The distributional range of the Citril Finch *Carduelis citrinella* – unsolved riddles and possible explanations

Hans Märki, Gaston Adamek

This report is an overview pointing to still unresolved issues in the evolution of the distributional range of the Citril Finch *Carduelis citrinella*. The current distribution, abundance, and genetic differences between Spanish and central European populations indicate that the glacial refuge of the Citril Finch was on the Iberian Peninsula. In contrast to other subalpine species, the Citril Finch did not colonise a zone of about 200 km length of suitable habitats directly adjacent to its distributional range in the northern part of the eastern Alps. Both density and occurrence decrease towards the east, and from north to south in the central and eastern Alps. Following a brief discussion of the advantages and limitations of genetic methods and distribution modelling on the Citril Finch and its postglacial dispersal, we explain the importance of vegetation. Only mast years of pine and spruce lead to strong population increases throughout the range. Currently, pine forests in Spain that regularly bear fruit are ideal habitats for the Citril Finch. In contrast, spruce forests in the Alps seem suboptimal due to their long intervals between years with full mast seeding. Reproduction and survival rates are probably better in pine habitats than in spruce habitats. The decreasing density from north to south and the distribution in the central and eastern Alps correlates with limestone and dolomite zones. The herb layer on limestone and dolomite is more species-rich than on crystalline bedrock and probably provides seeds continuously and in sufficient quantity, with dandelions serving as the most important food for nestlings. Finally, open questions about the size of the wintering area as well as physiological limitations on migration are discussed. The interaction of historical and current ecological factors, including the small wintering area and the low genetic variability of the central European population, are likely to lead to low population pressure and may explain the irregular and decreasing distribution of the Citril Finch in the easternmost part of the Alps.

With the European Breeding Bird Atlas EBBA2 (Keller et al. 2020) and the national atlases, the distribution of the endemic Citril Finch is now well documented (Fig. 1). Out of its glacial refuge on the Iberian Peninsula (Förschler et al. 2011), the Citril Finch colonised central Europe from south-west. Today, their main populations are located in Spain and in the western and central Alps.

In the central European range, current trends clearly depict declining populations (Schmid et al. 1998, Förschler 2013, Knaus et al. 2018, Keller et al. 2020). The distribution of the Citril Finch in the eastern Austrian Alps does not coincide with the occurrence of suitable habitat in the subalpine zone: An area of about 200 km length of suitable habitats in the eastern Alps is not or only sporadically colonised (Märki 1976, Glutz von Blotzheim und Bauer 1997, Engler et al. 2014, BirdLife Österreich 2022).

In the following text, we discuss (1) the differences between the Iberian and the central European breeding areas, (2) the use of genetic methods and modelling of distributional ranges, (3) the postglacial spread of Citril Finches, (4) the role of vegetation, and (5) open questions about wintering distributions and migration. Overall, this review points out puzzling uncertainties about changes in the distribution of the Citril Finch.

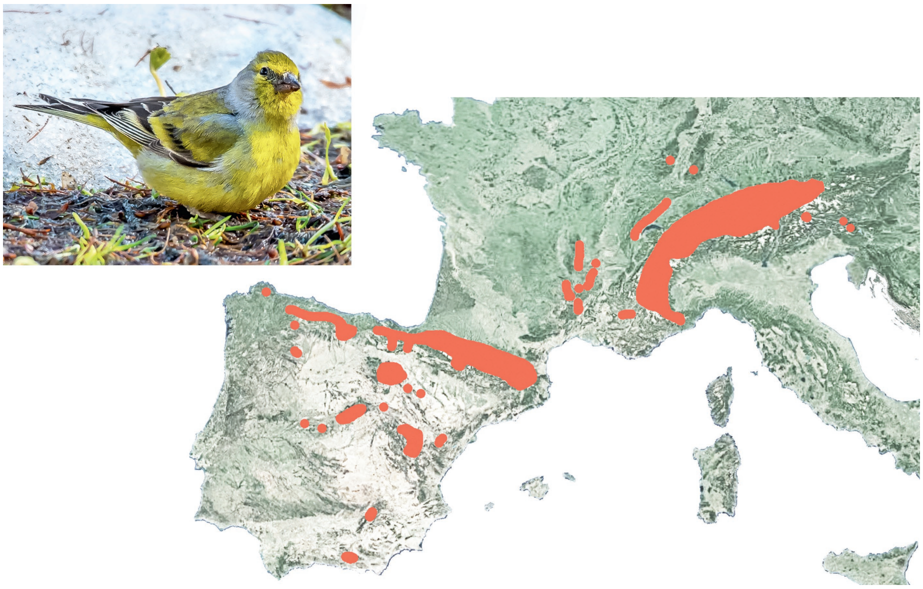

Figure 1. Distribution of the European endemic Citril Finch, compiled from various national publications and Keller et al. (2020); the basic map is from Google Earth. Photo Daniela Heldner.
Verbreitung des in Europa endemischen Zitronenzeisigs, zusammengestellt aus verschiedenen nationalen Veröffentlichungen und Keller et al. (2020); die Grundkarte stammt von Google Earth.

1. Current distribution and eastern borderline

In Spain, suitable mountain areas are colonised despite lowland gaps of up to 240 km. Citril Finches regularly occur both in the Mediterranean mountain climate at 2150 m a.s.l. in the Sierra Nevada, Andalusia, and in the Atlantic climate at 500 m a.s.l. in Galicia (Vázquez Pumariño 2004, Pérez-Contreras et al. 2005, Märki et al. 2012), but their optimal habitats are located in the Pyrenees.

In France, most Citril Finches breed in the western Alps and in the Pyrenees, as well as partly in the Massif Central.

In the central and eastern Alps, population density decreases from north to south, with suitable habitats in the south (Knaus et al. 2018, BirdLife Österreich 2022; Fig. 3). Currently, populations are declining mostly in the Swiss and French Jura, in the Vosges and in the Black Forest (Keller et al. 2020) – the potential loss of the species as a breeding bird in the Black Forest is expected within the next ten years (Förschler 2013). Scattered observations of Citril Finches in the Harz Mountains (500 km further north than the Black Forest) are available, with long intervals from the 19th century to the 1960s. Based on the observation of a large number of young birds (Ringleben 1968), it can be assumed that the species bred there in the 1960s.

Unlike other subalpine species like Ring Ouzel *Turdus torquatus* (Fig. 2), the Citril Finch does not colonise an area of about 200 km length of suitable habitats in the north-eastern Alps, and no further continuous spread is observed. Isolated breeding places in the northern Austrian Alps are not regularly confirmed (Glutz von Blotzheim and Bauer 1997).

Few recent data are available from the two south-eastern micro-occurrences in Slovenia (Tekavčič and Kljum 2019, Lunczer 2020) and in the Carinthian Dobratsch (Feldner and Rass 1999), which are isolated from the northern main Alpine area.

In Italy, the historical distribution seems to be similar to the present one, which is at the southern side of the central and eastern Alps as well as in the western Alps (Brichetti and Fracasso 2013).

2. Gene flow studies and distribution modelling on Citril Finches

The study by Förschler et al. (2011) by means of genetic markers is a pioneering effort to understand the post-glacial evolution of the present distribution of Citril Finches. Accordingly, the population north of the Pyrenees (at least of the French and northern Alpine area) is genetically different from the Iberian populations, suggesting a separation and subsequent range expansion towards central Europe. According to information from ring recoveries, it seems that northern populations barely mix with Iberian populations. The extent to which genetic differences correlate with behavioural differences (migratory behaviour, feeding habits) cannot be clarified by means of such haplontic differen-

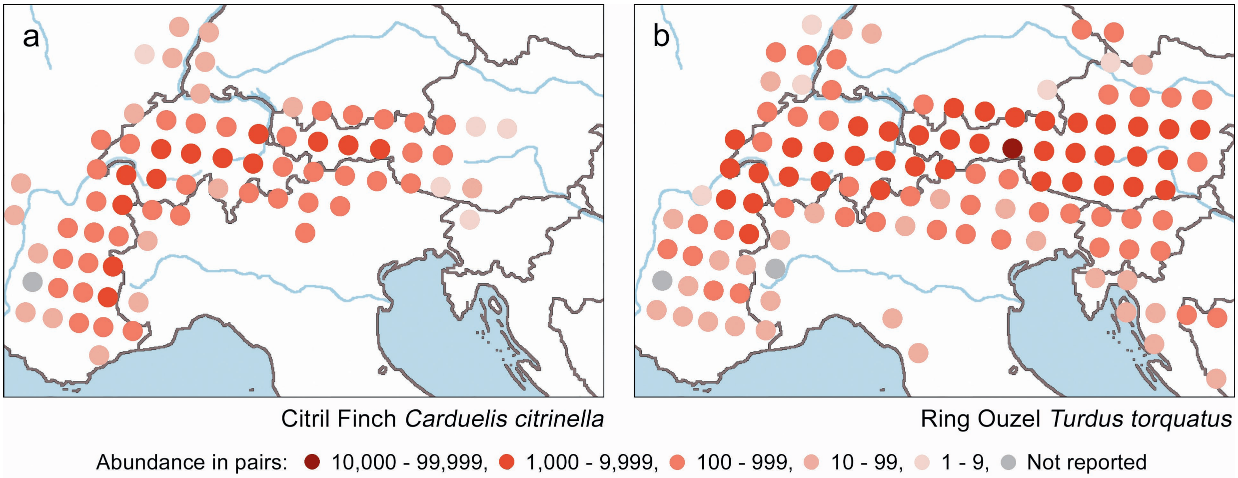

Figure 2. Abundance (breeding pairs) of the two subalpine species (a) Citril Finch and (b) Ring Ouzel in the Alps. Adapted from map sections in Keller et al. (2020).
Häufigkeit (Brutpaare) der beiden subalpinen Arten (a) Zitronenzeisig und (b) Ringdrossel in den Alpen. Adaptiert aus Kartenausschnitten in Keller et al. (2020).

tials; this would require extremely complex genomic and even epigenomic studies, like those currently being carried out for the Blackcap *Sylvia atricapilla* (Merlin and Liedvogel 2019, Langebrake et al. 2021).

It cannot be excluded that breeding birds of the northern part of the Alps cross the Alps or fly around them westwards and reach Italy. However, the north-south alpine crossing of Citril Finches in the central and eastern Alps seems to be only marginally substantiated based on the available observations and ring findings. Two birds captured in autumn at Col de la Golèze (border region between France and south-western Switzerland) and one bird captured in spring in the Swiss Alps (canton of St. Gallen) reached Italy (Maumary et al. 2007, Spina and Volponi 2008).

It cannot be ruled out that the Italian population (of the eastern, western, and southern Alps) split off early from the northward migrating population in the south of France. Interestingly, today's southern Alpine populations almost always show only short winter shifts from the breeding areas to the offshore lowlands (Brichetti and Fracasso 2013), as it is common in the Pyrenees (Borras et al. 2010) and less frequently observed in the north-western and western Alps (Issa and Muller 2015, Luisier 2022). It would therefore be interesting to study southern alpine Citril Finches genetically. If there were haplontic differences between the populations of the northern and southern Alps, it might also be possible to draw conclusions about the origin of the remaining populations of Slovenia and Dobratsch, whose origin is still unclear.

Modelling can be used to depict the current distribution of breeding populations and to estimate past or future distributions. In addition to a modelling study by Borras et al. (2010) on habitats used in winter in Catalonia (which we will not address here), we are currently aware of three publications with distribution models for the Citril Finch: A range and breeding density simulation for the Swiss population (Knaus et al. 2018) and two models for the entire European range (Huntley et al. 2007, Engler et al. 2014).

Knaus et al. (2018) were able to use an enormous amount of observations for their Swiss Breeding Atlas 2013–2016: 4–5 1-km² observation plots per 10 × 10 km square, covering the whole of Switzerland. The modelling, taking into account vegetation and elevation, resulted in the detailed map shown in Fig. 3a. Despite ideal basic data, the number of breeding pairs could only be roughly estimated at 10 000 to 20 000.

For their modelling of the distribution, Huntley et al. (2007) used data from the EBCC Atlas of European breeding birds (Hagemeijer and Blair 1997) and climate data over a 30-year interval. Their simulation of the current distribution (including the Corsican Finch *Carduelis corsicana*) looks reasonable, despite outliers from Scandinavia to Jan Mayen and Bjørnøya to the Black Sea coast. Based on a predictive simulation for the late 21st century, with an occurrence on Svalbard, the authors conclude that «less than 10% of the present range is remaining suitable, mainly in the Alps and northern Spain» (Huntley et al. 2007).

Engler et al. (2014), who are experts on the biology of the Citril Finch, carried out more sophisticated and elaborate modelling. Extremely precise data on the

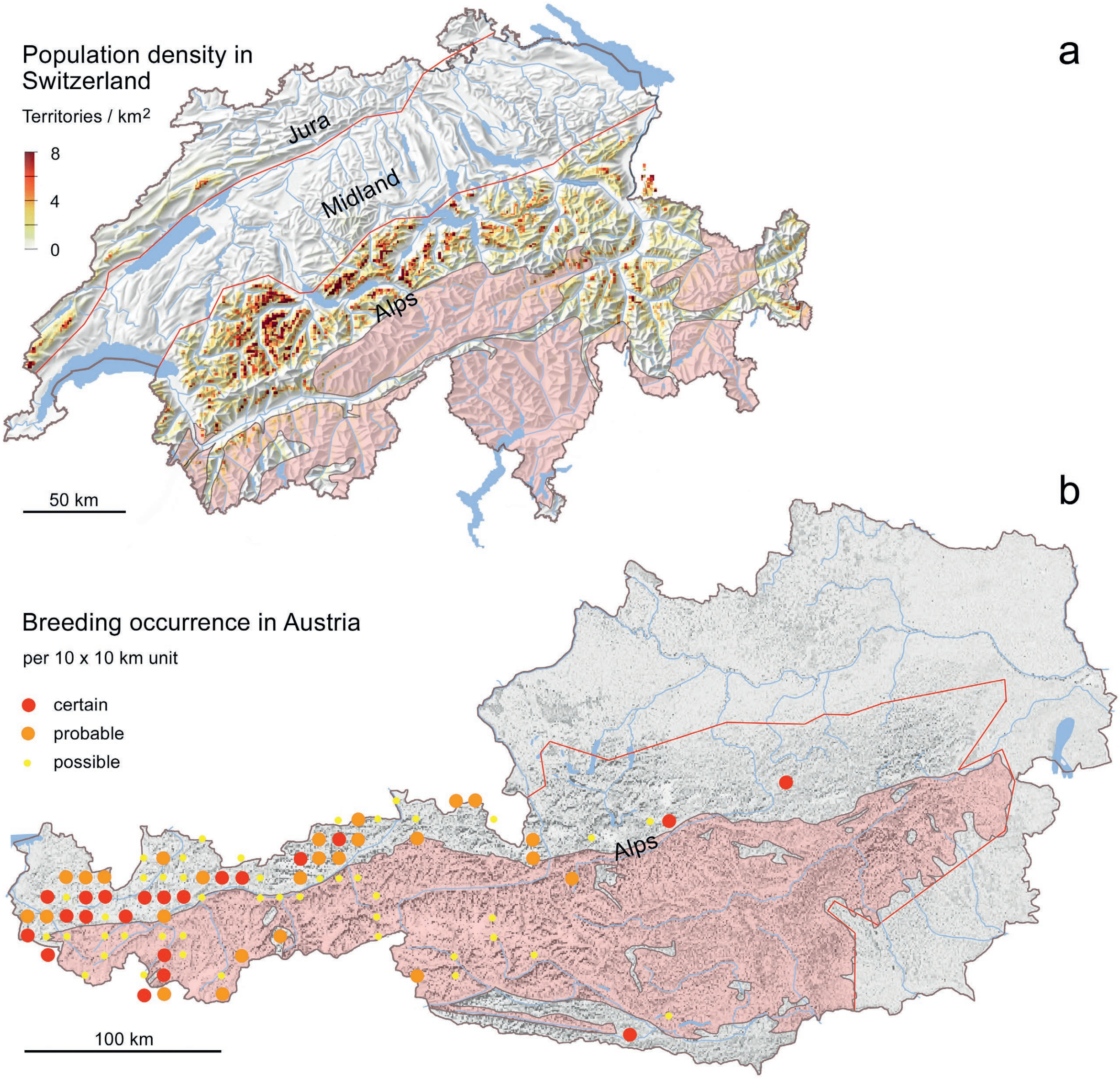

Figure 3. Distribution of the Citril Finch in Switzerland and Austria 2013–2016 in relation to the geological substratum. (a) Distribution and density in the Jura and the Alps of Switzerland. (b) Breeding occurrence in the Austrian Alps. Pink coloured areas: Crystalline substratum. Grey areas within the Jura and the Alps: Carbonate substratum such as limestone and dolomite (partly sediments). Basic maps are from Knaus et al. (2018) and BirdLife Österreich (2022). Geological areas are from Spiess (1993) and Schuster et al. (2013).

Verbreitung des Zitronenzeisigs in der Schweiz und Österreich 2013–2016 in Bezug auf den geologischen Untergrund. (a) Verbreitung und Dichte im Jura und in den Alpen der Schweiz. (b) Brutvorkommen in den österreichischen Alpen. Rosa gefärbte Gebiete: kristallines Substrat. Graue Flächen im Jura und in den Alpen: Karbonatsubstrat wie Kalkstein und Dolomit (teilweise Sedimente). Die Basiskarten stammen aus Knaus et al. (2018) und BirdLife Österreich (2022); die geologischen Gebiete sind aus Spiess (1993) und Schuster et al. (2013).

range of breeding and wintering areas were collected. Using suitable precipitation and temperature data and «coniferous forests» and «mixed forests» selected as relevant habitat classes, they made interesting simulations, and deviations from the real distribution were discussed in detail. However, the authors acknowledge that more accurate data are lacking on the microhabitats of the birds both for breeding and wintering areas, where «microhabitat» is defined as «open and semi-open conifer forests consisting mainly of spruce *Picea* and pine *Pinus* species».

3. Postglacial spread

To understand the current distribution of the Citril Finch, we have to take into account the spread of the species from the last ice age onwards (Förschler et al. 2011). The glacial refuge of the Citril Finch was probably on the Iberian Peninsula, which was also a refuge for several *Pinus* species used by the Citril Finch at least today (Benito-Garzón et al. 2008, Desprat et al. 2015, Di Pasquale et al. 2020), including *Pinus nigra* that has a three times higher grain weight than *P. mugo/uncinata* and *P. silvestris* (ETHZ 1995). We may assume that the glacial refuge is where Citril Finches developed a preference for *Pinus* seeds, which are not only energy-rich but also available long-term and regularly (Fouarge 1980, Borras et al. 2003). Postglacially, Citril Finches then probably migrated with the first spreading sparse birch-pine forests (*Pinus sylvestris* and *mugo/uncinata* are difficult or largely impossible to distinguish in pollen analysis) to central Europe, possibly reaching areas further in the north and east than today. Whether the south-eastern occurrences in Slovenia (Tekavčič and Kljum 2019) and Carinthian Dobratsch (Feldner and Rass 1999), which are isolated from the main Alpine area, were reached in the course of postglacial dispersal or were colonised more recently is difficult to reconstruct. Förschler et al. (2011) studied this range expansion by means of genetic markers. They found hints of a relatively rapid post-glacial expansion, followed by a strong and relatively recent bottleneck event with a sudden decrease of crucial resources during the Mid-Holocene and a subsequent breakdown of the population. This decrease was probably linked to a postglacial warm period with its increased humidity, resulting in fundamental changes of the forest vegetation of central Europe and a reduction of *Pinus* remnants even in the mountains (Rey et al. 2013). The immigration of Citril Finches into the Alps after the postglacial warm period probably occurred simultaneously with spruce, which migrated slowly from the east (Rey et al. 2013).

4. The role of pines, spruce and herb layer for population dynamics

The diet of the Citril Finch is well studied (K. Sabel in Glutz von Blotzheim and Bauer 1997, Borras et al. 2003, Förschler 2001, 2007, Förscher et al. 2006, Förschler and Kalko 2006). Despite the opportunistic nature of its food choice, the Citril Finch uses only a few species whose seeds are easily accessible and available in large numbers. From spring to summer, Citril Finches feed increasingly on the ground or in the herb layer, but still profit from pine seeds until early summer (Borras et al. 2003).

For Spanish populations, pine seeds are a key resource, and mass fructification is the reason for opportunistic first breeding at low elevations, followed by the subsequent broods in the subalpine zone (Borras and Senar 1991, Borras et al. 2003). It seems reasonable to assume that the Citril Finch originally adapted to the more regular fructification of pine species in its refugial area on the Iberian Peninsula. Pine seeds are a food source that is regularly available from winter to July (Fouarge 1980, Borras et al. 2003), while in central Europe, spruce seeding is variable, and mast seeding of spruce can lead to strong but intermittent population increases in the Citril Finch (Glutz von Blotzheim and Bauer 1997, Kilzer et al. 2002, 2011). In contrast to pine species in Spain, full mast of spruce in central Europe is thus less regular, and there are regional differences on the occurrence of mast seeding: in the Black Forest every 3–5 years (Marc Förschler, personal communication), in Switzerland (above 800 m) very irregularly from a three-year period to only every 10 or even 17 years (Anton Burkart, personal communication, and in Burri et al. 2016). Fructification failures in spruce are due to long wet and cold periods or late frosts in spring. Failure is most pronounced at high elevations (Anton Burkart, personal communication), which severely affects Citril Finches with their predominance in the subalpine zone. In Switzerland, which is the main breeding area in central Europe, the density of *Pinus mugo/uncinata* stands is very low (Knaus et al. 2018, Landesforstinventar 2022), and the *Pinus* species are found at the upper forest boundary more rarely than spruce. Thus, Citril Finches encounter less stable food conditions in central Europe than in Spain. In contrast to the Spanish population, when returning from wintering grounds, finches of the central European population must often content themselves with the tiny seeds of herbaceous plants that they pick from the ground (Fig. 4), which represent a much poorer nutritional basis for egg production than the *Pinus* seeds available to Spanish populations.

Figure 4. Citril Finch feeding on spruce *Picea* sp. cones (a) and dandelion *Taraxacum* sp. seeds (b). Photos BirdID and Valéry Schollaert.
Zitronenzeisige an Fichtenzapfen Picea sp. (a) und an Löwenzahnsamen Taraxacum sp. (b).

Not all good mast years of spruce lead to an increase of Citril Finch populations; but a good supply of spruce seeds is necessary for any annual increase in population density, for breeding outside the boundaries of the usual range, and/or for breeding at lower elevations (Nothdurft 1972, Cercle Ornithologique de Fribourg 1993, V. Dorka in Glutz von Blotzheim and Bauer 1997). However, study conclusions on the role of spruce seeds are contradictory. Already Jouard (1930) associated a high density of Citril Finches and the occurrence of winter broods, which were particularly common in 1959 in the Alps and in the Swiss Jura (J.-P. Zinder, J. Burnier in Glutz von Blotzheim 1962), with an abundant supply of spruce seeds. The recent broods east of the Alpine range at Hochkar in Austria typically occurred in a year with spruce mast seeding (Harald Pfleger, personal communication). V. Dorka (in Glutz von Blotzheim and Bauer 1997) states that the Citril Finch is widespread in the Black Forest after two years with a good supply of spruce seeds, but, in years with failure of seed production, retreated completely to the mountain pine forests. In contrast, Förschler et al. (2006) found no increase in the population of Citril Finches in the Black Forest between 1992 and 2002 in spruce mast years. They assume that, in comparison with Eurasian Siskin *Carduelis spinus* and Common Crossbill *Loxia curvirostra*, Citril Finches have stronger specialisation on mountain pine seeds even in spruce mast years, as well as less nomadism, less exploration behaviour, and higher breeding-site fidelity.

In fact, due to the hanging cones, spruce seeds are more difficult to reach for the rather clumsy Citril Finches than the seeds of *Pinus* species. Citril Finches pick up spruce seeds mainly on the ground. Other bird species consuming spruce seeds are more numerous and present during the whole winter period and are clearly superior to the Citril Finch in exploiting seeds in the cones. In addition, spruce seeds on the ground are often consumed by small mammals (Ruhm 2012). Another cause for a lacking correlation between spruce mast and increasing Citril Finch populations may be climate warming, leading to spruce seeds dropping out prematurely, as is frequently observed in years with sunny and dry autumn periods (Anton Burkart, personal communication).

Further, there is a striking correlation between the occurrence of Citril Finches and the geological substratum: Citril Finches are usually much more abundant on carbonate rocks (limestone and dolomite) than on crystalline substratum (Fig. 3). Carbonate rocks have a more species-rich herb layer than crystalline rocks (Ewald 2003). We assume that the herb layer on carbonate rock is providing seeds continuously and in sufficient quantities. For example, the dandelion *Taraxacum* sp. (Fig. 4), whose milk-ripe fruits are the most important food for nestlings, occurs more frequently on carbonate than on crystalline rock and is also favoured by the increasing use of fertilizers (Ellenberg et al. 1992). The extent to which a species-rich herb layer affects breeding success and population dynamics is difficult to assess. However, we think that a rich herb layer is unlikely to have the same impact as spruce masts and will not compensate for the lack of spruce seeds.

5. Wintering range and migration

The Citril Finches of the central Alps population mostly winter in the south of France (Märki 1976, Zink and Bairlein 1995, Bairlein et al. 2014). Population dynamics depend on a complex combination of factors, such as food resources, breeding success, survival rates, and genetic variability. For example, Rappole et al. (2003) suggest that winter range size may be an important limiting factor for the population of the Golden-cheeked Warbler *Dendroica chrysoparia*. In addition, the resources in the small wintering range of the central European population of the Citril Finch could play a role in the non-colonisation of potentially suitable breeding habitats in the eastern Alps and the decreasing occurrence and density in this region. It is an open question whether extreme deforestation in the 18th and 19th centuries in the wintering area in southern France (Blondel 1976, Coutancier and Huguenin 2007, Märki and Adamek 2013) reduced the Citril Finch population. The eastward advancement of the Alpine population in the early 20th century, starting from Switzerland to the Bavarian Alps and further east (Remold 1958, Nitsche and Plachter 1987), could be related to the massive reforestation in the wintering area, leading to population increases. The recent decline of the Citril Finch population in central Europe, on the other hand, could well be related to the recent massive damage and death of Scots pine *Pinus sylvestris* and spruce in France, especially in the classical wintering areas of southern France (IFN-DSF 2007, Saintonge 2020).

In this context, Engler et al. (2014) suggested that the possible migration distances hardly exceed more than 500 km in the Citril Finch, and the distance to the main wintering areas might become too large for expanding eastern and northern range limits. In contrast, the migration distances covered by other finches of comparable sizes are much greater (Zink and Bairlein 1995, Bairlein et al. 2014). Theoretically, Citril Finches could progress in the adjacent areas in the eastern Alps step by step without exceeding their physiological capacities; also, migration behaviour is usually flexible and can be adapted to environmental factors (Lack 1968, Berthold 2000, Bairlein 2022). The fact that Citril Finches of southern populations, which generally migrate less than their northern conspecifics, can migrate up to 1000 km (Borràs et al. 2012), is not in agreement with the hypothesis of physiologically limited migration distances.

Förschler et al. (2011) and Engler et al. (2014) have made important contributions in disentangling the complex factors controlling population dynamics in the Citril Finch. However, quantifying the contribution of all factors controlling population dynamics is likely to be an almost impossible task.

6. Conclusions

In Spain and central Europe, Citril Finches depend on an abundant supply of conifer seeds. Pine-dominated habitats in Spain are ideal for the species that likely adapted to pine seeds in the ice ages. Consequently, we expect that reproduction and survival rates are better in pine habitats than in the typical spruce-dominated habitats in the Alps, where fructification of spruce is less frequent and regular than fructification of pines in Spain.

This relative shortage of preferred food, combined with the lower genetic variability of the central European population and possibly the limited capacity of the small winter range as well as the migration distances, are all factors that probably lead to low population pressure in central Europe, so that no range expansion is to be expected in the future. Moreover, under current climate warming, the species starts losing its marginal populations north of the Alps, in addition to a decline in other central European habitats. The case of the Citril Finch demonstrates that the distribution of a species varies not only as a response to current ecological factors, but also depending on its history, reflected by range expansions and range reductions due to multiple causes.

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Zusammenfassung

Märki H, Adamek G (2022) Die Verbreitung des Zitronenzeisigs *Carduelis citrinella* – ungelöste Rätsel und mögliche Erklärungen. Ornithologischer Beobachter 119: 366–375.

Bei diesem Bericht handelt es sich um einen Überblick, der auf noch immer ungelöste Fragen bei der Entwicklung des Verbreitungsgebiets des Zitronenzeisigs hinweist. Das derzeitige Verbreitungsgebiet, die Abundanz und die genetischen Unterschiede zwischen den spanischen und mitteleuropäischen Populationen deuten darauf hin, dass das eiszeitliche Refugium des Zitronenzeisigs auf der Iberischen Halbinsel lag. Im Gegensatz zu anderen subalpinen Arten besiedelt der Zitronenzeisig in den nördlichen Ostalpen eine Zone von rund 200 km Länge mit geeigneten Habitaten nicht, die direkt an das bisherige Verbreitungsgebiet anschliesst. Die Dichte und das Vorkommen nehmen in Richtung Osten und, in den zentralen und östlichen Alpen, von Norden nach Süden ab. Nach einer kurzen Darstellung der Vorteile und Grenzen genetischer Methoden und der Modellierung des Verbreitungsgebiets beim Zitronenzeisig und bei seiner postglazialen Ausbreitung wird die Bedeutung der Vegetation näher erläutert. Mastjahre von Kiefern und Fichten sind im ganzen Areal der Schlüssel zu starken Populationsanstiegen. Aktuell bilden Kiefernwälder (Schwarzkiefer, Bergkiefer, Waldkiefer) in Spanien, die regelmässig Samen produzieren, die idealen Lebensräume. Für den Zitronenzeisig sind Fichtenwälder in den Alpen vermutlich suboptimal, weil es grosse Abstände zwischen den Jahren mit Vollmasten gibt. Die Reproduktions- und Überlebensraten sind in Kiefernhabitaten wahrscheinlich besser als in Fichtenhabitaten. Die von Norden nach Süden abnehmende Dichte und die Verbreitung in den Zentral- und Ostalpen korrelieren mit Kalk- und Dolomit-Zonen. Die Krautschicht ist dort artenreicher als jene auf kristallinem Untergrund. Sie liefert wohl kontinuierlich und in ausreichender Menge Samen, wobei der Löwenzahn als wichtigste Nahrung für Nestlinge dient. Schliesslich werden offene Fragen zur Kapazität und Grösse des Überwinterungsgebietes sowie zu einer physiologischen Limitierung der Zugdistanzen angesprochen. Das Zusammenwirken historischer und aktuell wirkender ökologischer Faktoren könnte, zusammen mit dem kleinen Winterquartier und der geringen genetischen Variabilität der mitteleuropäischen Population, zu einem geringen Populationsdruck führen und die unregelmässige und abnehmende Verbreitung im östlichen Teil der Alpen erklären.

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Authors

Hans Märki studied biology at the University of Bern and has been a volunteer collaborator of the Swiss Ornithological Institute since 1964. Since 1972, as an amateur, he specialised on the biology of the Citril Finch. He closely collaborates with Italian, Spanish and German specialists of the species and visited Mediterranean breeding and winter sites of the Citril Finch. Gaston Adamek is a biologist with a focus on ecophysiological and biochemical cell-biological work. He was a teacher of biology and chemistry and is an amateur ornithologist since his youth. Furthermore, he led seabird field trips with the first author for three decades.

Hans Märki, Tännlenenweg 20, 3152 Mamishaus, Switzerland, e-mail maerki.h@bluewin.ch;
Gaston Adamek, Flurstrasse 25, 3014 Bern, Switzerland, e-mail g.adamek@bluewin.ch