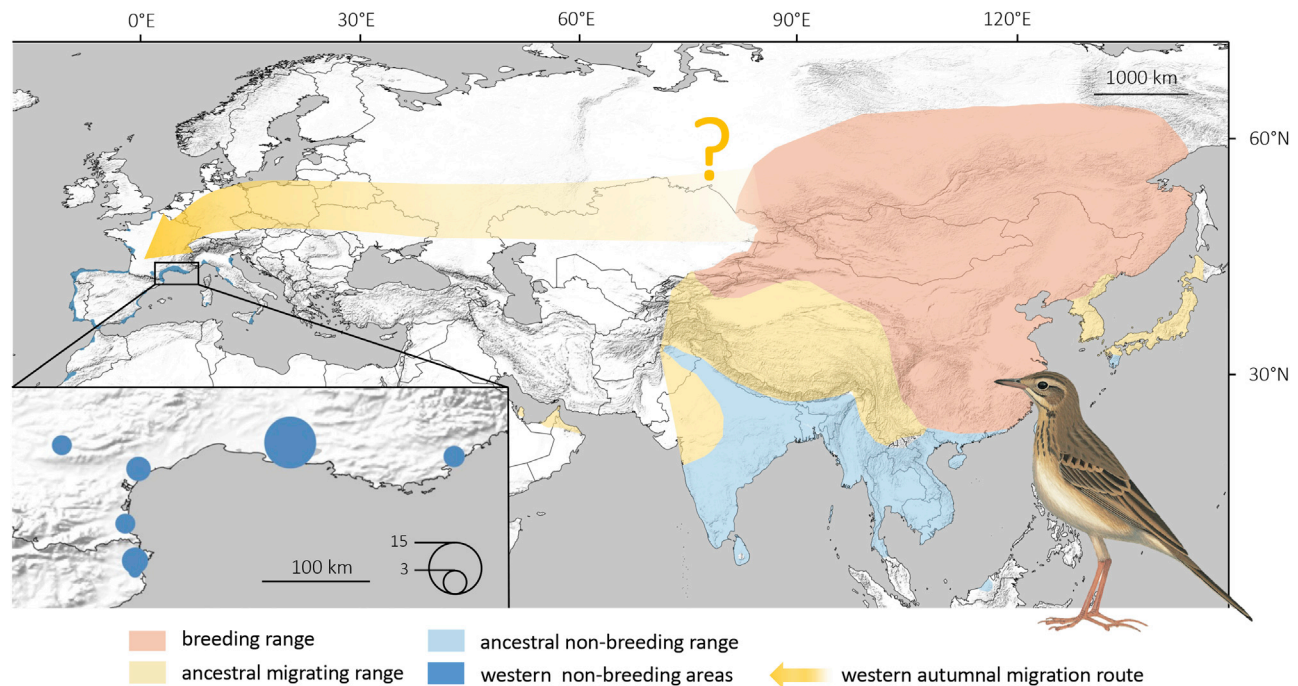
Figure 1. Distribution ranges and migratory movements of Richard's Pipit
Breeding, migrating, and ancestral non-breeding ranges are taken from BirdLife International.[18] Suspected new non-breeding areas are defined from occurrences collected from the Global Biodiversity Information Facility (GBIF) for countries that regularly host the species in winter.[13,17,19] Locations of the monitored sites are indicated by blue dots in the zoomed panel, with the size representing the mean annual numbers of birds caught per season. The yellow arrow illustrates the suspected new migratory route that birds should undertake to reach southern Europe. Note that there is no clear evidence that central Asian populations migrate through or west of the Himalayas to reach ancestral non-breeding areas and could instead head a south/southwest direction, thereby avoiding the Gobi Desert, the Tibetan Plateau, and the Himalayas.[13,20]
Illustration © Per Alström. Related to Table S2.

Among 81 birds examined in the hand in southern France and northeastern Spain, 28 (34.6%) were found to be adults: a high proportion similar to that observed in regular wintering species in southern Europe (e.g., European Robin *Erithacus rubecula*[23]) and supporting the migration hypothesis. In addition, from the 68 individuals that were color-ringed during the first two seasons, 11 were re-sighted or re-trapped the following winters (four of them over two consecutive seasons; Table S2), providing further empirical support to the migration hypothesis.

To determine whether birds that winter in France originate from the known breeding area or from a previously undetected breeding population, we equipped seven individuals with global location sensors (GLSs) during winter 2019/2020 (Table S2). The following winter, we re-captured three of these individuals (recapture is needed for data retrieval with GLS). All three birds spent the summer at the western edge of the known breeding range in a small area of the Novosibirsk Oblast in Russia (Figure 3) where light data indicate that at least one individual engaged in breeding behavior (Figure 3F), supporting the hypothesis that these birds were regular migrants rather than vagrants. During the spring migration, the three individuals used three different stopover locations for more than 24 h; the second-year individual first headed north and stopped in Sweden before redirecting eastward to reach a likely breeding site where it lingered until the GLS stopped (Figure 3E). These three individuals thus traveled 5,750, 7,045, and 7,320 km during their spring migration

between southern France and Siberia along a migratory route that crosses countries where the species is rarely sighted.

To determine whether regular migrants are also present in other parts of the western non-breeding range (Figure 1), we tested for the presence of adult birds in these locations using pictures from citizen-science databases to estimate the age ratio. On good-quality pictures, first-generation wing coverts (grown in the nest) can easily be distinguished from second-generation feathers (Figure S2), allowing safe aging of birds with first-generation coverts as young birds (i.e., less than 1 year old). However, some young birds molt all wing coverts during the autumn, resulting in an adult-type plumage in winter that cannot be separated from adults without in-hand examination. To estimate the proportions of the different molt stages among young birds, we examined 78 in-hand and aged birds caught in France and northeastern Spain to classify them into three molt phenotypes (full juvenile, extended molt, and adult type; Figure S2), all of which can be determined based on pictures. Of 50 young birds examined, six were of the full-juvenile type (12%), 39 belonged to the extended-molt type (78%), and five to the adult type (10%; see Figure S2 for details). Within 33 adult-type birds (which of course include all adults), five (15%) were found to be young birds upon in-hand examination. Molt phenotype thus provides imprecise but meaningful information about age. We then scored pictures of 331 individuals across Europe and North Africa to estimate age-ratio variation. In northern
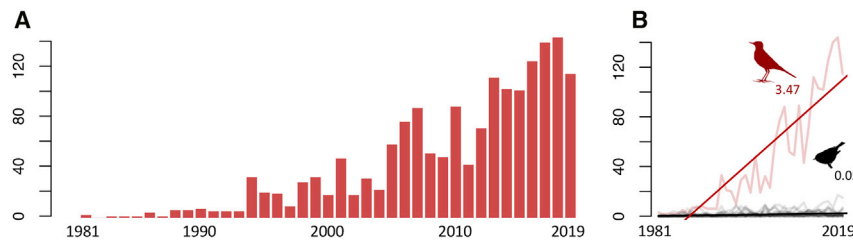
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Figure 2. Trends in Richard's Pipit occurrences in France during the last decades
(A) Barplot representing the temporal evolution of the number of Richard's Pipits observed in France between 1981 and 2019.
(B) Graphic comparing the trends in the number of Richard's Pipits (red line) versus other vagrant species of eastern origin (black line) regularly observed in France over the same period (1981–2019). Other vagrant species were used as a proxy for the evolution of the observer effort. Regression lines and coefficients are shown. For vagrant species, the coefficient represents the mean value for all vagrant species.
Related to Figure S1 and Table S1.

Europe, adult-type birds are rare (10% in autumn, 15.2% in winter) and their number is not significantly different from the number of adult-type birds expected if all birds were young birds (7 adult-type birds out of 46 scored individuals versus 5 adult-type birds among 50 in-hand aged juveniles; Fisher's exact test, p = 0.55). In southwestern Europe and North Africa, however, adult-type birds are more common (48.5% in autumn, 59% in winter; Figure S3), significantly more common than expected if all birds were young (winter period, 57 adult type out of 97; chi-square test = 54.1, p < 0.001). The proportions of adult-type molt phenotypes in citizen-science pictures thus demonstrate the regular occurrence of adult birds, and hence likely regular migrants and wintering individuals, in the Iberian Peninsula, North Africa (Morocco), western France, and Italy.

Can vagrancy promote the emergence of new migratory routes?

The change in status of Richard's Pipit from vagrant to regular migrant in southwestern Europe opens up the question of the role of vagrancy in the establishment of new migration routes. Large angle misorientation, also known as reverse migration[11] or mirror-image migration,[24] has been proposed to explain the occurrence of Siberian vagrants in Europe, particularly for populations breeding in the western part of their distribution[15,25,26] (but see Lees and Van der Werf[27]). Such errors in migratory orientation have usually dramatic consequences on fitness,[28] especially in passerines where the energy cost of long migratory flights is very high,[29] and vagrants are therefore usually thought to perish.[14,30] The ability of vagrants to establish new migration routes may thus depend crucially on the wintering conditions they encounter in the areas where they end up (i.e., overwinter survival) and on their ability to perform a successful return journey and transmit their migration route to their offspring (via genetic inheritance as migration direction is genetically determined in songbirds; e.g., Helbig,[31] Lundberg et al.,[32] and Delmore et al.[33]).

In Richard's Pipit, the main wintering grounds are in southern and Southeast Asia (Figure 1).[13] Thus, the most parsimonious hypothesis is that the species' ancestral wintering grounds are in Asia and that the European wintering range represents a derived state that was recently established, or at least recently increased. To investigate the factors that may have favored the observed change in migration strategy, we examined the wintering niche conditions in the ancestral and derived ranges.

When citizen-science occurrences data were plotted in a two-dimensional space defined by principal component analysis (PCA) axes on climatic and habitat variables (Figure 4A),[13,34] we found that the niche of the European wintering range is broadly similar but not identical to the niche used in Asia: niches overlapped with a Schoener's D value of 0.31 (D = 0, no overlap; D = 1, complete overlap) and 68.8% of the European niche was included within the Asian niche. We also performed two niche distribution models, one calibrated in Europe and one calibrated in Asia, then projected them under current conditions (Figures 4B and S4). The projection of the Asian calibrated model under current conditions over Europe mainly predicted wintering in western Iberian Peninsula and North Africa (Figure 4B), confirming that the species encounter slightly different (but still overlapping) climatic conditions in southern France and northeastern Spain compared to the ancestral wintering areas in Asia. To test for recent changes in European wintering conditions, we projected a European calibrated model over two periods in 1961–1990 and 1990–2018 and found an extension in suitable wintering areas (mostly due to increasing temperature; Figure S5) between these periods, especially in northern Spain, southern and western France, and Italy (Figure 4C). Vagrant Richard's Pipits migrating west from Asia may thus have found suitable environmental conditions to survive the winter in large areas of North Africa and Iberian Peninsula (see Cramp and Simmons[12]), after which environmental changes (here climate change) might have increased wintering opportunities for Richard's Pipit in southern Europe.

If these results suggest that the emergence of new migratory routes can ensue from the survival and successful return migration of vagrants to Europe, to what extent natural selection may explain the emergence and spread of this new wintering range remains to be investigated. In particular, although proximate mechanisms of vagrancy remain largely unknown to date, it should be verified that vagrancy is to some degree hardwired (otherwise this new migratory orientation could not be transmitted to young) and that some forms of reproductive isolation exist between individuals migrating west and east (otherwise panmixia would prevent the stability of migration to Europe).[5,6] We suppose that a migratory divide could exist in this species with individuals at the western margin of the species' range, which should constitute a distinct population, all having a westerly migratory route,[35,36] but this would need to be tested by deploying data loggers in breeding populations.
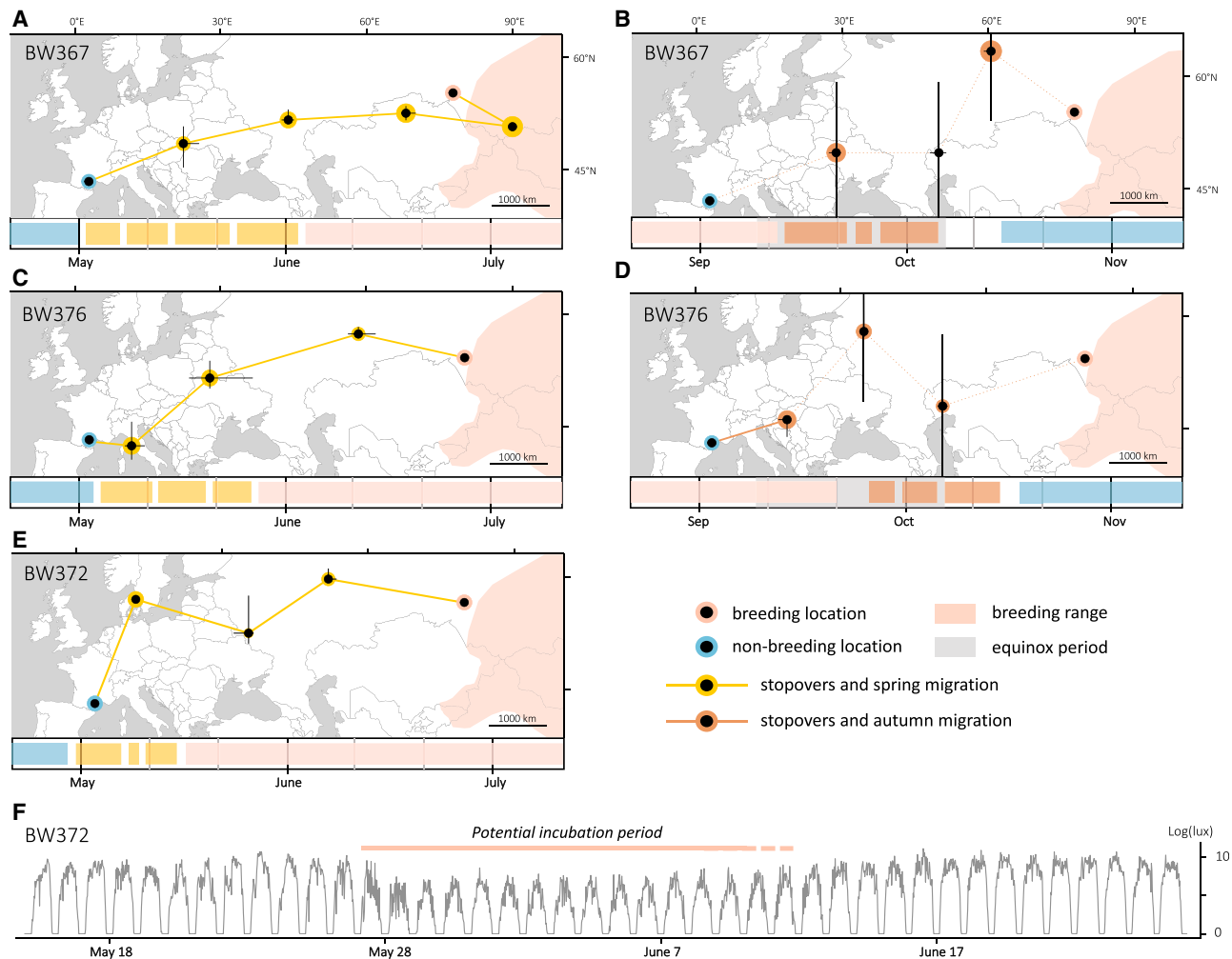
Figure 3. Migration routes, stopovers, and breeding sites of three GLS-tracked Richard's Pipits
Individuals are identified by their GLS numbers: BW367 (A and B), BW376 (C and D), and BW372 (E). (F) indicates the light intensity (log-transformed) recorded by GLS BW372 in May to June. Blue dots indicate the wintering location in southern France (Labruguière for BW376 and BW372, Lespignan for BW367) where the GLSs were deployed. Pink dots indicate the estimated breeding location from the retrieved GLS (55.35 N ± 0.8 SD, 77.53 E ± 1.3 SD, 54.45 N ± 0.4, 79.82 E ± 0.6, and 56.74 N ± 0.3, 79.54 E ± 0.9 for the three birds, respectively), at the limit of the known breeding distribution represented by the pink polygon.[18] The change of pattern in light intensity data (F) suggests that this individual was likely incubating and thus engaged in breeding behavior. Other dots (with error bars corresponding to standard errors of longitude and latitude estimates) indicate stopover sites where the bird stayed more than 24 h. The sizes of these dots are proportional to the duration of the stopover. For each individual, the migration phenology is indicated alongside the map where colored bars indicate stopovers and white spaces between them represent movement periods between the stopovers. The equinox period (22 September ± 14 days) is indicated for the autumn migration (B–D). Since birds undertook most of their autumn migrations during this period, latitudinal positions have large errors.

Ancient literature suggests that this species may have been observed with some regularity in few European localities during the 19th century.[37,38] Although we showed that Richard's Pipit numbers have undoubtedly increased in recent decades, particularly in southwestern Europe and probably due to changing temperatures, we cannot rule out the hypothesis that a westward migratory route had existed for a long time and that we observed an increased use of this route in recent decades.

Concluding remarks
In this study, we show that the occurrence of Richard's Pipit in southwestern Europe is, at least in part, due to a population performing a regular seasonal migration, and cannot solely be

explained by disoriented vagrant individuals. While the role of vagrancy in colonization of new breeding range has been documented in several species,[39–42] our results support the idea that vagrancy may also promote the establishment of new migratory routes.[4] This idea was also proposed to explain one of the few known contemporary changes[2,3] in migration route in passerines: the change from southwestern to northwestern orientation in central European Blackcap *Sylvia atricapilla*,[1,5,6] selected as a response to changing environment that increased overwinter survival.[43,44] Increased overwinter survival, helped by climate change, may also explain recent increases in autumn and winter numbers of other Siberian species in Europe (e.g., Yellow-browed Warbler *Phylloscopus inornatus*, Siberian
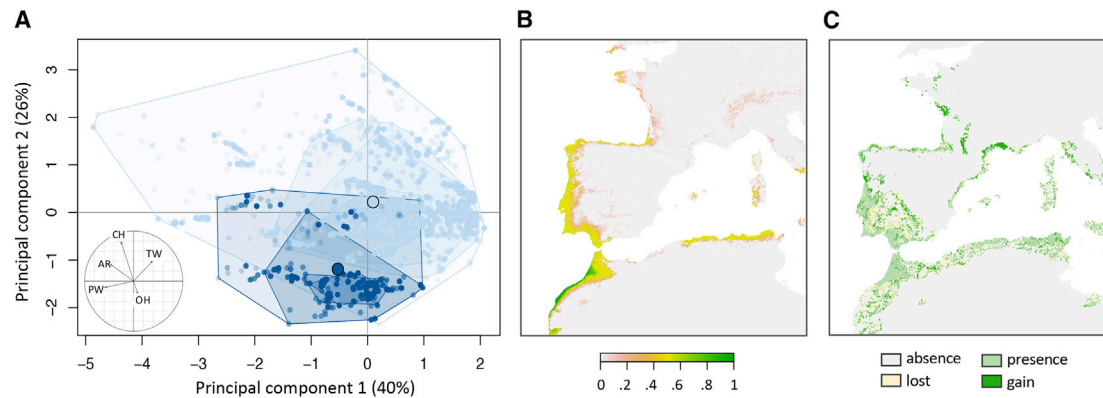
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Figure 4. Wintering niche comparisons and niche-based distribution modeling

(A) Niche comparison between wintering areas in Europe and North Africa (dark blue) and Southeast Asia (light blue). The convex hulls indicate the prevalence (25%, 50%, 75%, and 100% of locations included) of the environmental conditions. Small dots indicate GBIF occurrences and black-circled dots represent the centroids of these occurrences. The correlation circle (inset) indicates the loading of environmental variables onto the first two PCA axes: PRW (precipitation during winter months), TW (temperature of winter months), AR (aridity), OH (open habitats), and CH (closed habitats). The first axis (PC1, 39.6% of total variance) differentiated the environmental spaces between wintering ranges with warmer and less humid winters in Asia than in Europe. The second axis (PC2, 26.4%) is associated with the opening of habitats, with the Asian niche of the species being characterized by more closed habitats than in Europe.

(B) Map representing the projection over Europe and North Africa under current conditions of the niche model calibrated with Asian occurrences. Colors from white to green represent an increasing scale of suitability. The coastal plain in northwest Morocco and to a lesser degree the Portugal coast and the coastal plain area between Alger and Tunis (in Algeria and Tunisia) corresponds to the environmental conditions experienced by Richard's Pipits in their ancestral wintering areas.

(C) Map representing the change of suitability based on the projection over two periods (1961–1990 and 1990–2018) of a niche model calibrated with European occurrences. Dark green represents gain of suitable areas between these periods.

Related to Figures S4 and S5.

Chiffchaff *Phylloscopus collybita tristis*, and Olive-backed Pipit *Anthus hodgsoni*) that may also be currently establishing new secondary migration routes to Europe. The lack of records of these species during the spring migration was perceived as undermining the "pseudo-vagrancy" theory,[4] but we have shown here that such spring return migration can be particularly under-detected. The Richard's Pipit might thus be the most prominent example of a phenomenon that could change current paradigms on the flexibility and constraints of avian migration. Indeed, there is no passerine species confirmed to undertake such longitudinal migration to European wintering grounds, and most similar routes concern species with East African wintering grounds that probably spread eastward from an ancestral breeding range in Europe to breed in the eastern Palearctic but return to winter in same locations.[7,8] Such examples of apparent failure to discover new, less energetically demanding wintering areas explain why migration orientation is usually perceived as highly constrained in passerines.[28,31] Our results suggest that we need to temper this view and that vagrancy due to misorientation during migration is more than a mere natural curiosity without much scientific interest.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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  - Data and code availability
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  - Birds aging and molt scoring
  - Assessing the geographical distribution of molt phenotypes from pictures
  - Tracking the breeding range of Richard's Pipits with archival light loggers
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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.09.086.

AUTHOR CONTRIBUTIONS

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. J.R., M.G., P.D.-V., and P.D. collected occurrences and environmental data. M.G. and P.D. ran the analyses. P.D. wrote the first version of the paper and all authors contributed substantially to the revisions.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw geolocator data	This paper	Study ID: 1720094461
Software and algorithms		
R package TwGeos	[45]	https://github.com/slisovski/TwGeos
R package FLightR	[46]	https://cran.r-project.org/web/packages/FLightR/
R package geosphere	[47]	https://cran.r-project.org/web/packages/geosphere/
R package spThin	[48]	https://cran.r-project.org/web/packages/spThin/
R package ade4	[49]	https://cran.r-project.org/web/packages/ade4/
R package biomod2	[50,51]	https://cran.r-project.org/web/packages/biomod2/
Other		
Intigeo geolocators	Migrate Technology Ltd, Cambridge, UK	INTIGEO P65C2-7 0.74 g

RESOURCE AVAILABILITY

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

Materials availability
This study did not generate new unique reagents.

Data and code availability
Raw geolocator data have been archived on https://www.movebank.org/cms/movebank-main (study ID: 1720094461). Occurrences data are from published or downloadable online sources (e.g., Global Biodiversity Information Facility). Environmental data used in this paper are freely available and downloadable from the web, the R code for running niche modeling analyses is available on Zenodo: https://doi.org/10.5281/zenodo.5500364.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

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

METHOD DETAILS

Estimating trends in Richard's Pipit occurrence
To check whether the number of Richard's Pipits occurring in Europe actually increased over the last few decades, we studied the trend in occurrence numbers in France between 1981 and 2019. We focused on France because the country hosted the first documented wintering record for Europe[16] and because data have been meticulously collected over a period of about 30 years. The French Birds Rarities Committee collected data between 1981 and 2005 when the species was still rare to scarce. From the 1990s onward, numbers of occurrences started to increase and data on the species were collected by another committee between 2005 and 2010, after which the citizen-science databases took over. To avoid double-counting, we used the maximum number of individuals simultaneously recorded on a given locality and on a given year.

To test whether the species increasing trend is entirely driven by an increase in observer effort, we compared linear regression coefficients of number of individuals over time for Richard's Pipit and other vagrants of eastern origin. As these data have always been collected using the same methodology by the French Birds Rarities Committee, we assumed no reporting bias over time and we considered these data as an approximation of observer effort. We excluded the rarest species from the dataset (less than 5 records over the 1981-2019 period; the list of species and numbers of individuals can be found in Table S1). We repeated these analyses for the Mediterranean region of southern France (defined as departments bordering the Mediterranean Sea) as this region

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hosted the first and most of the wintering sites and includes several localities where observation pressure had remained strong over this period.

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

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

Ringing campaigns

We caught Richard's Pipits over the course of three wintering periods between 2018 and 2021 on several locations along the Mediterranean coast of France and Spain (see Figure 1 and details in Table S2). Since capture success of the capture sessions was strongly dependent on weather, the effort of capture was heterogeneous between sites and between wintering seasons. Birds were attracted with conspecific call playback and caught using vertical monofilament mist nets or (in Spain only) spring traps, mainly at dawn or dusk. Due to a very variable attraction success of call playback, capture rates were also very variable and null on several sessions. All captured birds were measured, ringed with a metal (left leg) and a Darvic band (engraved with a unique alphanumeric code; right leg), photographed, and a feather sample (one greater covert) was taken before birds were released after ca. 5 min of handling. There is no known reliable way to determine the sex in this species from in-hand examinations and we thus have no information on the sex of the birds we caught.

Birds aging and molt scoring

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

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

Assessing the geographical distribution of molt phenotypes from pictures

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

For the winter period, we assessed whether the proportions of molt phenotypes in northwestern Europe (Norway, Sweden, Denmark, Germany, the Netherlands, the United-Kingdom, Ireland, Switzerland and Western France) and southwestern Europe (Southern France, Italy, Catalonia, Spain, Portugal, Morocco) are different from the expected proportions under the full vagrancy hypothesis (i.e., under the hypothesis that only young birds are seen in Europe) by performing a Fisher' exact or Chi-square test on contingency tables summarizing observations (the choice of the test depending on the number of observations per category). We thus compared the proportions of molt phenotypes from the 50 young birds examined in the hand with the proportions of molt phenotypes estimated from pictures in Northwestern and Southwestern Europe. A significant test would indicate that the proportions of molt

phenotypes differ from those observed in a sample of juvenile birds. If only vagrant birds were involved, we would expect that all or most are juveniles.

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

During the 2019-2020 winter period, we deployed seven INTIGEO P65C2-7 Global-Location-Sensors (GLS) in Southern France (Migrate Technology, 0.74 g; Covid-19 lockdown stopped the fieldwork season in early 2020). GLS are small electronic devices that record time and light intensity, enabling the calculation of the approximate position of the logger given the duration of the day and the time of solar noon, both depending on latitude and longitude for a given calendar day.[52] Due to the small body size of the Richard's Pipit, there were no other technology available at the time to track the movements of the species during the annual cycle. Since GLS do not remotely transmit positions, they have to be retrieved to download the data and birds must thus be captured again. Due to the equivalent day length everywhere on Earth at the autumnal and spring equinoxes, latitudinal positions within 15 days on each side of the two equinox dates cannot be estimated accurately.[53] The error of GLS locations during migration is known to vary up to 200 km[53] but the precision increases (in the order of a few dozen kilometers) when the bird stays several days at the same location.[54] Using the same technique as explained above, we equipped four adults and three young birds with leg-loop harnesses made from rubber bands to attach the loggers. The device and fitting material represented less than 3% of a bird's weight (average weight: 31.9 ± 2.2 g, n = 78; unpublished data). We retrieved three devices the next winter, containing data from at least one complete migration per bird (Table S2). Return rates of GLS-equipped birds did not differ obviously from those that have been colored-ringed during winter 2018-2019 and re-sighted during winter 2018-2019 (42% of returning GLS-equipped bird and 33% of returning color-ringed individuals, but note small sample sizes).

We followed the method described in Lisovski et al. (2020)[55] to analyze the light data recorded by GLS devices. We first looked for changes in light intensity pattern that could provide evidence for an incubating behavior (i.e., for a bird hidden in the vegetation). Then, we used the *TwGeos* R package[45] to define twilights with the *preprocessLight* function, using a threshold of 2.5 lux. We manually removed obviously erroneous twilights and applied an additional automated screening using the *twilightEdit* function (settings were window = 4, outlier.mins = 45 and stationary.mins = 25). We then used the *FLightR* package[46] to determine migration timing. Since, the package requires calibration periods during which the bird is stationary in a known location, we ran the model a first time using the month of March as calibration period and with a particle filter of 10^4 particles (color-ringed birds were observed throughout March on their wintering site, *pers. obs*). We refined the calibration period using the *plot_lon_lat* function (plot of latitude and longitude in horizontal layout). We defined the *FLightR* search grid between 35° S and 65° N latitude and 0° W and 100° E longitude and ran the particle filter with the recommended 10^6 particles. We estimated the breeding location, migration timing, potential stationary periods and their locations using the *stationary.migration.summary* function by defining a minimum duration of stationary period of 24 h and testing different values of minimum probability of movement (*prob.cutoff*). We estimated the migratory route and the distance traveled via the shortest route (i.e., a great circle route; *distHaversine* function in the *geosphere* R package)[47] between these different stationary locations.

Wintering niche comparison

To compare environmental niches of birds wintering in their ancestral Asian areas and birds wintering in Europe, we collected occurrences of Richard's Pipit from the Global Biodiversity Information Facility (https://www.gbif.org/). We selected occurrence data for the wintering period alone (from December to February) and from countries known to host the species regularly during this period (Europe and North Africa: France, Spain, Portugal, Italy, Morocco; Asia: Taiwan, Thailand, Hong-Kong, China, India, Myanmar, Vietnam, Laos, Cambodia, Sri Lanka; see Alström and Mild[13]). We retained verified and georeferenced occurrences, resulting in 1,268 occurrences for Europe and North Africa and 6, 717 occurrences for Asia, derived from citizen science databases widely used by the ornithological community (mostly eBird.org, iNaturalist.org, observation.org and the various Biolovision national reporting systems). For Europe, these databased are usually well curated by validation committees that operate at local (regional) or national scales. Data were then thinned prior to analyses to reduce the effect of biased species occurrence collections, using the *spThin* R package[48] with a thinning parameter of 0.5 km, leaving a total of 1,638 occurrences.

Since environmental conditions seem to play a key role in the selection of species' wintering grounds, particularly for finding the resources necessary for winter survival,[34] we collected several climatic and habitat variables related to the species preference.[13] We downloaded the temperature and precipitations of the winter months (between December and February), an aridity index (the ratio of the mean annual precipitation on the mean annual potential evapo-transpiration) and a discrete variable characterizing open and closed habitats. The climatic data were collected from the CHELSA database v1.2 (https://chelsa-climate.org/) at a resolution of 30 arc seconds, with monthly mean temperature and precipitation averaged over the period 1979– 2013.[56] The aridity index was collected from the CGIAR-CSI Database (https://cgiarcsi.community/) at a resolution of 30 arc seconds for the period 1970–2000[57] and habitat variable from the Global Land Cover Map (GlobCover).[58] The habitat variable was coded as "open" and "closed" habitats based on GlobCover categories; crop and mosaic habitats with more than 50% of cropland or grassland were considered as open habitats whereas mosaic habitats with less than 50% of cropland or grassland and more than 50% of forest or scrubland were considered as closed habitats. We checked that variables were not collinear (correlation coefficients < 0.50) using occurrences in both European and Asian regions, resulting in five variables to represent environmental variation among regions: PRW (precipitation during winter months), TW (temperature of winter months), AR (aridity), OH (open-habitats) and CH (close-habitats).

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Environmental niche variation was evaluated using principal component analysis (PCA) implemented in the *ade4* R package.[49] We assessed the variation between the European-North African and Asian wintering ranges by comparing the coordinates of occurrences in a two-dimensional environmental space (PC1 x PC2). We evaluated the niche overlap between the Asian and the European niches using Schoener's D.[59] We also evaluated the percentage of inclusion of the European niche within the Asian niche by measuring the intersection between each convex hull defined by 100% of occurrences.

To investigate if vagrant birds may have found suitable wintering conditions in Europe, we performed niche distribution models with the *BIOMOD* R package[50,51] implemented in the *biomod2 R* package. For each region, an ensemble of projections from four statistical models was obtained, including random forest (RF), generalized linear models (GLM), generalized additive models (GAM) and general boosting method (GBM).[60] Models were calibrated for the baseline period using 70% of observations randomly sampled from the initial data and evaluated against the remaining 30% data using the true skill statistic (TSS)[61] and the area under the curve (ROC).[62] For each model, the relative importance of each environmental variable was assessed by calculating the Pearson's correlation between the standard predictions (i.e., fitted values) and the predictions after randomly permuting the values of the variable. The ensemble forecasting was then built by assigning weight to each individual model depending on its quality (TSS) and taking the weighted sum of occurrence probabilities. Both calibrated models were projected under current conditions over Europe – North Africa and Asia.

To evaluate changes in suitability across Europe over the period 1960-2018, we also performed niche distribution models using the same methodology with environmental variables available for this time period. We thus downloaded the temperature and precipitation of the winter months (between December and February) from the CHELSA database v1.2 (https://chelsa-climate.org/) at a resolution of 30 arc seconds, with monthly mean temperature and precipitation averaged for the 1961-2018 period.[56] The aridity index (CGIAR-CSI Database) and habitat variable from the Global Land Cover Map (GlobCover)[58] were not available for the entire study period. Therefore, we calculated the De Martonne index[63] as an aridity index, from monthly precipitation and annual temperature data for the 1961-2018 period. But we finally found high collinearity (correlation coefficients > 0.50) with precipitations data. The calibrated model based on two environmental variables (PRW and TW) was projected over Europe under conditions of the 1961-1990 and the 1990-2018 periods.

Supplemental Information

A new westward migration route

in an Asian passerine bird

Paul Dufour, Christophe de Franceschi, Paul Doniol-Valcroze, Frédéric Jiguet, Maya Guéguen, Julien Renaud, Sébastien Lavergne, and Pierre-André Crochet
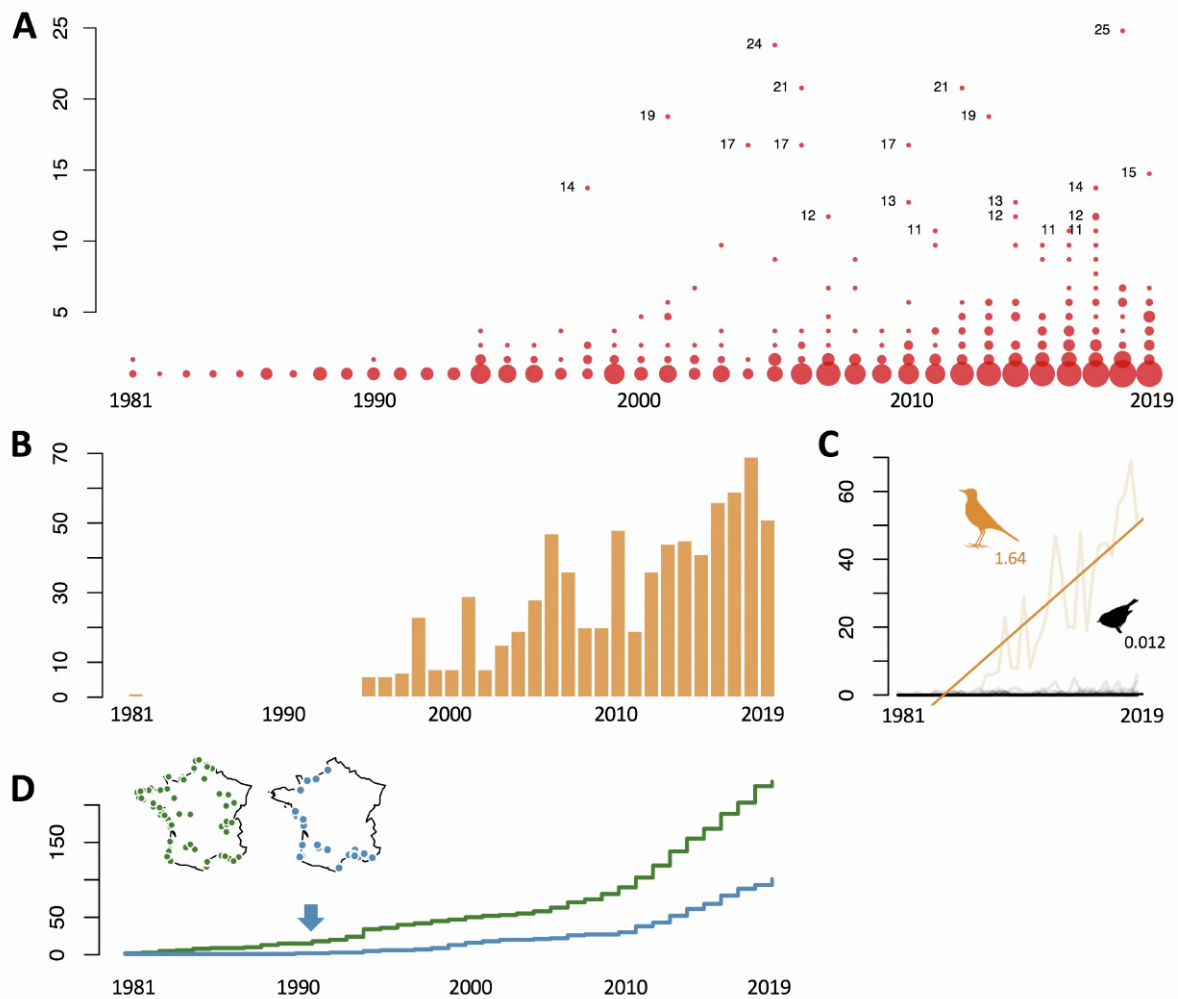
Figure S1. Trends in Richard's Pipit flock sizes and occurrence locations during the last decades. Related to Figure 2, Table S1 and STAR Methods.

(A) Sizes of groups for Richard's Pipit observations in France between 1981 and 2019. The size of the points represents the number of observations for a given flock size, this number has been log+1 transformed for visualization purposes. Numbers above 10 are indicated on the figure. (B) Barplot representing the temporal evolution of the number of Richard's Pipits observed in southern France (Mediterranean region: Languedoc-Roussillon and Provence-Alpes-Côte d'Azur) between 1981 and 2019. In several localities (Camargue and Crau notably), sites that now host the species during winter have been monitored constantly over this period. This is especially true for the Tour du Valat Biological Station in the Camargue where experimented ornithologists have been present without interruption since the 1960s and where intensive ringing programs took place until the 1970s, allowing the local observers to record the first occurrence of wintering Richard's Pipits followed by an increase in numbers in subsequent years.[S1-2] (C) Graphic comparing the trends in the number of Richard's Pipits

(orange line) versus other vagrant species of eastern origin (black line) observed in southern France over the same period (1981-2019). The list of vagrant species as well as the regression coefficients can be found in Table S1. (D) Evolution of the number (cumulative) of locations frequented by Richard's Pipits during the migration period (green; September-November and March-May) and the winter period (blue; December-February) over the period (1981-2019). The schematic maps indicate the approximate locations during both migration and winter period. The first case of wintering recorded in southern France in 1991 is indicated by the blue arrow.[S3]
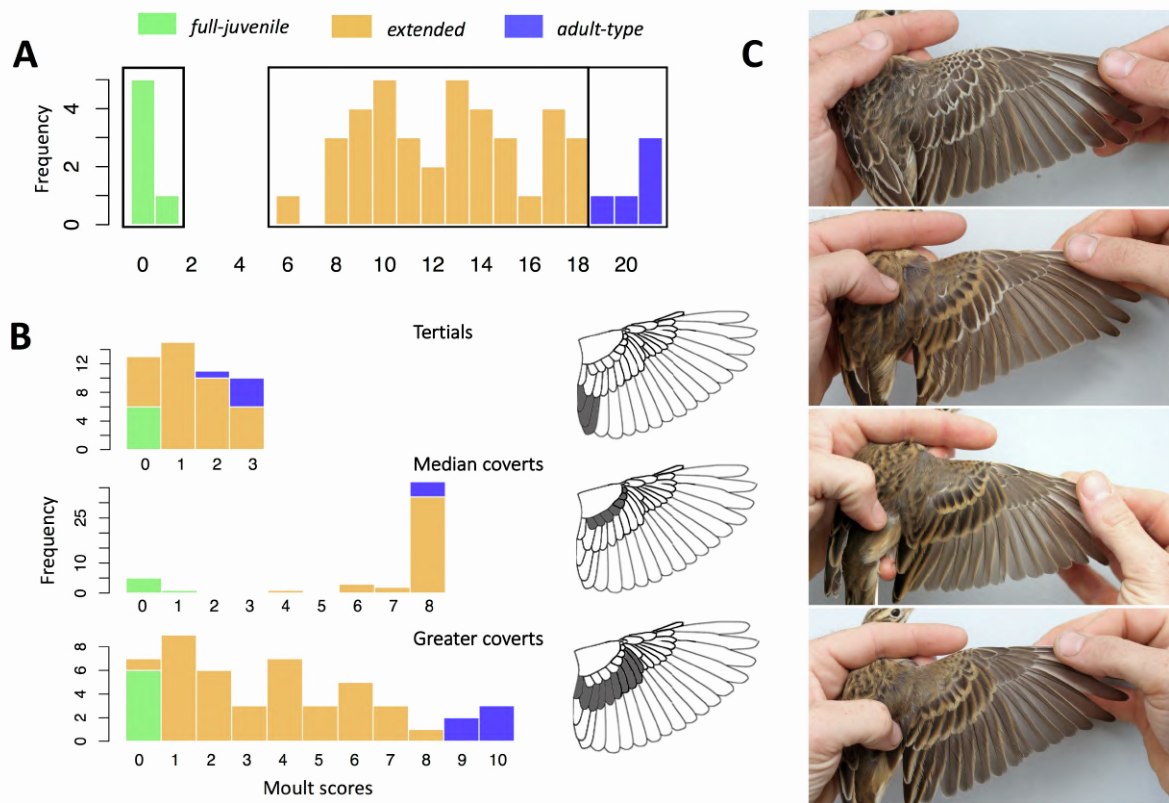
Figure S2. Molt scores and molt phenotypes observed in captured Richard's Pipits. Related to Figure S3 and STAR Methods.

(A) Barplot representing the total number of molted feathers in first-winter birds caught in this study from 0 (no feather molted) to 21 (all tertiaries, median and greater coverts molted; n = 50). Colours and the three boxes represent the three molt phenotypes identified: *full-juvenile*, *extended* and *adult-type*. (B) Barplots representing the number of molted feathers for each feather type: tertiaries, median and greater coverts. (C) Illustration of the different molt phenotypes identified in captured Richard's Pipits. From top to bottom: *full-juvenile*, *extended* molt phenotype, *adult-type* first-winter bird and adult bird for comparison. Photos Paul Dufour.
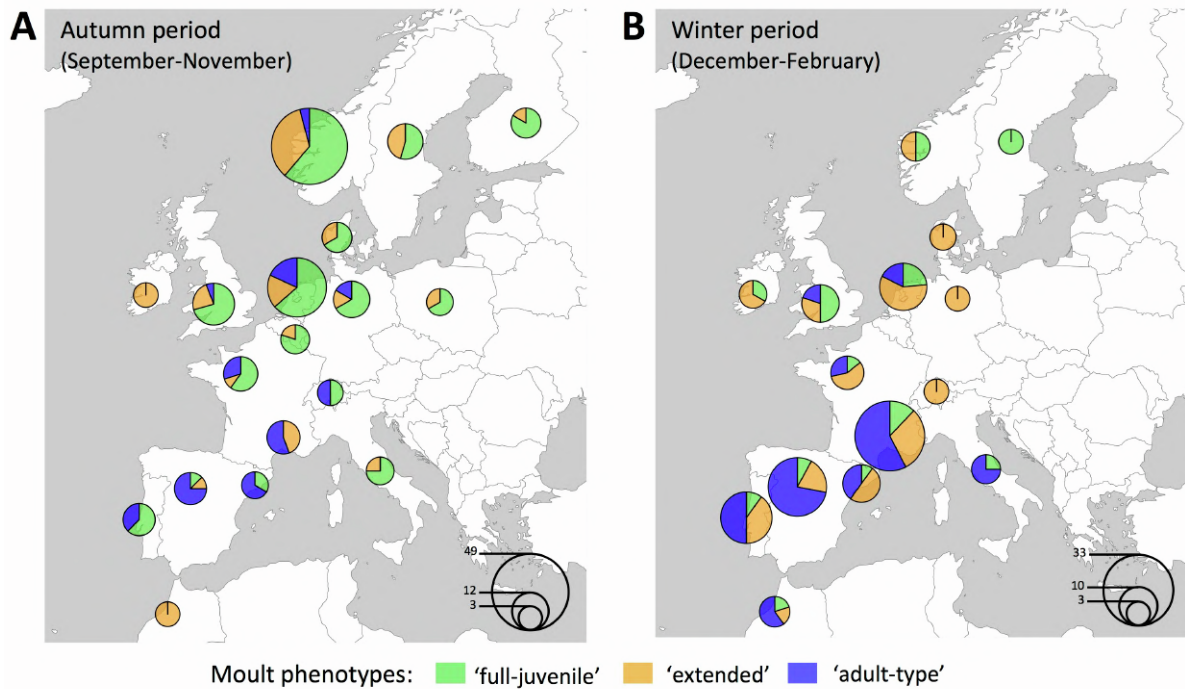
Figure S3. Geographical variation in molt phenotypes. Related to Figure S3, Table S2 and STAR Methods.

Molt phenotypes were assessed from pictures of Richard's Pipits taken in European and North Africa between 2013 and 2019 in autumn (A) or during winter (B). Molt phenotype is a proxy for age, with *full juvenile + extended* entirely made of young birds while *adult-type* is a mixture of adult and young birds (we found 17% of young birds within the adult-type birds in our captures). In addition of southern France, Iberian Peninsula, North-Africa (Morocco), western France and Italy likely host regular migrant Richard's Pipits during the winter period, but the low proportions of *adult-type* birds found in the United-Kingdom and the Netherlands could not exclude the presence of young birds having completed an extensive molt. Even if some of the birds observed in northwestern Europe may subsequently reorient towards wintering sites of southwest Europe, the high proportion of *full-juvenile* phenotypes (rare in southwestern Europe and on the species' classical wintering sites[S4]) suggests that they are mostly misoriented juveniles. The size of the pie charts depends to the number of pictures collected per country (see inset). France is divided between the Mediterranean coast and the rest of the country.
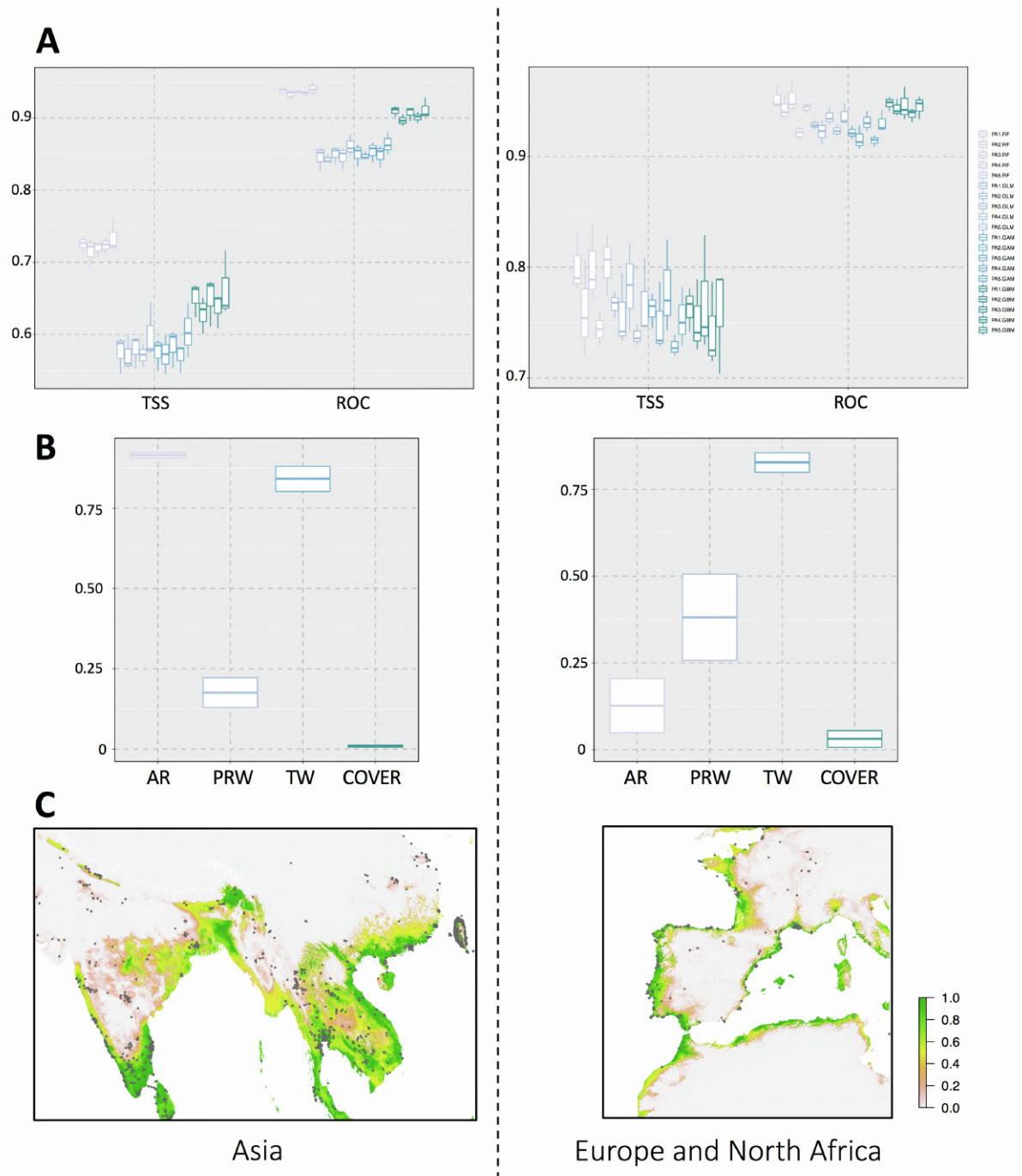
Figure S4. Niche distribution modeling values and projections under current conditions. Related to Figure 4. (A) True skill statistic (TSS) and area under the curve (ROC) values obtained for the four statistical models tested and calibrated in Asia and in Europe and North Africa. Models tested are random forest (RF), generalized linear models (GLM), generalized additive models (GAM) and general boosting method (GBM). (B) Relative importance (Pearson's correlation) of the four environmental variables used to project the potential distribution of Richard's Pipit and obtained from calibration in Europe and North-Africa and in Asia. PRW (precipitation during winter months), TW (temperature of winter months), AR (aridity), COVER (open and close habitats). (C) Maps indicate predicted areas from the

projection under current conditions of models calibrated in Asia and in Europe and North-Africa. Grey dots represent the GBIF occurrences (1 268 in Europe and North Africa, 6 171 in Asia) considered to construct the niche modelling. Colors from white to green represent an increasing scale of suitability.
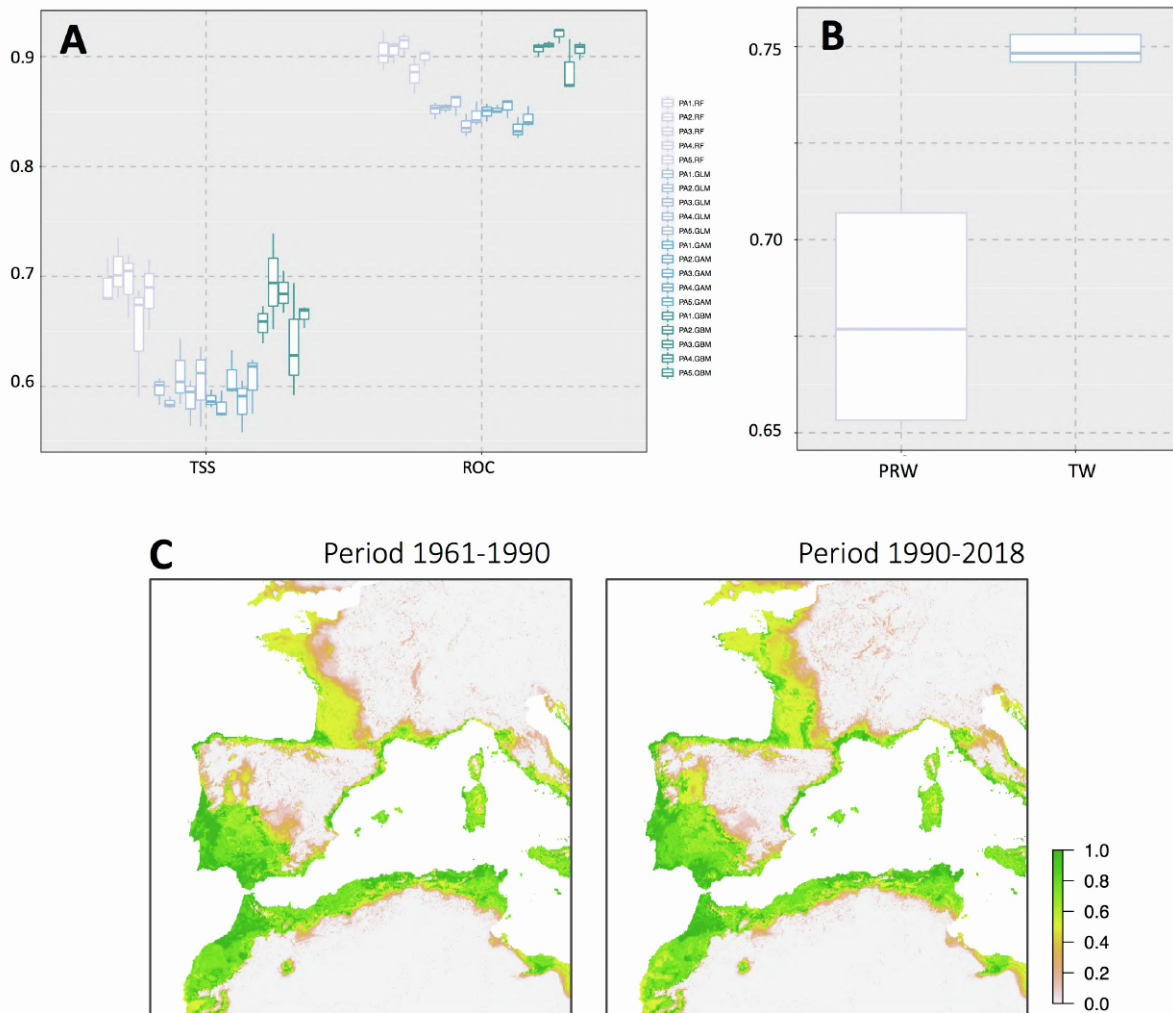

Figure S5. **Niche distribution modeling values and projections over 1961-1990 / 1990-2018 periods. Related to Figure 4.** (A) True skill statistic (TSS) and area under the curve (ROC) values obtained for the four statistical models tested and calibrated under current conditions in Europe. Models tested are random forest (RF), generalized linear models (GLM), generalized additive models (GAM) and general boosting method (GBM). (B) Relative importance (Pearson's correlation) of the two environmental variables. PRW (precipitation during winter months), TW (temperature of winter months). (C) Maps indicate predicted areas from the projection over two periods of a model calibrated under current conditions in Europe: 1961-1990 and 1990-2018. Colors from white to green represent an increasing scale of suitability.

Eastern origin species	France		Mediterranean regions	
	Total Record	Coeff.	Total Record	Coeff.
Acrocephalus agricola	62	0,070	18	0,020
Acrocephalus dumetorum	22	0,034	1	-
Anthus godlewski	18	0,033	3	0,004
Anthus hodgsoni	40	0,073	1	-
Emberiza leucocephalos	55	0,029	8	0,013
Emberiza pusilla	205	0,231	29	0,030
Emberiza rustica	33	0,005	0	-
Iduna caligata	14	0,015	0	-
Lanius isabellinus/phoenicuroides	13	0,020	3	0,004
Luscinia luscinia	9	0,007	0	-
Motacilla citreola	62	0,111	26	0,050
Phylloscopus borealis	17	-0,009	1	-
Phylloscopus fuscatus	87	0,103	6	0,010
Phylloscopus humei	38	0,060	3	<0,001
Phylloscopus proregulus	133	0,111	18	0,011
Phylloscopus schwarzi	19	0,015	0	-
Phylloscopus trochiloides	30	0,008	3	-0,003
Saxicola maurus	36	0,001	3	0,002
Sylvia nisoria	82	0,099	5	-0,003
Tarsiger cyanurus	19	0,040	3	0,006

Table S1. Trends in species from eastern origin recorded in France between 1981 and 2019. Related to Figure 2, S1.

List of species from eastern origin with the total number of individuals recorded in France and in southern France (Mediterranean regions) between 1981 and 2019 and the regression coefficient of record per year over the period. The Yellow-browed Warbler *Phylloscopus inornatus* is another passerine species that has become more common in recent decades in autumn and winter (see Results and Discussion), hence it was not considered here.

Sites	Country	GPS (lat, lon)	Winter 2018/2019		Winter 2019/2020				Winter 2020/2021			
			Total	Adult birds	Total	Adult birds	GLS-deployed	Control	Total	Adult birds	GLS-retrieved	Control
Crau plain	France	43.57°N, 4.87°E	21	2	21	4	-	2	5	2	-	2 (1)
Fréjus	France	43.41°N, 6.73°E	4	2	1	1	1	1	3	0	0	1 (1)
Alenya	France	42.65°N, 3.00°E	2	1	1	0	1	2	4	3	0	1 (1)
Labruguières	France	43.54°N, 2.28°E	3	1	2	1	2	2	2	2	1	1 (1)
Lespignan	France	43.27°N, 3.15°E	-	-	3	2	3	-	3	2	2	2
Fleury	France	43.25°N, 3.19°E	-	-	-	-	-	-	1	1	-	-
Vilanera	Spain	42.11°N, 3.11°E	1	1	-	-	-	-	-	-	-	-
Camp Túries	Spain	42.23°N, 3.11°E	4	3	-	-	-	1	-	-	-	-

Table S2. Monitoring sites and captures results over the three wintering seasons. Related to Figure 1 and STAR Methods.

Locations where Richard's Pipits were captured and GLS-equipped during the different winters. The total numbers of birds captured, the number of adult birds among birds captured, the number of GLS deployed and retrieved and the number of ringed birds re-sighted or recaptured in following winters are indicated. Note that the total numbers only concerned new ringed birds since control numbers may only represent visual controls. Numbers between brackets indicate the number of birds ringed during the 2018-2019 winters that have returned in 2019-2020 and 2020-2021. (-) indicates that no capture was made on the spot.

Countries	Websites	Pictures collected
France	https://www.faune-france.org/	59
Belgium	https://waarnemingen.be/	4
	https://www.trektellen.nl/	1
Holland	https://waarneming.nl/	44
	https://www.trektellen.nl/	6
Germany	https://www.ornitho.de/	13
Poland	http://www.clanga.com/	3
Denmark	https://dofbasen.dk/	9
Norway	https://www.artsobservasjoner.no/	53
Finland	https://www.tiira.fi/	6
Sweden	https://www.artportalen.se	11
	https://ebird.org/	1
Britain	https://www.birdguides.com/	22
	https://ebird.org/	5
Ireland	http://www.irishbirding.com/	2
	https://www.birdguides.com/	2
Italy	https://www.ornitho.it/	8
Switzerland	https://www.ornitho.ch/	3
Spain	https://www.reservoirbirds.com/	13
	https://www.ornitho.eus/	7
	https://ebird.org/	14
Catalonia	https://www.ornitho.cat/	13
Portugal	https://ebird.org/	32
Morocco	https://maroc.observation.org/	2
	https://ebird.org/	5

Table S3. Details on number of pictures collected per websites and per countries. Related to Figure S3 and STAR Methods.

Pictures were mostly collected from citizen-science databases and Internet picture repositories.

Supplemental References

S1.   Kayser, Y., Girard, C., Massez, G., Chérain, Y., Cohez, D., Hafner, H., Johnson, A., Sadoul, N., Tamisier, A., and Isenmann, P. (2003). Compte-rendu ornithologique Camarguais pour les années 1995-2000. Rev. Écol. (Terre Vie) *58*, 5–76. In French with English summary.

S2.   Kayser, Y., Gauthier-Clerc, M., Béchet, A., Poulin, B., Massez, G., Chérain, Y., Paoli, J., Sadoul, N., Vialet, E., Paulus, G., et al. (2008). Compte Rendu ornithologique camarguais pour les années 2001-2006. Rev. Écol. (Terre Vie) *63*, 299–349. In French with English summary.

S3.   Dulau, S. (1997). Nouveau cas d'hivernage du Pipit de Richard Anthus richardi dans le sud de la France. Ornithos *4*, 90–91. In French with English summary.

S4.   Alstrom, P., and Mild, K. (2003). Pipits and Wagtails of Europe, Asia and North-America Helm, ed.