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# Contradictions between current theory and historical evidence in the population dynamics and biogeography of the Ortolan bunting *Emberiza hortulana*

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**SUMMARY**

The Ortolan bunting is an Old World bunting distributed across 20.2 million km$^2$ in the Central and West Palearctic regions, breeding from sea level to 3,300 m. Most of the population is spending the winter in Sub-Saharan Africa north of 5°N migrating mainly along two flyways, on each side of the Mediterranean Sea. The current theory about the bird's population dynamics and biogeography has been developed from transitory research in geographically disconnected surveys on the European and African continent over the last 30 years, handled in stochastic models and population viability analyses. The theory posits that the species was abundant in antecedent times but the previously continuous population became fragmented and underwent a very steep decline in central and western Europe from the middle of the 20$^{th}$ century due to negative anthropogenic effects and hunting. The population segment in Fennoscandia has become isolated from the rest of Europe due to lack of contemporary gene flow from the south and the species is directly threatened with extinction. A review of 948 interdisciplinary literary sources across 435 years (1590-2025) from 18 European countries, the Americas, Africa, Asia and Australia was conducted to explore if the Ortolan bunting's population development could be understood differently with insight gleaned from empirical material on a large spatiotemporal scale. The review revealed that a hundred-years perspective is necessary to obtain a true picture as shorter time will only expose fractions of events interpreted out of context. Historical data disagree with the claim that current distribution is due to fragmentation of a continuous population. The distribution has been restricted to the same "geographical islands" now perceived as fragments across at least the last 300 years. The structure of the population does not indicate restricted gene flow to Fennoscandia from the south as historically the species has not been established in areas immediately south of the peninsula. It was colonized from the east. Antecedent hunting results cited in current scientific literature to validate immense harvest are erroneous, as are the annual catch estimates from France around the turn of the Millennium used to predict the bird's extinction in Fennoscandia. In the last 260 years the population in Europe has undergone temporally long fluctuations (range expansions and contractions) with transient shifts between occurrence and absence manifested by distinct peaks and nadirs in abundance, superimposed on a negative trend. The main drivers may have been a variable immigration rate (fluctuations) and asymmetric growth (negative trend).

## INTRODUCTION

According to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species[1] the Ortolan bunting *Emberiza hortulana* Linné 1758 is not threatened neither under the range size criterion (extremely large, 20.2 million km$^2$), nor the population size criterion (extremely large, 11-17 million mature individuals) or the population trend criterion (decrease in 10 years/3 generations is less than 30%). It is a species of least concern. Despite the status, Pan-European research was initiated in the 1990s (Steiner 1992) which is still ongoing (Piirainen et al. 2024) based on a perception that the population had suffered a massive, human induced decline in Western Europe due to habitat loss, hunting and pesticides (Appendix 1). The decline turned precipitous between 1980 and 2008 (Mentz & Arlettaz 2012) and there was a potential decrease of 50% between 2002 and 2014 (Jiguet et al. 2016a). Menz & Arlettaz (2012) suggested that the current, patchy distribution displayed by the range map (IUCN), which appears to be fragments from a previous continuous population, could be a possible broad scale metapopulation structure (Levins 1969, Hanski & Gilpin 1997). The research has been carried out to create a scientific foundation for remedial conservation efforts. However, extensive management of one of the main Ortolan bunting habitats in eastern Norway during 17 years from 1988 did nothing to curb the species' decline (DN 2009) and by 2025 only two singing males were recorded close to the Swedish border (Bekken 2025[2]). From 2009 farmland at Lake Kvismaren in south-central Sweden was managed according to recommendations from ornithologists to improve ortolan bunting habitat.This did not stop an ongoing 50-year decline from a status of fairly common in 1965 (Runesson & Jönsson 1987) to 5 nests in 2017 (Sondell et al. 2019).

Current research has suffered from short term bias which was evident at the last of four international Ortolan bunting symposia (1992-2009) held in Hitzaker, Germany, where about 80 ornithologists from 10 European countries attended (Bernady 2009). They presented 16 research papers with 432 citations where 83.2% of the sources were published after 1980, 70.4% after 1990 and 36.6% after 2000. None were published before 1900 (Sollien 2024). This short-term bias, which was acknowledged by Dale (1997) and Nævra (2002) warranted a detailed study of the species' biogeographical history to discover an alternative explanation to the population development and decline. During the last 20 years access to written historical sources has undergone substantial improvement. A plethora of ornithological publications, hunting statistics and avicultural data covering continents and centuries has been made available online making it possible to trace the history of bird species. A synthesis of information from these three fields across 435 years revealed that population development in the Ortolan bunting must be viewed across a large spatiotemporal scale. The study established that the population did not appear to have been adversely affected by negative anthropogenic effects. The patchy distribution in Europe has developed from colonization, not fragmentation and natural chains of events in population dynamics, i.e. spatiotemporal fluctuations and asymmetric growth, have been decisive in the Ortolan bunting's disappearance. This indicates that there may be different drivers behind the decline observed across Europe in the last 45 years than the ones analysed by conservation ecologists. Here, I present a literature review to document the historical evidence for such potential drivers for the Ortolan bunting's population decline.

## MATERIALS AND METHODS

The literature review is based on 948 publications from 18 European countries, the Americas, Asia, Africa and Australia across 435 years (1590-2025), of which 57.4% were published before 1950, 44.1% before 1900 (Fig. 1) and 417 are cited as directly relevant to the scope of this article. Of the 417 selected titles, 74.2% were published before 1950. Historical literature was extracted from online libraries, e.g. Google Books, Internet Archive, Hathitrust and Biodiversity Heritage Library with about 83 million titles combined. Metadata was searched by using historical and current names for the Ortolan bunting (Appendix 2). Cataloges of ornithological pioneers were screened, early researchers who had published in periodicals (Appendix 3), or released monographs in one or several volumes about status and development of the

[1]https://www.iucnredlist.org/species/22720916/281469459 Last accessed 6.9.26.

[2]https://artsobservasjoner.no/Sighting/39553933. Norwegian Species Observation Service. Ortolan bunting. Last accessed 7.23.26.

bird populations in their home country and/or in Europe. Current literature was obtained by internet search with the same names for the bird as for the historical literature except for the antecedent ones (Appendix 4) and adding relevant key words (Appendix 5). Further investigation was made in all literature cited in the publications found in the initial search. Publications from scientific fields other than ornithology (e.g. forestry history, archaeology and genetics) were screened if the content could help explain aspects of the bunting's population development and biogeography. The figures are created from data in historical and current empirical material and background maps are in the public domain. When referring to geographical combinations of countries in Northern Europe, Scandinavia is defined as the peninsula of Norway and Sweden while Fennoscandia is Norway, Sweden and Finland.

## RESULTS

### Impact from negative anthropogenic effects

The patchy distribution of the Ortolan bunting on "geographical islands" in western Europe displayed on the range map (IUCN) has been interpreted as heavy fragmentation of a historically continuous population caused by negative anthropogenic effects and habitat loss (Dale 1997, 2001, 2009, Stolt 1997b, Dale et al. 2005, Bülow et al. 2009, Deutch & Sudbeck 2009, Magyar 2009, Haldén 2012, Moussy et al. 2018).

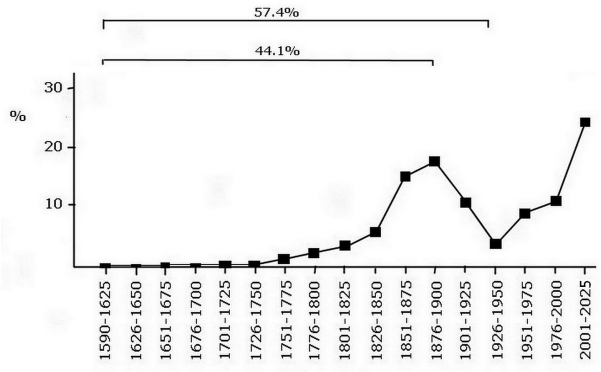


**Figure 1.** Temporal distribution of 948 publications reviewed from 1590 to 2025 in 25-year periods (except the first and last). 57.4% were published before 1950, 44.1% before 1900.

Hunting has been regarded as one of the major negative anthropogenic effects to impact the European population (Claessens 1992, Dale 1997, Stolt 1997a, Jiguet et al. 2019, CABS[3]). In the eastern flyway 80,000-200,000 birds were reportedly caught annually on glue sticks in Cyprus in antecedent times and exported to Europe (Tavernier 1676, Goeze 1795, Wilhelm & Leizelt 1795, Gloger 1834, Sundevall 1856, Holmgren 1866, Homeyer 1868, Rines & Beach 1904). From the western flyway, mainly in Landes County in southwest France, 50,000 (30,000-80,000) birds have been reported as an annual catch until the late 2010s (Claessens 1992, Jiguet et al. 2019, CABS). Population viability analyses of the lowest estimate revealed that the hunting was unsustainable. The population in Fennoscandia, passing through the hunting grounds in the fall, was viewed as directly threatened with extinction (Jiguet et al. 2019).

The Ortolan bunting's migration strategy is to fly singly or in very small flocks (Wolf 1724, Naumann 1824, Demidov 1840, Samat 1896, Haftorn 1971, Girardot et al. 2009, SBRC 2021) indicating that capture of the bird in such large numbers is highly improbable. All small, migratory birds caught in Cyprus were called ortolans (Wolf & Meyer 1805) and about 200 "ortolans" provided by the Cypriot bird catchers for identification were in fact Blackcaps *Sylvia atricapilla* (Linné, 1758) (Bucknill 1909). This is the main target for the hunt on the island (Jenkins et al. 2017, Shialis & Charalambides 2022, CABS). The reports about large catches in Landes County, France, appear to be confounded by the same error as the antecedent results from Cyprus. The estimated average of 50,000 birds (Claessens 1992) cited in contemporary scientific literature (Dale 1997, Stolt 1997a, Jiguet et al. 2019, CABS) was based on information from hunters (Claessens pers. info.), not compiled from ornithological surveys of hunting grounds or traps, and in Landes the hunters generally applied the name "ortolan" to any small bird put on the plate (Nöel Mayaud, co-editor of ALAUDA[4] and Robert-Daniel Etchécopar in independent, written statements to Kumerloeve 1953). At the meat and poultry markets in Marseilles, southeast France, any bird smaller than a skylark *Alauda arvensis* Linné, 1758 was traded under the moniker ortolan. Toussenel (1859) identified Greenfinches *Chloris chloris* (Linné,

[3] https://www.komitee.de/en/ Committee Against Bird Slaughter. Last accessed 6.9.26.

[4] https://www.seof.fr/service2 The journal of the French Ornithological Society. Last accessed 6.9.26.

1758), Chaffinches *Fringilla coelebs* Linné, 1758 and Common linnets *Carduelis cannabina* (Linné, 1758) among the birds on display. The traders remarked that this might be true in Paris (his home town), but in Marseilles they were all ortolans. In 1912 the Ortolan bunting was close to absent in southern France (Hess 1912), five years later exceptionally rare (Hermitte 1917). Paradoxically, the supply of ortolans to restaurants in Paris had not diminished (Hess 1912), indicating a common trade with a range of species under the ortolan umbrella name. The custom of giving the vernacular name "ortolan" to small migratory birds caught for the table was not restricted to Europe as the historical literature identified 35 species and subspecies on five continents labelled either ortolan or a moniker with ortolan included (Tab. 1, appendix 6). The transfer of the name to the United States by European immigrants and the confusion caused due to its use on several native American species was discussed at the World Congress on Ornithology in Chicago in 1893 (Praeger 1896).

**Table 1.** The historical literature identified 35 species and subspecies labelled ortolan or a moniker with ortolan included. Sources: Appendix 6.

| | |
|---|---|
| **EUROPE** | |
| Wryneck *Jynx torquilla* Linné, 1758 | Ortolan tire langue* |
| Water pipit *Anthus spinoletta* (Linné 1758) | Ortolan |
| Alpine accentor *Prunella collaris* (Scopoli, 1769) | Ortolan |
| Winchat *Saxicola rubetra* (Linné, 1758) | Ortolan |
| Northern wheatear *Oenanthe oenanthe* (Linné, 1758) | English ortolan |
| | Sussex ortolan |
| Blackcap *Sylvia atricapilla* (Linné, 1758) | Ortolan |
| Chaffinch *Fringilla coelebs* Linné, 1758 | Ortolan |
| Greenfinch *Chloris chloris*, (Linné, 1758) | Ortolan |
| Common linnet *Linnaria cannabina* (Linné, 1758) | Ortolan |
| Pine grosbeak *Pinicola enucleator* (Linné, 1758) | Ortolan |
| Lapland longspur *Calcarius lapponicus* (Linné, 1758) | Ortolan |
| Snow bunting *Plectrophenax nivalis* (Linné, 1758) | Ortolan |
| | Snow ortolan |
| | Mountain ortolan |
| | Migratory ortolan |
| Reed bunting *Emberiza schoeniclus* (Linné, 1758) | Reed ortolan |
| | Whooping cough ortolan |
| | Beach ortolan |
| | Coast ortolan |
| *E. s. passerina* Pallas, 1771 | Ortolan |
| *E. s. pyrrhuloides* Pallas, 1811 | Palud ortolan |
| Cretzschmar's bunting *E. caesia* Cretzschmar, 1827 | Ashy ortolan |
| | Grey ortolan |
| Yellowhammer *E. citrinella* Linné, 1758 | Ortolan |
| Pine bunting *E. leucocephalos* Gmelin, 1771 | Mountain ortolan |
| Cirl bunting *E. cirlus* Linné, 1766 | Ortolan |
| Black-headed bunting *E. melanocephala* Scopoli, 1769 | Ortolan king |
| Corn bunting *Emberiza calandra* Linné, 1758 | Ortolan |
| Rock bunting *E. cia* Linné, 1766 | Lorraine ortolan |
| | Migratory ortolan |
| | Dalmatia ortolan |
| | Trieste ortolan |
| Striolated bunting *E. striolata* (Lichtenstein, 1823) | Mountain ortolan |
| **U.S.A.** | |
| Sora *Porzana carolina* (Linné, 1758) | Ortolan |
| Common ground dove *Columbina passerina* (Linné, 1758) | Martinique ortolan |
| | Haiti ortolan |

| | |
|---|---|
| Bobolink *Dolychonix oryzivorus* (Linné, 1758) | American ortolan |
| | Carolina ortolan |
| Dark-eyed junco *Junco hyemalis* (Linné, 1758) | Jacobin ortolan |
| | Black snow ortolan |
| Saltmarsh sparrow *Ammospiza caudacuta* (Gmelin, 1788) | Louisiana ortolan |
| **CANADA** | |
| Horned lark *Eremophila alpestris* (Linné, 1758) | Ortolan |
| Dark-eyed junco *Junco hyemalis* (Linné, 1758) | Ortolan |
| American tree sparrow *Spizelloides arborea* (Wilson, 1810) | Ortolan |
| **SOUTH AMERICA** | |
| Stripe-tailed yellow finch *Sicalis citrina* (Pelzeln, 1870) | Brasil ortolan |
| **ASIA** | |
| Ashy-crowned sparrow-lark *Eremopterix griseus* (Scopoli, 1786) | Ortolan |
| Greater short-toed lark *Calandrella brachydactyla* (Leisler, 1814) | Ortolan |
| Richard's pipit *Anthus ricardi* Vieillot, 1818 | Ortolan |
| **AFRICA** | |
| Cape bunting *E. capensis* Linné, 1766 | Cape of Good Hope Ortolan |

*With protruding tongue

**Table 2.** A summary of 11 hunting results from the western flyway of 409,500 birds between 1611 and 1885 showed a total of only about 600 Ortolan buntings (0.15%). Surveys of 165,771 birds in the eastern flyway (hunting and ringing) between 1937 and 2012 showed a proportion of Ortolan bunting of 0.02% - 1.5% at an average of 0.45%, equating to 0.6 - 120 birds annually.

| Location | Temporal range | No. of years catching | Migrants / Year | Ortolan buntings / Year | % Ortolan buntings |
|---|---|---|---|---|---|
| WESTERN FLYWAY 409,500 BIRDS | | | | | |
| France, Germany and Italy | 1611-1885 | 51 | 8,029 | 12 | 0.15 |
| EASTERN FLYWAY 165,771 BIRDS | | | | | |
| Cyprus | 1968 | 1 | 25,235 | 39 | 0.15 |
| Egypt | 1937-1952 | 16 | 1,265 | 10 | 0.8 |
| Eilat, Israel | 1984-2000 | 13 | 8,235 | 120 | 1.5 |
| Egypt, Sinai Peninsula | 2008-2012 | 5 | 2,646 | 0.6 | 0.02 |

The true number of Ortolan buntings caught and killed during hunting seems to have been very small. Commercial hunting ended in Germany about 1755 due to lack of profitability (Naumann 1824) and by the end of the century no more than 50-60 birds were caught annually in the entire country (Goeze 1795). A summary of 11 hunting results from Germany, France and Italy in the western flyway counting 409,500 birds caught during 51 seasons between 1611 and 1885 showed an estimated 600 Ortolan buntings (0.15%) (Giglioli 1891, Vallon 1891, Hennicke 1895, Salvadori 1898-1899, MacPherson & Momber 1909) (Tab. 2). Wandsbeck (1893) regarded the Ortolan bunting as rare and from a twenty-year survey of hunting facilities in southern France, Algeria Tunisia, Sicily, Italy, Corsica and Switzerland (1870-1890) he mentioned the species as a decoy bird only once, at a large facility in Italy between Lakes Lugano and Maggiore in October of 1884. In the eastern flyway four surveys (hunting and ringing) of 165,771 birds running for 1-16 years from 1937 to 2012 showed a proportion of Ortolan bunting of only 0.02% - 1.5% at an average of 0.45%, equating to 0.6-120 birds annually (Watson 1971, Hubbard 1982, Yosef & Tryjanowski 2002, Yosef et al. 2002, Eason et al. 2015) (Tab. 2). One of the surveys was carried out in Cyprus (1968) where an annual catch of 80,000 – 200,000 was claimed in antecedent times, but the proportions of the bunting in this survey and in the summary of the hunting

results from 1611 to 1885 in the western flyway were identical, 0.15%.

In Scandinavia the deleterious effect from seed grain laced with methylmercury ($CH_3Hg^+$) has been perceived to be a major influencing factor in the decrease of the Ortolan bunting population. The view is based on Swedish surveys where museum specimens of a range of species were tested across a timeline from 1840 to 1965, in addition to fresh kills. The results showed a sharp increase in methylmercury levels in feathers following the introduction in 1938 (Borg et al. 1965, Berg et al. 1966). A link was suspected between this increase and the increased spillage of grain during sowing by the change from horse-drawn to tractor-pulled seed drills (Tejning 1967). However, no Ortolan buntings occurred in the samples (Borg et al. 1965, Berg et al. 1966) and a 10-year survey at Uppsala, Sweden during the period of methylmercury application (1960-1969) concluded that it was improbable that the decrease in the population was due to the pesticide. The negative trend had been continuous from the late 1800s (Stolt 1974). Only one survey links the species to methylmercury poisoning, at Närke, south-central Sweden in 1955 where it was suspected that the seed grain had been exposed by long term rain (Otterlind & Lennerstedt 1964).

Accordingly, there is no indication of a link between methylmercury introduction and population decrease in Norway. The most significant decrease nationwide took place from 1895 to 1940 (Sollien 2024) and methylmercury was introduced in 1952 and banned in 1966 (Bylterud 1972). Two surveys of 506 birds of 47+ species (found dead or killed) were undertaken between 1965 and 1971 and there were no Ortolan buntings in the samples (Holt 1972). The apparent lack of impact on Norwegian birds was attributed to the agricultural strategy. Only 14% of the grain growing region was subjected to methylmercury application. On the 14% only half of the seed grain was treated, and this half sown only biennially. In the intermittent years the treated fields were used for alternative crops (Bylterud 1972). If exposed to methylmercury-laced grain the Ortolan bunting could also possibly have avoided most of the pesticide. The liquid metal was applied by friction to the outside of the grain only, blending the two in a specially designed barrel mixer (TeKrony 1976). The bunting has a hulling technique of long grains by which it cracks the hull perpendicularly and then removes it with the tongue before consuming the endosperm (Ziswiler 1965). Consequently, the hull covered in methylmercury would have been discarded.

**Distribution is due to historical colonization**

Menz & Arlettaz (2012) suggested that the current distribution could be a possible broad scale metapopulation structure (Levins 1969, Hanski & Gilpin 1997). To test this hypothesis 205 local and regional population estimates across 176 years (1724-1900, appendix 7) where the bird was quantified as absent, rare, common or very common were plotted and superimposed on the current distribution map of central- and western Europe. A pattern emerged showing that the Ortolan bunting has been breeding on the same "geographical islands" for the last 300 years, which are currently perceived to be metapopulations from a recent fragmentation. The distribution has been geographically specific regardless of population level and the bird has also conspicuously not occupied areas between the "islands", where it continues to be absent today (Fig. 2).

The pattern is explained by the Ortolan bunting's colonization of Europe. According to vogelwarte.ch[5] the species began its dispersal across the continent in the 1600s. However, recent phylogeographic research on the genus *Emberiza* confirmed expansion from western Asia/the Mediterranean during Pliocene (5.4 MA-2.5 MA BP) or Pleistocene (2.5 MA–11.7 KA BP) (Fjeldså et al. 2020), an origin suggested by Marshall (1887). The Ortolan bunting is distinctly a valley colonizer (Ekman 1922) utilizing river valleys as directive- or leading lines (Kumari 1961, Schweppenburg 1963, Bylin 1975, Lomolino 2020). The area of origin and the colonizing along river valleys point to an initial route to central- and western Europe along the river Danube which has headwaters in the Black Forest of Germany, runs through 10 countries, has tributaries in 9 more and discharges into the Black Sea. The northern catchment area is intertwined with the major rivers of Poland and Germany, the Danube sharing a basin with the Elbe. Progression by the Ortolan

[5] https://www.vogelwarte.ch/en/birds-of-switzerland/ortolan-bunting/ Last accessed 6.3.26

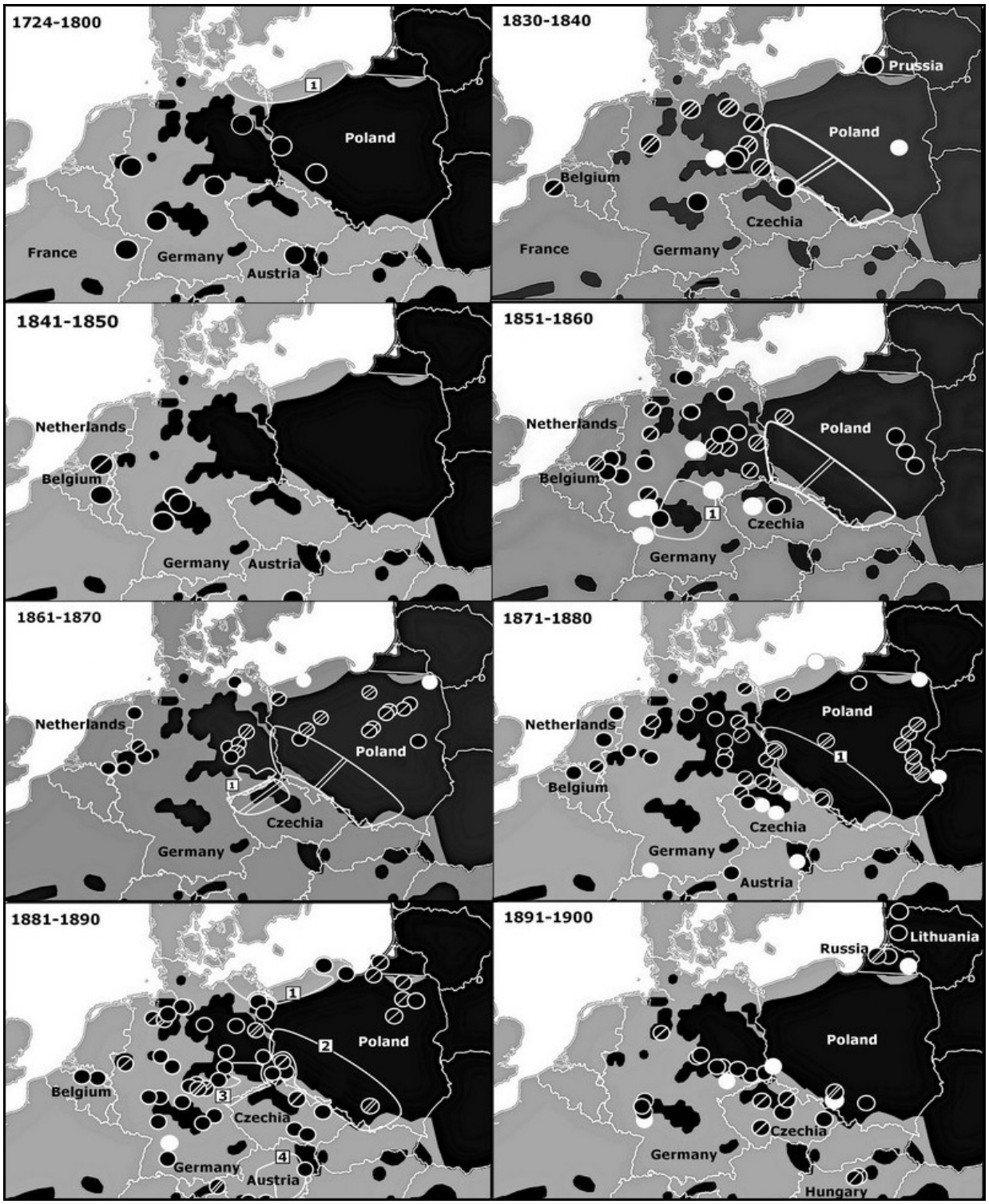


**Figure 2.** Plotted population estimates at 205 locations from 1724 to 1900 on the current range map (black) shows that the Ortolan bunting distribution has been restricted to the same areas for 300 years. White circle or area encircled with a numbered white line (1, 2, 3, 4 inside a square on the line): Absent. Black circle: Rare. Black circle or encircled area with 1 white crossbar: Common. With 2 white crossbars: Abundant. Sources: Appendix 7. Background map: https://sk.wikipedia.org/wiki/Redaktor:SanoAK. https://www.iucnredlist.org/species/22720916/166422798. CC BY-SA 3.0. Lines, numbers, letters and circles are added.

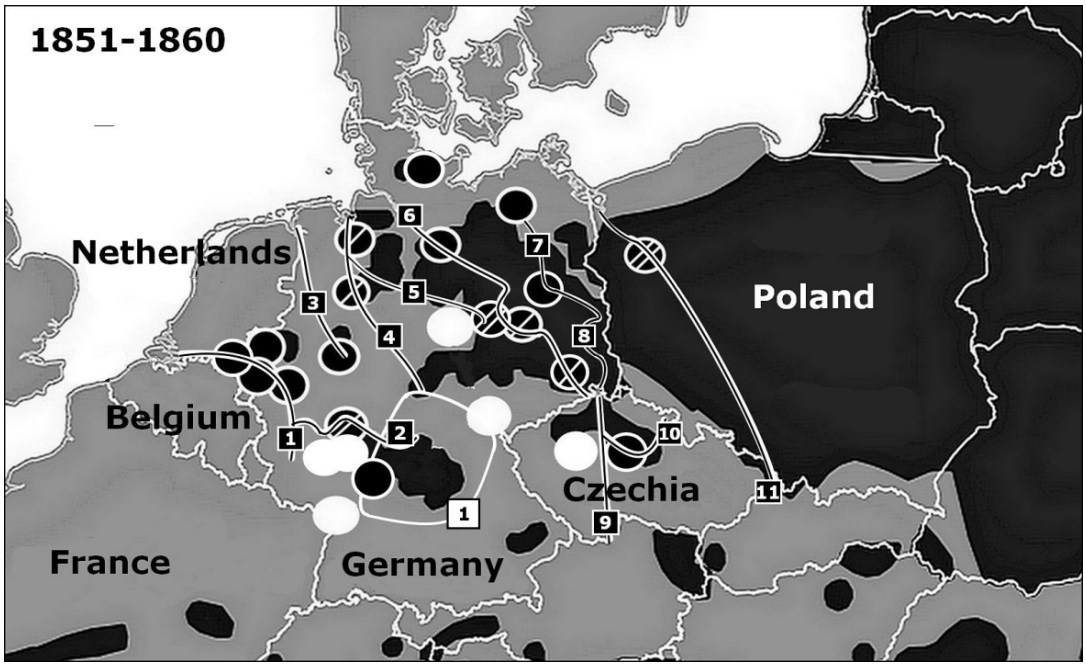


**Figure 3.** The pattern of colonization and distribution is indicated by superimposing a stylized map of the major rivers in central- and western Europe on the current range map with plotted historical breeding sites for Ortolan Bunting 1851-1860 as an example of how it developed. The rivers are: 1 the Rhine, 2 the Main, 3 the Ems, 4 the Weser, 5 the Aller, 6 the Elbe, 7 the Havel, 8 the Spree, 9 the Vltava, 10 the Elbe within the Czech Republic, 11 the Oder. Sources: Appendix 7. Background map: https://sk.wikipedia.org/wiki/Redaktor:SanoAK. https://www.iucnredlist.org/species/22720916/166422798. CC BY-SA 3.0. Lines, numbers, letters and circles are added. Legend for breeding status: Fig. 2.

bunting from the Danube across this catchment area is indicated by the direction of the colonization in Germany and Poland. In Germany the species advanced from southeast (Homeyer 1868), in Poland it came from southwest (Taczanowski 1888, Zedlitz 1921). In spite of an apparent contradiction, the statements were correct. All major river valleys in Germany run from southeast to northwest and from the south end of the Oder Valley, which at the time of Homeyer's statement was on German territory, the bunting could continue into Poland along the rivers Warta, Noteć and Brda to the largest and longest river, Vistula, the colonization then running from southwest to northeast. The pattern of colonizing along valleys emerges when a stylized map of the major rivers in Central- and Western Europe is superimposed on the current range map (IUCN) and plotted breeding locations 1851–1860 are used as an historical example showing how the three overlap (Fig. 3).

The Ortolan bunting had crossed Europe reaching the extreme western periphery of the range (France) at the latest during the mid-Pleistocene. This is verified by the oldest fossil discoveries, in Grotte du Lazaret by Nice, dated at 144 KA–108 KA BP (Tyrberg 1998, Valensi 2000). It sets the arrival in the Eemian, the penultimate interglacial 130 KA–115 KA BP and implies that the bird was hunted for food by archaic humans, *Homo neanderthalensis* King, 1864 inhabiting the cave at that time (Michel et al. 2011). This discovery, together with five more in southeast France but nowhere else in more than 1.300 digs across the country (inpn.mnhn.fr[6]), indicates colonization from northern Italy as suggested by Buffon (1778) and Deterville (1803).

**Spatiotemporal fluctuations in Europe**

The Ortolan bunting has exhibited unpredictable, temporally long fluctuations during the last 260 years (Appendix 8). No other *Emberiza* species displays such transience between occurrence and absence and at least in Europe it has repeatedly contracted and expanded the range, disappearing from large areas only to remigrate after years or even decades making

[6] https://inpn.mnhn.fr/ National Inventory of Natural Heritage, France. Last accessed 4.19.22.

the boundary oscillate across the entire continent (Stresemann & Portenko 1960). Three cases illustrate the pattern.

The Oder Valley encompasses the old province of Silesia which is now located in Poland (previously in Germany). While absent at the turn of the 17th century (Schwenckfeld 1603) the Ortolan bunting was established a century later (Wolf 1724). Between 1830 and 1840 it was very common (Fig. 2) and by the mid-19th century Silesia was claimed to have the highest abundance in central Europe (Pöppig 1851, Floericke 1892). Breeding sites on "geographical islands" were selected during colonization and seven distinctly separate sites were recorded with the highest abundance at the sites furthest north (Floericke 1892) (Fig. 4). Twenty years later the Ortolan bunting had disappeared (Fig. 2).

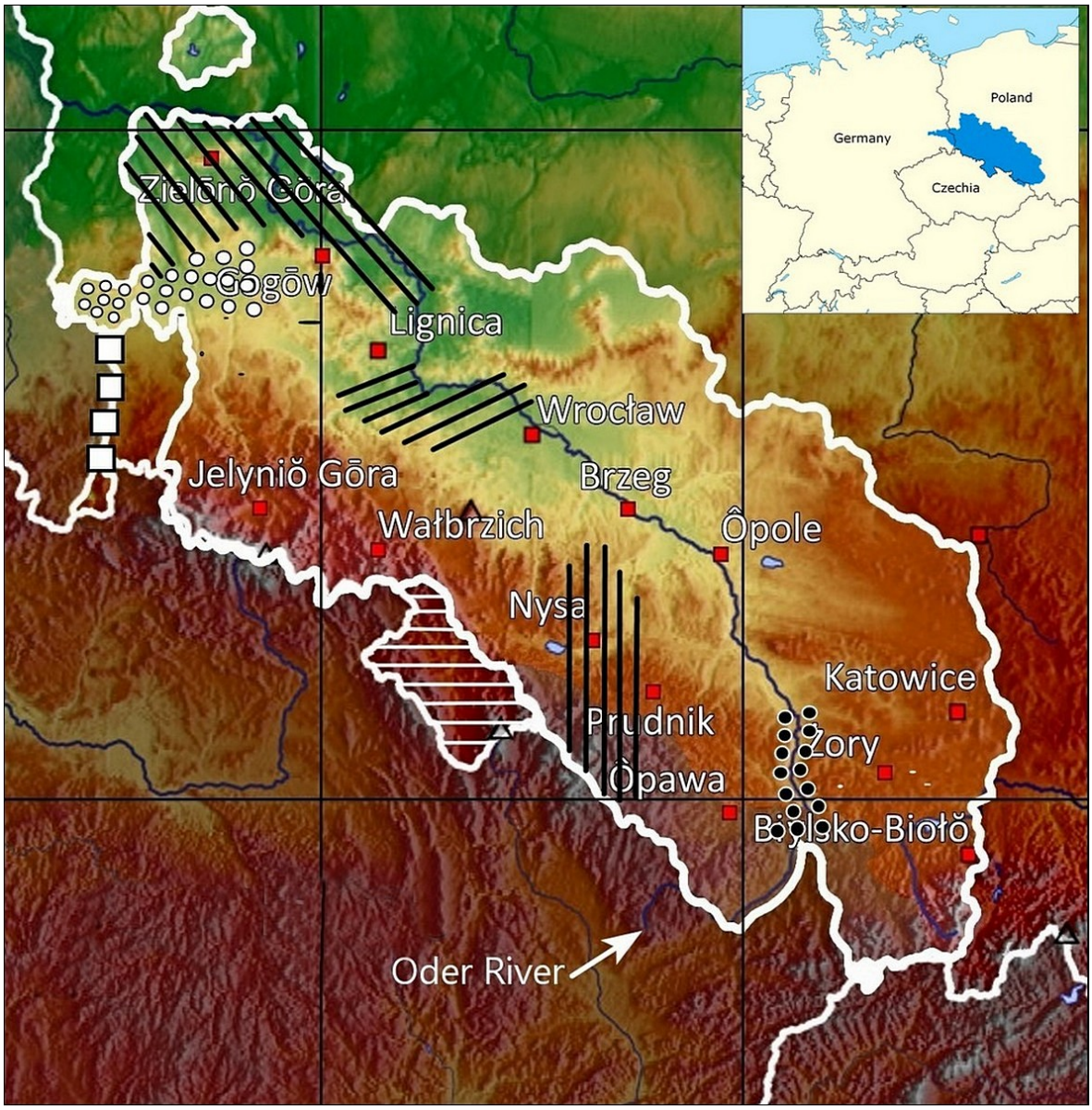


**Figure 4.** When the Ortolan bunting colonized Silesia along the Oder River toward the first half of the 19th century it occupied 7 distinctly different locations (bars, circles and squares) where it was claimed to have the highest abundance in Europe, with the most populous sites furthest north. By 1870 it had disappeared. Background map: https://commons.wikimedia.org/wiki/File:Silesia_topo_2.jpg. Inset: Silesia in Europe. https://en.wikipedia.org/wiki/Silesia#/media/File:%C5%9Al%C5%AFnsk_1335-1675.png. CC BY-SA 3.0. Letters, lines, circles and squares are added.

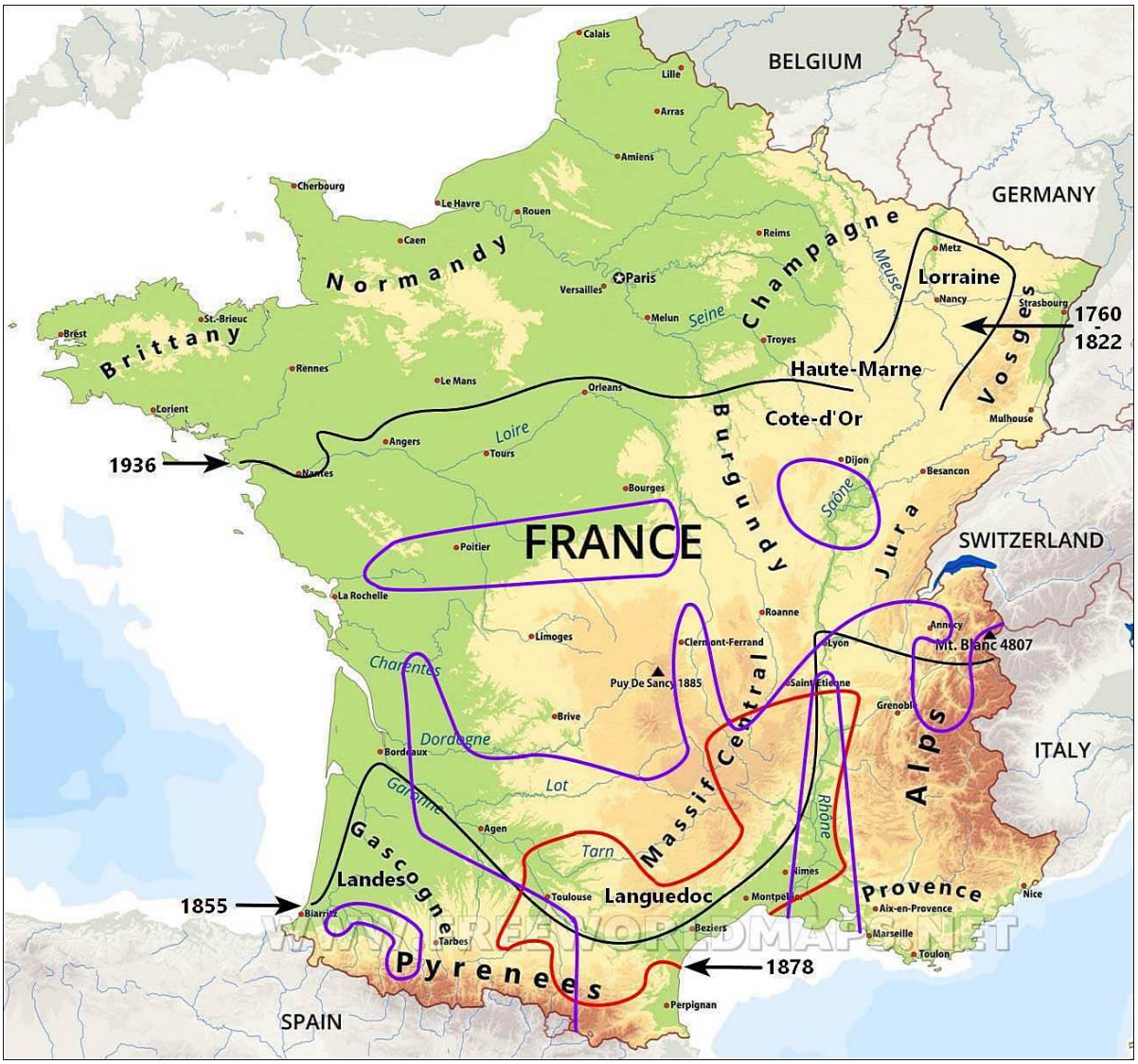


**Figure 5.** Fluctuations in France from 1760 to 2019. Lorraine was colonized about 1760 from where the Ortolan bunting retracted about 1822 and in 1855 was established south of a boundary running from the river Adour on the west coast to the river Durance in the east. By 1878 most of the population was confined within the province of Languedoc (red line line) and in 1912 the bird was close to absent. Following a new expansion, in 1936 the periphery was established along the vineyard boundary north of the Loire Valley east to Champagne/Haute-Marne/Côte-d'Or. Purple lines show the present distribution. Background map: https://freeworldmaps.net/europe/france/map.html CC BY-SA 2.5. Numbers, letters and lines are added.

In France, on the extreme western periphery, data indicate two expansions and contractions the last 260 years. About 1760 the Ortolan bunting advanced northward to establish in the former province of Lorraine, close to the German border, where it remained for more than 60 years (Buchoz 1771, AVL-O 1780, Buffon 1793, Bomare 1800, Colchen 1803, Deterville 1803, Gerardin 1805, Cuvier 1817, Bonnaterre et al. 1823) (Fig. 5). By the early 1820s it had retracted from Lorraine (Serres 1822) and by 1840 it was only observed as a rare migrant (Fournel 1840, 1856, Malherbe 1843). In 1855 the northern boundary ran between the rivers Adour in southwest and Durance in southeast skirting the Cévennes Mountains (the southeast edge of the Massif Central) passing the city of Lyon (Olphe-Galliard 1855, Toussenel 1855). By 1873 the population had contracted inside the old provinces Languedoc and Gascogne close to the Spanish border (LaCroix 1873). Later it was established almost exclusively within Languedoc (Brévans 1878, Pairault 1885) (Fig. 5) although a few patches were established

along the west- and northwest coast disconnected from the eastern segment (Lemmeteil 1868, Savatier & Foucard 1889, Granger 1893 Hamonville 1897, 1898). In 1912 the bunting was virtually absent from the south of France (Hess 1912), five years later exceptionally rare (Hermitte 1917). An expansion must have taken place as by 1936 the Ortolan bunting was re-established to the vineyard boundary running northwest of the Loire Valley, continuing east through Champagne, Haute-Marne and Côte-d'Or while being rare in the north and east (Mayaud 1953, 1960) (Fig. 5). From there it had a major range contraction and by 1990 was again almost confined to the southern half of the country (Claessens 1992, Cramp & Perrins 1994). The mechanics behind a retraction of the range periphery, observed as decrease in abundance and distribution, were explained in the third case by Grimm (2008) during a fluctuation in the federal state of Thuringia, central Germany. At both ends of the 18th century the Ortolan bunting was common in the state (Wolf 1724, Bechstein 1791-1795). A contraction appears to have happened as it was later reported as very rare (Naumann 1824), then as absent ("not immigrated yet") in east Thuringia (Liebe 1878). Immigration was expected due to a recent establishment at Halle on the Saale River, 70 km east of the Thuringian border and 55 years later the bunting reached the Kyffhäuser-Unstrut region from the east and continued into the inner Thuringia Basin (Fenk 1932) (Fig. 6). In the 1930s the southern boundary of the central European part of the range ran along the German "Mittelgebirge", the uplands between the German Plain and the Alps running east/west from the Czech border to the Belgian Ardennes (Niethammer 1937), in Thuringia the Schiefergebirge and the Thuringian Forest. From the 1940s a considerable growth took place along the boundary apparently moving through the valleys of the rivers Saale, Unstrut, Ilme and Weisse Elster.

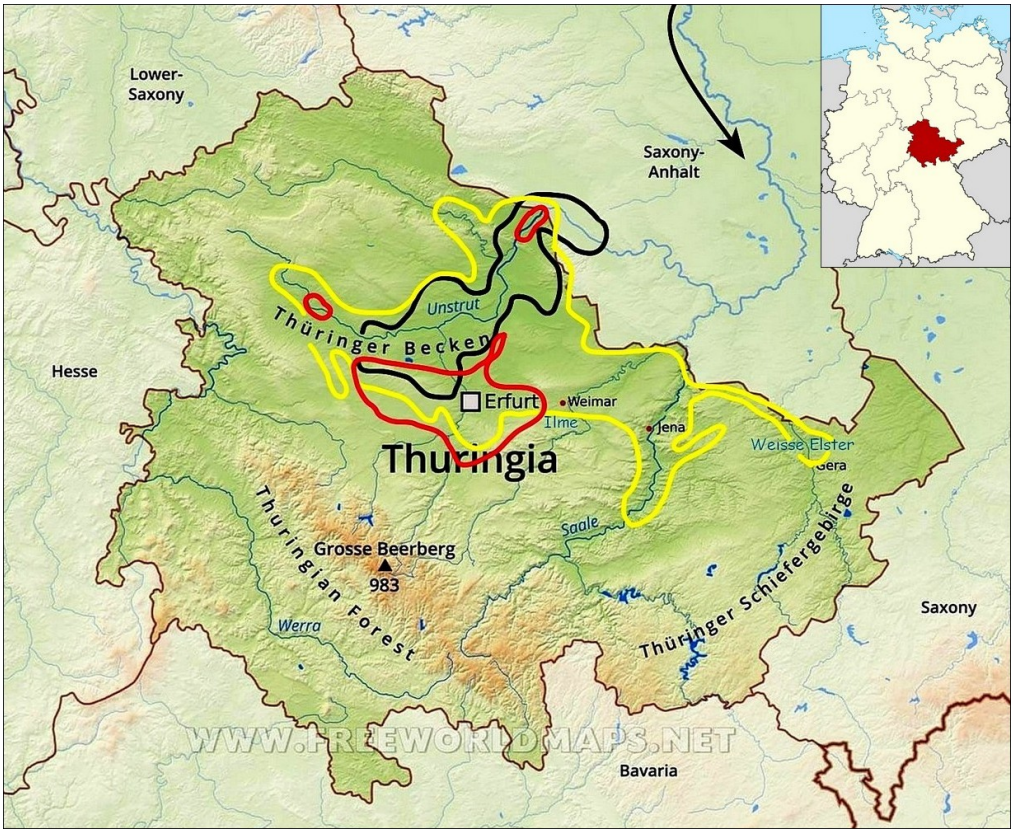


**Figure 6.** Fluctuation in Thuringia, Germany from the 1930s to the 1990s. From an establishment at Halle on the Saale River 70 km east of Thuringia before 1880 the population reached a maximum in the Thuringian Basin in the 1950s/1960s followed by complete abandonment in the 1990s. Black arrow: expansion along the river Saale from Halle. The black line is a stylized indication of the boundary in the 1930s/1940s, yellow line 1950s/1960s, red line 1970s/1980s (information from Grimm 2008). Background map: https://www.freeworldmaps.net/europe/germany/thuringia.html CC BY-SA 2.5. Black, yellow and red lines are added. Inset: Thuringia in Germany. https://upload.wikimedia.org/wikipedia/commons/d/d5/Locator_map_Thuringia_in_Germany.svg.

The population in Thuringia peaked in the 1950s/1960s and breeding was confirmed until 1987 when the bird initially disappeared from a few sites and in the 1990s vanished completely. According to Grimm (2008) the last areas to be settled were the first to be abandoned, indicating that a retraction of the range periphery may be explained as a sequential reversal of site occupation during colonization.

**Development in Fennoscandia**

Since large-scale changes leading to long-term negative trends are more likely to be detected at the periphery of a species' range than at the core (Torrenta et al. 2022), the temporal end-to-end development in Fennoscandia makes a compelling case that recent changes in the Ortolan bunting population is not due to negative anthropogenic effects but to spatiotemporal fluctuations and asymmetric growth. According to Moussy et al. (2018) the population in Fennoscandia has suffered from lack of contemporary gene flow (immigration) from the south due to fragmentation, extinctions and quasi-extinctions in several European countries including the closest neighbour, Denmark. However, except for one single nest at Tykskov Krat, Ejstrup Parish on the Jutland Heath July 8th, 1902 (Winge 1903), no breeding has been confirmed in Denmark the last 260 years (Brunnichii 1764, Kjærbølling 1852, Kjærbølling & Collin 1875-1877, Winge 1888, Jespersen 1946, dofbasen.dk[7]). As the Ortolan bunting was abundant in the south- and southwest of Sweden in the 19th century (Nilsson 1817-1821, 1824, 1858, Kjærbølling & Collin 1875-1877, Malm 1877, Carlson 1894) while simultaneously absent in Denmark, and it has also been a rare breeding bird in Pomerania along the northern coast of Poland and Germany for the last 300 years (Fig. 2) it is unlikely that the population in Fennoscandia colonized from the south across Öresund Sound or the Baltic Sea. Constriction of gene flow from the south is hence highly improbable as there have been no proximate populations subjected to decline.

The Ortolan bunting originated in western Asia/the Mediterranean (Fjeldså et al. 2020) and archaeological discoveries in Crimea from the lower Aurignacian culture period (late Pleistocene) 33 KA-26 KA BP (Tyrberg 1998) suggest a colonization of Fennoscandia from the east, for which Ekman (1922) provided a large, supporting empirical material. Most likely the Ortolan bunting advanced from the Black Sea along the river Dnieper and from the Caspian Sea along the river Volga reaching Fennoscandia via the extensive river system in the Baltic Region. Genetic research has confirmed that migration routes may trace ancestral routes of dispersal (Newton 2010) and the two rivers are mapped as established migration routes for birds from the Baltic Region to the Black- and Caspian Seas (Clarke 1912). Heavy fall migration of Ortolan bunting has been recorded along the Volga through Samara, Volgograd and Astrakahn about 950 km (Samara) to 80 km (Astrakahn) northeast of the Caspian Sea (Güldenstädt 1795, Pallas 1831, Dementiev & Gladkov 1970).

Although the bird colonized France at the latest in the Eemian interglacial about 130 KA-115 KA BP (Tyrberg 1998, Valensi 2000), colonization of Fennoscandia has been dated to the Holocene, less than 5.7 KA BP, a sub-fossil discovered in Sweden was 700-1.000 years old (Ericson & Tyrberg 2004). However, about 128 KA BP the White Sea Waterway which separated the Fennoscandian Peninsula from the Eurasian continent closed due to eustatic emergence creating a watershed at Lake Onega in Karelia (Funder et al. 2002, Grøsfjeld et al. 2006). This indicates that colonization across a land bridge could have happened in the Eemian Interglacial also in Fennoscandia. Kalela (1952) noted that expansion in Finland moved the boundary toward northwest, the direction of the main waterways, which points to an original entry from the southeast through Karelia. Separate post-glacial re-colonization routes are indicated by two easily distinguishable song dialects in the north and south of the country apparently belonging to two geographically disconnected segments of the population with little or no interaction (Piha & Seimola 2021). The southern part of the Ortolan bunting population would have advanced northeast along the ice edge from refugia in south- and southwest Europe during glacial retreat, entering through the Karelian Isthmus. The northern birds would have colonized via the original eastern route from refugia in the Balkans and Western Asia, entering east of Lake Ladoga.

Further advance toward the north end of the Gulf of Bothnia brought the Ortolan bunting into northern Sweden. After passing around the bottom of

[7] https://dofbasen.dk/danmarksfugle/art/18660 Danish Species Observation Service. Last accessed 1.13.26.

the gulf and continuing south along the coast it ascended the river valleys running northwest where it encountered the most impenetrable dispersal barrier in Scandinavia: The mountain range along the border of northern Norway rising to 2,000 m. From breeding sites on the extreme north-western periphery in Norway it can be determined that the Ortolan bunting succeeded in penetrating the barrier and colonize/re-colonize through low altitude passes of 400-700 m along four specific routes of connected valleys (Fig. 7): B, from Torneå to Bardu/Målselv (Garnes 1988[8], Størkersen et al. 2005), C, from Luleå to Steigen (Olsen 2012), D, from Skellefteå to Saltdal Valley (Hagemann 1883, 1886, Asphjell 1979, Baines et al. 2015) and E, from Umeå to Hattfjelldal/Hemnesberget (Collett 1921, Furuhatt 1961). No other breeding sites are known from this part of northern Norway and the distances from the northernmost region in central Norway with a prior continuous population of Ortolan bunting (Trondheim) are 250, 450, 520, and 650 km as the crow flies, too scattered to indicate colonization from the south. The routes from the source area on the Swedish coast between Torneå and Umeå through the valleys to the four Norwegian sites can be traced by plotting pre-1920 breeding sites (Linné 1732, Löwenhjelm1843, 1845, Wheelright 1864, Dresser 1871, Bau 1876, Kolthoff & Jägerskiöld 1898) (Fig. 7, 1-4). A similar colonization happened in the Trondheim Region where several low-altitude passes through the mountain range provided access from Sollefteå and allowed a continuous population to develop (Storm 1881) (Fig. 7, F). Furthest north in Norway the Ortolan bunting accessed Pasvik (Wessel 1904, Schaanning 1907, 1916a) from the outlet of the river Kemi, Finland (Fig. 7, A).

Throughout the 19th century the population in Fennoscandia experienced an expansion. Following a sparse occurrence in Finland and Sweden in the 18th century (Scheffer 1704, Linne 1732, Linne & Eckmark 1757) the population in Sweden increased from about 1815 (Nilsson 1817-1821, 1824, 1858, 1879). In 1832 the Ortolan bunting was established along a gradient running from Mounio on the Swedish border in northern Finland (Wright in Pleske 1886) 650 km southward along the Swedish coast where it was very common to Umeå (Wright 1832, Sundström 1887, 1888, Gylling 1898, Fisendahl 1907, Kolmodin 1907, all in Ekman 1922) (Fig. 8). In 1871 it was recorded along the Gulf of Bothnia northward from Turku, Finland, the abundance increasing with increasing latitude, being particularly high north of Oulu located in the colonization route from Karelia. The high abundance extended northeast to Rovaniemi and west around the north end of the gulf and, confirming previous information, continued southward into Sweden between Torneå and Umeå where it was exceptionally common (Dresser 1871) (Fig. 8). This is the source area for the four breeding sites in northern Norway (Fig. 7). Simultaneously, in Norway the population grew from sporadic in eastern Norway west to the Dovre Mountains in 1816 (Nilsson 1879) to the highest abundance ever recorded on the Scandinavian Peninsula by Nilsson (1858) at Gol and Ål in the Hallingdal Valley, south-central Norway in 1826. It was subsequently recorded as very common (Rasch 1838) and in 1856 one of the most frequently observed birds during a journey through Norway (Gould 1873). By 1895 the Ortolan bunting had expanded the range periphery all the way to the west coast. It was established along about 1.050 km from Ryfylke (59º23' N, 6º25' E) to Saltdal Valley (66º55' N, 15º33' E) (Schlegel 1854-1858, Storm 1881, Hagemann 1883, 1886, Collett 1894a, Bahr 1896, Chapman 1897) and so common it was regarded as one of four character species in the Førde Valley (Chapman 1897). In the north it had reached Pasvik (Wessel 1904) (Fig. 8).

**Negative trend is due to contraction**

The structural changes in the Ortolan Bunting population in Fennoscandia the last 125 years give a distinct impression of a contraction of the range periphery toward the entry point in Karelia, accounting for the negative trend on the peninsula. Cramp & Perrins (1994) noted a marked decrease in central- and western Europe with a contraction in northwest. Grimm (2008) described the retraction of the range periphery as a sequential reversal of the site occupation during colonization. Consequently, the contraction in northwest (Fennoscandia) following the last peak abundance in the 1890s would have been initiated as a decrease along the Norwegian west coast and the periphery moving eastward. Temporally parallel or subsequent contractions

[8] https://artsobservasjoner.no/Sighting/2893307. Norwegian Species Observation Service, Ortolan bunting. Last accessed 6.8.26.

would have happened in Sweden (northward) and Finland (southward) and the abundance would progressively increase with decreasing distance to the entry point in Karelia. The population in Finland would at any time have been larger than the Swedish population, which would have been larger than the Norwegian. This is the recorded development.

In 1895 the population in Norway stretched 450 km from the Swedish border across the entire southern part of the country to the west coast (Schlegel 1854, Storm 1881, Hagemann 1883, 1886, Collett 1894a, Bahr 1896, Chapman 1897) barring mountains above 1,000 m (Sollien 2024) (Fig. 8). Twenty years later the Ortolan bunting was absent from the west coast between Ryfylke and the Trondheim region (Schaanning 1916b), a region where the previously common bird (Storm 1881) now was reported as rare (Storm 1913). At Ål in the Hallingdal Valley the population was monitored from 1826 across 200 years (Nilsson 1858, Collett 1894b, Strand 1901, Odden (in Breiehagen 1994), T. Breiehagen pers. info. 2025). While decreasing from the highest abundance Nilsson (1858) had recorded on the Scandinavian Peninsula it was still assessed as common at the end of the 19th century (Strand 1901), but by 1938 the bird had completely disappeared (Odden in Breiehagen 1994). In 2009 the remaining population in Norway was concentrated in a small area close to the Swedish border (DN 2009) (Fig. 8), in 2025 reduced to two singing males (Bekken 2025).

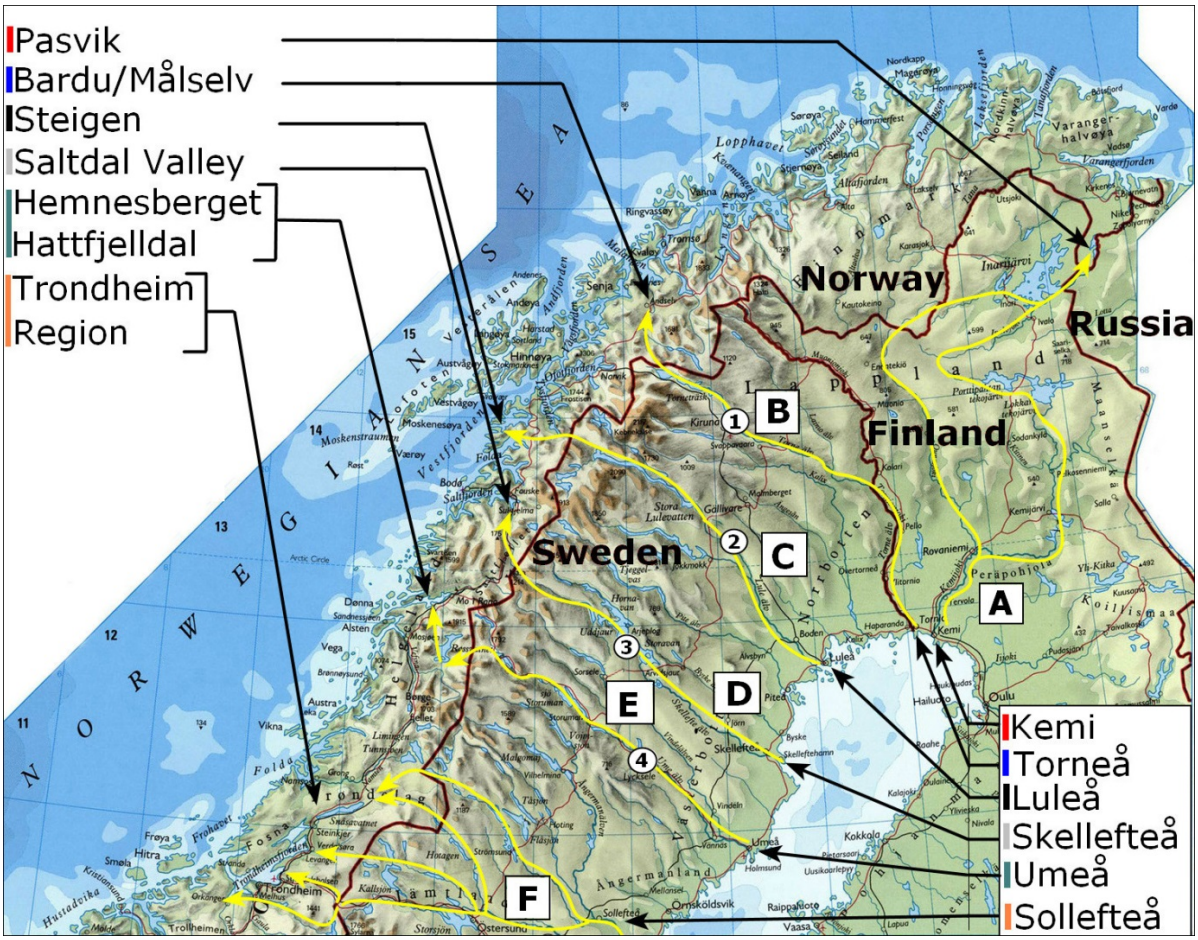


**Figure 7.** The Ortolan bunting's colonization of Norway through valleys from Sweden is illustrated by four routes starting between Torneå and Umeå (B, C, D, E) which can be traced via pre-1920 breeding sites (white circles, 1, 2, 3, 4) to the only known sites in Northern Norway (except Pasvik, furthest to the north). Start- and end locations have correlating color codes. The four sites are separated by considerable distances (80-225 km) and located 250-650 km north of the northernmost previous continuous population (the Trondheim Region), which indicates that colonization did not occur from the south. In the Trondheim region (F) the species had a multi-pronged advance from Sollefteå due to its access to a range of low altitude valleys. The northernmost site at Pasvik (A) was colonized from the outlet of the river Kemi in Finland. Background map: https://www.kartverket.no/en. Lines, circles, squares, names and numbers are added.


**Figure 8.** The last major expansion in Fennoscandia showed simultaneous growth in the three countries from about 1815 to about 1895 with exceptionally high abundance around the north end of the Gulf of Bothnia and in south Central Norway, with the bird established along 1.050 km of the Norwegian west coast from Ryfylke to Saltdal Valley by 1895 (black line). Through the interior of the peninsula it had advanced north to Pasvik. By 1960 the population in Norway had retracted southeast of the white line and was in 2009 concentrated in a small area close to the Swedish border where only two territorial males were recorded in 2025. White arrows indicate colonization routes through Karelia. Background map: https://sk.wikipedia.org/wiki/Redaktor:SanoAK. https://www.iucnredlist.org/species/22720916/166422798. CC BY-SA 3.0. Lines, numbers and letters are added.

Temporally parallel events took place at the peripheries in Sweden and northern Finland. From a high abundance north of the Gulf of Bothnia in the late 19th century (Fig. 8), at the beginning of the 20th Century the Ortolan bunting was regarded as rare. A small number of individuals and nests were recorded (Davies 1905, Munsterhjelm 1910, 1911, Schultz 1911, Finnilä 1913, 1914) and Montell (1916) had no observations in 13 years (1903-1916). From high abundance in the counties in south- and southwest Sweden in the 19th century (Nilsson 1817-1821, 1824, 1858, Kjærbølling & Collin 1875-1877, Malm 1877, Carlsson 1894) the population underwent a major decrease after the turn of the 20th century (Engström 1952). By the turn of the 1960s the bunting had virtually disappeared from almost all of southern Sweden (Runesson & Jönsson 1987, Tyrberg[9]) (Fig. 9). A noticeable decrease had also been recorded in central Sweden (Otterlind & Lennerstedt 1964, Stolt 1974) and in the mid-1970s the population estimate was 40,000 pairs (Ulfstrand

[9]https://takern.se/Bilagor/TTs%20p%C3%A4rm/TTs%20p%C3%A4rm%20OCR/del_5.pdf. Tåkern Field Station's list of birds. TT:s (Tommy Tyrberg's) binder, part 5. Last accessed 1.19.26.

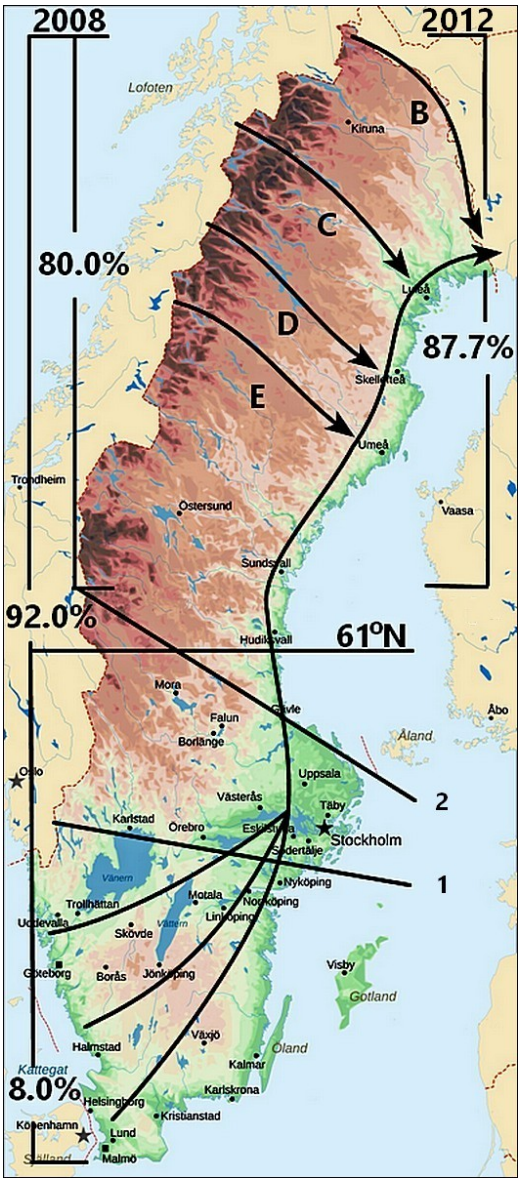


**Figure 9.** The contraction in Sweden following the last expansion in Fennoscandia, initially noticed as a major decrease in the southern part of the country (south of line 1) from the turn of the 20th century, continuing through the central part (between lines 1 and 2) up to the 1970s. From Northern Norway the bird would have retreated along colonization routes B, C, D and E in Fig. 7 toward the source area from Torneå to Umeå, and also from the Trondheim Region and Pasvik. By 2008, 92% of the population was established north of the 61st parallel with only 8% south of the line and 80% in the three northernmost counties. In 2012 the part of the population in the three northern counties had increased to 87.7%. Background map: http://www.aquarius.ifm-geomar.de/. Lines and numbers are added.

& Högstedt 1976). By the late 2000s the population was about 6,300 pairs established mainly along the coast, 92% in northern Sweden, approximately 80% in the three northernmost counties and only 8% south of the 61st parallel (Ottvall et al. 2008). When the population further decreased to about 3,700 pairs in 2012 the proportion in the three northern counties consequently increased to 87.7% (Haldén et al. 2017), the century-long chain of events indicating a northward contraction.

A smaller expansion in Finland before the final contraction probably started in the 1930s/ 1940s (Kalela 1952, Vepsäläinen et al. 2009) and did not appear to extend to Sweden and Norway. The population grew from an estimated 100,000 pairs (1941-1956, Merikallio 1958) into a range of 100,000-200,000 pairs in the late 1980s (Cramp & Perrins 1994, Vepsäläinen et al. 2009). The development has been monitored across the last 50 years (1974-2025, Lintuatlas[10]) showing a decrease of 90% in approximately 35 years (Tucker & Heath 1994, Burfield & Bommel 2004, Vepsäläinen et al. 2009, Jiguet et al. 2016a). The abundance has progressively decreased from north to south (Fig. 10), which has left the remainder of the population established mainly along the coast from Oulu to Karelia, in 2020 estimated at 1,700 pairs (Piha & Seimola 2021). The highest abundance was eventually recorded closest to the initial entry point in Karelia, in two regions of singing groups furthest southwest and south (Piirainen et al. 2024).

## Interminable contraction is due to asymmetric growth

Bird populations can progressively disappear from a region from reasons other than habitat fragmentation, but the development still mirrors the one expected in a decline where fragmentation is known to be the driver (Newton 1998). There are clear indications that the driver behind the long-term decrease leading to the disappearance of the species in Fennoscandia, which also applies to central- and western Europe, is asymmetric growth. The development of the Ortolan bunting population appears to follow the concept of the abundant center (Brown 1984), displaying chains of events expected from a source-sink dynamics.

[10] https://digitalis.fi/lintuatlas/lajit/?type=C&taxon=MX.35154 Results of bird atlas surveys, Finnish Museum of Natural History, Helsinki. Last accessed 1.19.26

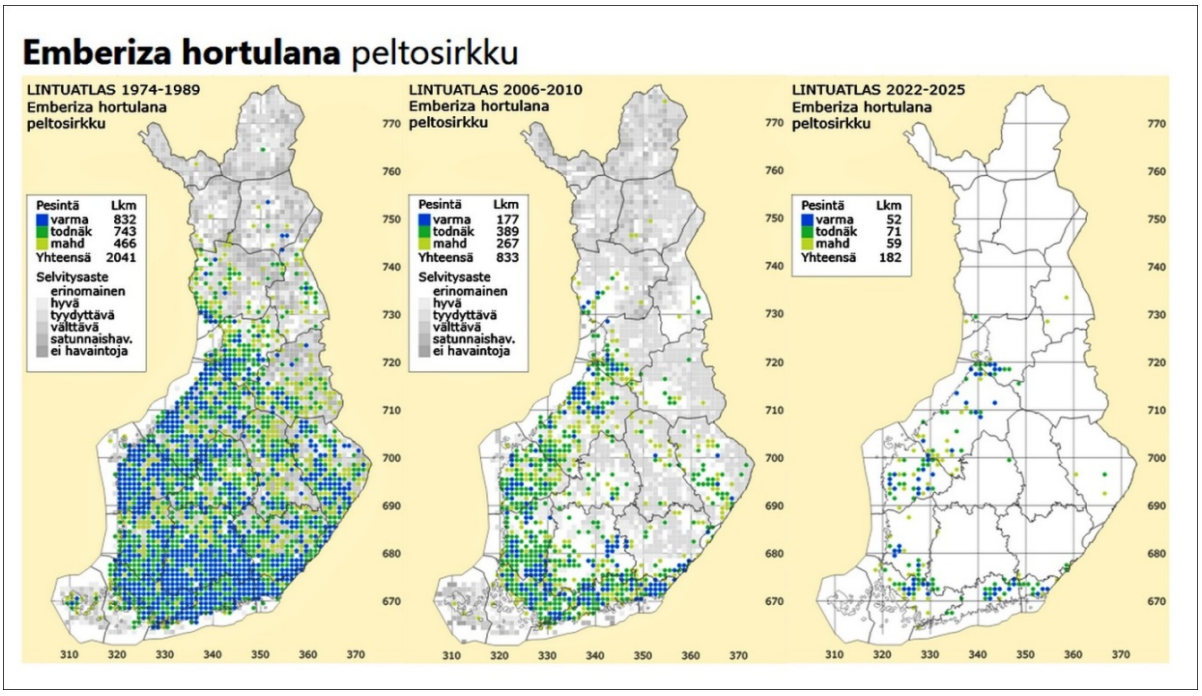


**Figure 10.** Progressive decrease in abundance from north to south in the Finnish population of Ortolan bunting between 1974 and 2025. Eventually two major regions of singing groups in the south of the country had the highest abundance, one of which is located closest to the colonization entry point in west Karelia. Blue squares: Confirmed occurrence. Dark green squares: Probable occurrence. Light green squares: Possible occurrence. Maps: Results of bird atlas surveys, Finnish Museum of Natural History, Helsinki. https://digitalis.fi/lintuatlas/lajit/?type=C&taxon=MX.35154. Left and middle map CC BY-SA 3.0, map to the right CC BY-SA 4.0.

This concept can be applied on various spatial scales from territories at the same location to different habitats in a region to separate parts of a geographical range (Pulliam 1988). From an origin in western Asia/the Mediterranean the abundant center moved NNE and it is now located in Russia, a country with the largest population in the range estimated at 2.0-4.3 million pairs (Jiguet et al. 2016a). This center is a source for Europe and exhibits an exceptionally high emigration rate from the east toward central- and western Europe of 30.13% (migrants derived from another population per generation) with 35.67% of the birds in the west traceable to an eastern origin (Moussy et al. 2018). This implies that Europe may function as a sink or a pseudo-sink (Newton 1998) fully or partially dependent on emigration from the east.

In spite of the high emigration rate which potentially could make the European population grow, it has continued to decrease. Cramp & Perrins (1994) noted an increase with expansion in the east of the range and by superimposing 14 estimates of the boundary in the south, east and north between 1795 and 1999 on the current range map (IUCN), the common denominator is that the eastern boundary has moved about 1,600 km further east the last 230 years (Fig. 11, A-I). That is equal to the distance from the Dutch coast to Western Ukraine and points to a movement of the population center eastward, consequently retracting the western periphery from western/central Europe. Dissimilar estimates of the boundary in north and south may be due to the species' exceptional expansions and contractions making it difficult to draw a well-defined line or that the entire perimeter is broken up in "geographical islands" similar to the distribution in western Europe.

The probable underlying cause for the asymmetric growth was explained by Johansen (1944). At the end of the 18$^{th}$ and beginning of the 19$^{th}$ centuries the eastern boundary ran along the river Ob (Goeze 1795, Pallas 1831, Gloger 1834) (Fig. 11, A). The taiga was then deforested from logging 500 km eastward from the river Ob to the river Yenisei, exactly to where the Ortolan bunting had expanded by 1913 (Suschkin 1914) (Fig 11, F). The bird had progressively advanced off of the Kazakh Steppe onto the forest clear-cuts as they emerged. A similar development has recently been recorded in Sweden.

The major part of the Ortolan bunting population has moved onto forest clear-cuts in the northern part of the country (Stolt 1994, Ottvall 2008), a habitat the bird could not have utilized before 1948 because it did not exist. Clear-cutting was a forestry management policy decision implemented that year, made possible by the introduction of the chainsaw (Holmberg 2005). As in Siberia it gave the Ortolan bunting an opportunity to colonize the clear-cuts which it did in the course of 40 years or less. The pronounced decrease recorded from the mid-20th century in countries on the western periphery of the population, where the effects of asymmetric growth would be noticed first and most, may have been due to further deforestation in Siberia. From the 1950s logging of the taiga continued on to Irkutsk (Sheingauz 2004). The forest fires in this region would also have facilitated the opening of these areas, approximately 1,000 a year along a line from Khatanga in the north through Bratsk and Katchoug to Irkutsk in the south (Belykh 2020, Drozdova & Sorokovikova 2021). From the previous boundary on the river Yenisei (Suschkin 1914, Johansen 1944) the Ortolan bunting has now advanced up to this line, which currently delineates the eastern boundary of the range (IUCN) (Fig. 11, I).


**Figure 11.** The common denominator in 14 estimates of the boundary across the last 230 years is an eastward expansion of 1.600 km (A-I). This equals the distance from the Dutch coast to Western Ukraine (white arrow) which probably accounts for the decrease in the population in Europe the last 125 years from asymmetric growth. A: Goeze 1795, Pallas 1831, Gloger 1834. B: Harvie-Brown 1877. C: Radde & Walter 1889, Sully (in Sharpe 1891), Dresser 1902. D: Giglioli 1907. E: Dunker 1912. F: Suschkin 1914, Johansen 1944. G: Vaurie 1959. H: Mullarney et al. 1999. I: IUCN 2019. Background map: https://sk.wikipedia.org/wiki/Redaktor:SanoAK.https://www.iucnredlist.org/species/22720916/ 166422798. CC BY-SA 3.0. Lines, circles and letters are added.

## DISCUSSION

It seems clear that the development and dynamics of the Ortolan bunting population in Europe has been misunderstood due to a range of assumptions deriving from short term bias (Bernady 2009), reliance on erroneous data in models (Jiguet et al. 2019) and research restricted to regions (within each country) rather than across its entire geographic range (Tucker & Heath 1994, Burfield & Bommel 2004, Jiguet et al. 2016a). The underlying causes which have led to the current distribution have been perceived as fragmentation of a previously continuous population from habitat loss, negative anthropogenic effects and hunting, hence the development has been interpreted in the paradigm of metapopulation theory (Dale 2001, 2009, Dale et al.

2005, Bülow et al. 2009, Deutch & Sudbeck 2009, Magyar 2009, Menz et al. 2009, Haldén 2012, Menz & Arlettaz 2012, Moussy et al. 2018). However, metapopulation theory is unlikely to be helpful if immigration rate is high and it applies only to birds with species specific habitat requirements (Hanski & Gilpin 1997), both of which exclude the Ortolan bunting.

With the exceptionally high emigration rate of 30.13% at range level from the east toward western Europe (Moussy et al. 2018), demographic changes in the abundant center resulting in a variable emigration rate would in Europe be recorded as a variable immigration rate which could have been a driver for long-term fluctuations. Population surveys have shown that the rate of immigration can explain trend and abundance and immigration preventing populations from going extinct and also support recovery (Ward 2005, Lieury et al. 2016, Tenan et al. 2017, Millon et al. 2019, Horswill et al. 2022). Development of the Ortolan bunting population appears to be significantly impacted by the immigration rate (Steifetten & Dale 2006, Dale 2009, 2016). Dale (2009) and Dale & Steifetten (2011) surveyed a population in Norway across 7 years. Despite reproduction parameters indicating a slow growth of 0.2-1.0%, a decrease of 29.0% was recorded. The parameter which explained the size and trend across the survey best, was the immigration rate measured by the dispersal of adult males. Due to this male dispersal the periphery of the range is likely to be very volatile. If males are unsuccessful in attracting females, they can embark on exceptionally long dispersals from the second and subsequent territories, even switching territories within the same season. In eastern Norway, on the current extreme periphery in northwest, dispersal of 45 km has been recorded with 22 km in a single day (Dale et al. 2005, Dale 2009). Since unpaired males may make up 38%-63% of singing individuals (Cramp & Perrins 1994, Dale 2011, Dale et al. 2005, Steifetten & Dale 2006, Piirainen et al. 2024) the dispersal of unsuccessful males established along the boundary could quickly expand and contract the range.

The Ortolan bunting is extraordinarily habitat flexible (Appendix 9) and in spite of extensive studies few have linked growth in the population to habitat quality (Skokanova 2016, Piha & Seimola 2024, Piirainen et al. 2024). According to Dale & Christiansen (2010) 83% of the males change habitat after natal dispersal. The habitat at the birthplace did not appear to have impact on the new choice and 62-71% of the birds changed habitat during several dispersals the following years, 86% at least once in their lifetime. Habitat flexibility is enabled by a wide range of ethological and physiological traits. The bird is an opportunist, exemplified by its ability to quickly merge onto newly opened habitats like fire burns (Dale 1997, Brotons et al. 2008) and forest clear-cuts (Johansen 1944, Stolt 1994, Ottvall 2008). Opportunism is expressed in a bird's behavior: It is largely non-confrontational on the breeding grounds and when confined in cages with other birds (Bettoni & Dressler 1865, Lemetteil 1868, Piera 1873, Collett 1921, Durango 1948, Cramp & Perrins 1994), it lacks shyness (Gould 1856, Bettoni & Dressler 1865, Kjærbølling & Collin 1875-1877, Posser 1880, Samat 1896, Collett 1921) and consequently lacks neophobia, which leads to a high rate of innovation (Kayello 2013). It is also a generalist which is indicated by the highly varied omnivore diet (Cramp & Perrins 1994). Dietary generalism, combined with the elevated rate of innovation characterizing an opportunist, provide the ability to quickly change to alternative food sources and specialize should they suddenly become available in abundance (Kayello 2013). Such specialization is reported from Switzerland where Busch crickets Tettigoniidae spp. Krauss, 1902 can make up about 70% of the juveniles' food (Keusch & Mosimann 1984 in Menz & Arlettaz 2012) and at one nest were fed almost exclusively to the nestlings (Kunz 1950). In Sweden oats were offered from a feeder during the breeding season and used by one pair at almost 25% of the visits when feeding the juveniles (Sondell et al. 2019). The Ortolan bunting has physiological versatility to adapt to a wide range of environmental conditions. According to Durango (1948) it is a sun-loving bird, but it has a temperature tolerance range of minus 15° C to 35° C and if necessary can function normally over an extended period of time at minus 5° C (Wallgren 1954). A male was singing in a snow storm in the Könkämä Valley, Northern Finland at 68°25' N on April 27th, 1904 (Davies 1905) (Fig. 8) and an individual visited a bird feeder in Porsanger, Norway at 70°15' N on November 5th, 2023 (Pedersen 2023 ) (Fig. 12). The previous night low was minus 5.6°C (Yr.no). Although the species is said to avoid coastal areas (Madge & Sharpe 2020) as it prefers breeding locations with less than 600 mm annual precipitation (Durango 1948), in the late 1800s it was established along the west coast of Norway to Saltdal Valley (Schlegel 1854, Storm

1881, 1913, Hagemann 1883, 1886, Collett 1894a, Bahr 1896, Chapman 1897). At two of the breeding sites, Førde and Etne (Fig. 8), the annual precipitation is 2.780 mm and 2.755 mm (Yr.no). Simultaneous with the establishment on the Norwegian west coast it was breeding in the river Guadalquivir marshes Las Marismas on the southwest coast of Spain (Chapman & Buck 1893). The seasonal precipitation (April-June) rather than the annual may be the key to establishment on the coast. At Førde the precipitation during the three months is 164, 142 and 142 mm, at Etne it is 157, 136 and 158 mm (Yr.no).

Due to its physiological versatility (Wallgren 1954), exceptional habitat flexibility (Appendix 9, Dale & Christiansen 2010), opportunism and generalism (this study) the Ortolan bunting has been able to expand across and occupy more than 20 million km$^2$ in the Palearctic region (IUCN) for no less than 120,000 years (inpn.mnhn.fr). Expansion and contraction of the range has happened multiple times, both on a small scale across limited areas during decades or a century (Stresemann & Portenko 1960) and on large scale across the continent during interglacial- and glacial periods (Tyrberg 1998, Valensi 2000, Erickson & Tyrberg 2004). Asymmetric growth must have happened at least once before, since the origin was in western Asia/the Mediterranean (Fjeldså et al. 2020) while the population center now is located 2,500 km further NNE, in Russia (Jiguet et al. 2016a, Moussy et al. 2018). This study reveals that the population again is undergoing asymmetric growth, this time toward the east. This explains the disappearance in Europe better than changes in anthropogenic biomes across a century, which is likely to be inconsequential for a bird with the Ortolan bunting's traits and history.


**Figure 12.** Ortolan bunting at Igeldas, Porsanger, Norway at 70°15' N on November 5th, 2023 eating sunflower seeds from a feeder. Note the snow on the ground. The previous night low was minus 5.6° C and the temperature at 12:00, ½ hour after the picture was taken, minus 2.8° C. (Knut Pedersen).

## CONCLUSIONS

The literature review revealed that the population dynamics and biogeography of the Ortolan bunting is better understood in light of historical empirical material on a large spatiotemporal scale than viewed in the paradigm of metapopulations. Current research has been based mainly on data gathered after 1980 which has omitted a history of extended temporal fluctuations necessary to be cognizant of to understand the present status and make future predictions. Ethological and physiological traits allow the bird to oscillate the boundary within its maximum potential range independent of large blocks of species-specific habitat making habitat loss an improbable driver for population decrease. Information from the literature indicates that neither anthropogenic effects nor hunting have had significant impact on the development. Empirical data strongly suggest that the negative trend in Europe has been caused by asymmetric growth due to expansion in the eastern part of the range, predicting that recovery to previous population levels and distribution in the west is unlikely. Similar reviews of other species' history could help explain how their respective populations developed to the current state. This would make it simpler to discern which ones are in real need of attention from conservation ecologists, and which are not.


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## APPENDICES

**Appendix 1**. Claessens 1992, Dale 1997, Stolt 1997a, Noorden 1999, Nævra 2002, Dale & Steifetten 2005, Magyar 2009, Menz et al. 2009, Haldén et al. 2017, Moussy et al. 2018, Jiguet et al. 2019, Piirainen et al. 2024.

**Appendix 2**. Bras y gerddi, Bruant Ortolan, Cerla e kopshtit, Därza stërste, Dultittlingur, Emberiza hortulana, Emberiza hortelano, Escribano hortelano, Fettammer, Garden bunting, Gartenammer, Green-headed Bunting, Hortolà comú, Hortulan, Hortulana, Hortelano, Hortulansparv, Hortulanus, Hortulon, Kertí sármány, Kiraz kusu, Kornfinke, Ortolan, Ortolaan, Ortolan Bunting, Ortolano, Ortolan sparf, Ortolansparv, Ortolanstreepkoppie, Peltosirkku, Sodinė starta, Sombria-brava, Strnad zahradní, Strnádka zahradna, Triguero hortelano, Verdaula, Vinogradska strnadica, Vrtna strnadica, Vrtni strnad.

**Appendix 3**. E.g. A. Hugo's Jagt-Zeitung, Actes de la Société de Linnéenne de Bordeaux, Allgemeine Deutsche Ornithologische Gesellscaft zu Berlin, Aquila, Bulletin de Musée Royal d'Historie Naturelle de Belgique, Der Zoologische Garten, Die Gefiederte Welt, Die Schwalbe, IBIS, Jahresbericht Tijdschrift der Nederlandsche Dierkundige Vereeniging, Journal für Ornithologie (published from 1853, from 2006 Journal of Ornithology), Naumannia, Ornis, Ornithologische Monatsschrift des Deutschen Vereins zum Schutze der Vogelwelt, Revue des Sciences Naturelles de l'Ouest, Revue Française d'Ornithologie, Ziva.

**Appendix 4**. Green-headed Bunting, Hortelano, Hortulanus, Hortulansparv, Hortulon, Kornfinke, Ortolan sparf, Triguero hortelano, Verdaula.

**Appendix 5**. Action plan, biogeography, decline, dispersal, distribution, ecology, habitat, migration, population dynamics, report, scholarly article.

**Appendix 6**. Tertre 1667, Labat 1724, Brisson 1763, Chanvalon 1763, Borbone 1771, Buffon 1778, 1853-1857, Latham 1783, Bechstein 1791-1795, Deterville 1803, Gérardin 1805, Meyer 1815, Forster 1817, Buliard 1822, Bonnaterre 1823, Selby 1825, 1833, Wagler 1827, Millet 1828, Lesson 1831, Hugo 1835, Eyton 1836, Ray 1843, Bishop 1852, Sundevall 1856, Loche 1858, Tschudi 1858, Toussenel 1859, LeMoine 1860, 1861, Albrecht 1861, Coues & Prentiss 1861, Prevost & Lemaire 1865, Brehm 1871, Dresser 1871, Yarrell 1871, Goodrich 1872, Gould 1873, Rolland 1877, 1879, Blanchére 1878, Brevans 1878, Smith 1879, Giglioli 1886, 1890, Olphe-Galliard 1890, Newton & Gadow 1896, Blanchan 1898, Hett 1902, Bucknill 1909, Dahl 1912, Schaanning 1913, Ramsay 1923, Wetmore 1930.

**Appendix 7**. **1724-1800**: Wolf 1724, Fritsch 1734/Kramer 1756/Merrem 1789 (in Kumerloeve 1953), Bechstein 1791-1795, Buffon 1793, 1799, Goeze 1795, Latham 1801, Yarrell 1839. **1830-1840**: Degland 1831, Gloger 1833, 1834, Buhle 1835, Reider & Hahn 1835, Naumann 1851, Bishop 1852, Fritsch 1870, Taczanowski 1877, Marshall 1895. **1841-1850**: Longchamps 1842, Seidensacher 1858,

Wolley & Newton 1864-1902, Müller & Müller 1882, Michel 1890. **1851-1860**: Baldamus 1851, 1853, Fuhlrott 1851, Naumann 1851, Pöppig 1851, Tobias 1851, Bolsmann 1852 (in Kumerloeve 1953), Borsmann 1852, Kjærbølling 1852, Ruhl 1852, Herklots 1853, Negelein 1853, Pralle 1853, Schlegel 1854-1858, 1860, Schpeersneider 1854, Hintz 1857, 1863, Pässler 1857, Boie 1858, Wolley & Newton 1864-1902, Fritsch 1870, Taczanowski 1888, Jäckel 1891, Marshall 1895. **1861-1870**: Homeyer 1863, 1865a, b, 1867, 1870, 1871, Hintz 1864, 1865, 1868, Altum 1865, Pässler 1865a, 1867, Preen 1865, Reichenbach 1866, Tschusi 1867, Droste 1868, Schlegel 1868, Fritsch 1870, Taczanowski 1888. **1871-1880**: Borggreve 1871, Dresser 1871, Fritsch 1871, Homeyer 1872, Rey 1872, Droste 1873, Harting et al. 1876, Schmidhoffen 1876, Bau et al. 1877, Taczanowski 1877, Basius et al. 1878, Goeldlin 1879, Koch 1878, 1881, Altum 1880 (in Kumerloeve 1953), Balen 1880, Taczanowski 1888 Marshall 1895, Lydekker 1899. **1881-1890**: Blasius 1884, Homeyer 1884, 1887, ADOGzB 1886, Krezschmar 1886, Čapek 1887, Hartert 1887, Tschusi & Dalla-Torre 1887, Middendorf 1888, 1890, Taczanowski 1888, Talsky 1888, Dalla-Torre 1890, Flöricke 1890, Keller 1890, Tschusi 1890, Preuschen 1891, Pražak 1893, Marshall 1895, Schuler 1899, Bährmann 1917. **1891-1900**: Preuschen 1891, Kněžourek 1892, Pražak 1893, Szielasko 1893, Wentzel 1895, Blasius 1896, Floericke 1896, Koepert 1896, Chernelháza 1897, Kayser 1898, Kleinschmidt 1898, Lindner 1898, 1901a, b, c, Parrot 1899, Schuler 1899, Kollibay 1904, Löns 1905, Hilgert 1908, Natorp 1909, Bährmann 1917.

**Appendix 8**. Buchoz 1771, Bomare 1800, Colchen 1803, Deterville 1803, Gerardin 1805, Cuvier 1817, Serres 1822, Bonnaterre 1823, Fournel 1840, 1856, Malherbe 1843, Jäckel 1849, Naumann 1851, Schlegel 1854, Nilsson 1858, Altum 1863, Holmgren 1866, Dresser 1871, Fritsch 1871, Homeyer 1872, Rey 1872, Taczanowski 1888, Keller 1890, Floericke 1892, Marshall 1895, Natorp 1909, Bährmann 1917, Stolz 1917.

**Appendix 9**. Chomel 1709, Hohental 1750, Linné & Ekmarck 1757, Borkhausen 1797, Gerardin 1805, Wolf & Meyer 1805, Meyer 1815, Cuvier 1817, Millet 1828, Schinz 1830, Degland 1831, 1841, 1849, Gloger 1834, Hugo 1835, Yarrell 1839, Bechstein 1840, 1885, Crespon 1844, Mühle 1844, Serres 1845, Baldamus 1851, 1853, Naumann 1851, Schlegel 1854, Olphe-Galliard 1855, 1891, Hoy (in Hewitson 1856), Dubois 1857, Moquin-Tandon 1858, Nilsson 1858, Toussenel 1859, Morris 1862, Wheelright 1864, Bettoni & Dressler 1865, Hintz 1865, Pässler 1865a, b, 1867, Prévost & Lemaire 1865, Degland & Gerbe 1867, Lemmeteil 1868, Fritsch 1870, 1871, Dresser 1871, Homeyer 1873, Krüper 1875, Schalow 1876, Sintenis 1877, Pleske 1878, Goeldlin 1879, Radde 1884, Krezschmar 1886, Baca 1887, Savatier & Foucaud 1889, Kerville 1890, Floericke 1892, Sandman 1892, Chapman & Buck 1893, Pražak 1893, Aurivillius 1894, Chapman 1897, Hamonville 1898, Deyrolle 1903, Hantzsch 1903, Kollibay 1904, Oddi 1904, Wessel 1904, Löns 1905, Munsterhjelm 1910, Delmas 1911, Detmers 1912, Grafsmann 1914, Hermitte 1916, Schaanning 1916b, Stolz 1917, Stresemann 1920, Mayaud 1933, Kumerloeve 1953.

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