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RESEARCH PAPER

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Flyways of Common Cranes *Grus grus* breeding in Fennoscandia

Flyttleder för tranor Grus grus *som häckar i Fennoskandia*

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KNOWLEDGE of migration patterns plays an essential role for understanding spatiotemporal distribution of birds. Here we used >15,000 sightings of 1,473 colour-ringed Common Cranes *Grus grus* to study migration patterns of birds breeding in five regions along a longitudinal gradient of Fennoscandia. Our results confirm that Fennoscandian cranes mainly use either a Western European flyway (W-flyway), to winter mainly in France or Spain, or a Central European flyway (C-flyway), to winter in Hungary or Israel. Finnish cranes showed the greatest variation in migration patterns in terms of distance and direction and only Finnish cranes were recovered in Africa. Many of the Finnish cranes, starting along C-flyway change to the W-flyway and winter in SW Europe or NW Africa. On the other hand, the Scandinavian cranes are rarely observed along the C-flyway. However, substantial numbers of cranes from NE Sweden cross the Baltic Sea and migrate via Finland but then follow the W-flyway from Germany and southwards, especially during autumn. These results can be used for conservation and management, e.g. to coordinate monitoring. They are also relevant for land use planning, e.g. to avoid windfarms at sites important for migrating soaring birds while crossing seas, so-called 'thermal bottleneck sites.'

Keywords: migration pattern | migratory flyway | ringing | banding | ringing recovery

Introduction

In the temperate zone, migration plays an essential role for birds as it is forming the conditions for survival, reproduction, spatiotemporal distribution and consequently fitness and population dynamics (Treves *et al.* 2006, Runge *et al.* 2014). A consequence of migration is that migrating birds are dependent on suitable habitats in different regions, often across several country and administrative borders, during the annual lifecycle. An understanding of migratory patterns of a species thus also provides information pertinent for conservation and management, e.g. for protection of suitable habitats, identification of important thermal sites for soaring birds along the migration routes, decide rates of sustainable harvest, mitigate negative impacts on human livelihoods, and disease transmission (Martin *et al.* 2007, Singh & Milner-Gulland 2011, Madsen *et al.* 2017).

Bird migration is a complex phenomenon where routes, stopover sites and phenology vary among species and subpopulations (Kirby *et al.* 2008, Runge *et al.* 2015). Migration strategies may vary even among individuals and with time due to factors such as age, social learning, weather conditions, human land use, disturbance and habitat restorations (Klaassen *et al.* 2006, Alonso *et al.* 2008, Pearse *et al.* 2010, Mueller *et al.* 2013, Runge *et al.* 2014). However, even though migration can show high degree of spatiotemporal variation, many individuals and populations also show high degree of fidelity to specific sites and routes (Alonso *et al.* 2008, Wakefield *et al.* 2015, Nilsson *et al.* 2018). For example, suitable stopover sites is often a limited resource along the migratory routes which may result in aggregations of large numbers of staging individuals repeatedly returning year after year (Runge *et al.* 2014, Nilsson *et al.* 2019).

To acknowledge the full range of variation, the flyway concept, defined as 'the entire range of a migratory species or distinct population through which it moves on an annual basis' has been established (for a review, see Boere *et al.* 2006). The flyway concept is a way to simplify the actual complexity of migration to assist decision-making and cooperation between countries and continents over the management of bird populations and habitats (Boere *et al.* 2006, Singh & Milner-Gulland 2011). However, defining species and subpopulation-specific flyways demands a lot of effort to gain sufficient information about migration patterns, population dynamics and annual life cycles of the species concerned (Johnson *et al.* 2014, Madsen *et al.* 2017). The techniques used when studying migration patterns and flyways of birds have evolved during the last decades, from direct observations by counts and radar to tracking individuals by ringing and different biologgers (Alerstam & Hedenström 1998, Fiedler 2009, Nilsson *et al.* 2018). Satellite- and GPS-based tracking techniques have developed rapidly and provide continuous movement data and opportunities for studying migration in detail. On the other hand, ringing with individually identifiable colour-rings may allow larger sample size as more individuals tagged due to lower cost compared to biologgers and tracking over longer time periods (not dependent of batteries) (Fiedler 2009, Thorup *et al.* 2014). In this study, we use colour-ringing data to describe migration routes and flyways of Common Cranes *G. grus* originating in Fennoscandia.

The distribution of common cranes ranges from Northern Europe to Eastern Russia with wintering areas in South and central Europe, North Africa, Central and Eastern Asia (Johnsgard 1983). The Western European crane population has increased rapidly during the last decades due to legal protection and intensification of agriculture providing high quality food (EC 2009, Harris & Mirande 2013). The population along the Western European flyway was estimated to approximately 500,000 individuals in 2015 (IUCN 2020), with hundred of thousands individuals occasionally aggregating simultaneously at specific stopover sites (e.g. 268,120 individuals were counted in Arjuanx, France, Nov. 2019; (LPO 2020)). A large proportion of the European Common Crane population breeds in Fennoscandia. The increase has led to increased crop damage (Salvi 2010, Montràs-Janer *et al.* 2019) but also increased numbers of observations of cranes predating on eggs and chicks of other bird species even though the effect on populations still is unclear (Wirdheim 2019, Fraixedas *et al.* 2020). Due to these recent changes in population numbers, knowledge about migration patterns of cranes will not only lead to an increased understanding of the ecology of the species, but can also be important for future conservation and management strategies (Nilsson *et al.* 2019, Hemminger *et al.* 2022).

The Common Crane can in general terms be described as a short to long distance migrant using thermal flights, gathering in large aggregations at specific stopover sites along the flyways. The stopover sites are often characterized by wetlands and shallow waters for night roosting and surrounding agricultural land for foraging (Vegvari & Tar 2002, Skyllberg *et al.* 2005, Vegvari *et al.* 2011, Hemminger *et al.* 2022). Colour-ringing of Common Cranes started more than 30 years ago, with the main purpose of studying their migration and foraging behaviour (Alonso *et al.* 2018). Due to great interest among the public and ornithologists at many of the stopover sites (Lundin 2005), large numbers of colour-ringed cranes are observed and reported to national and international databases, such as the Internet-based Crane Observation Ring Archive (Crane Conservation Germany 2020) that holds more than 200,000 resightings of birds.

Substantial data on distribution and migration of Common Cranes is therefore available across large of the annual range. A few studies have earlier described migration patterns of Common Cranes origin in Fennoscandia (Saurola *et al.* 2013, Nilsson *et al.* 2019, Ojaste *et al.* 2020), but no large scale study to delineate the migration routes of the Fennoscandian Common Crane has been made. Despite this, generalised maps of European migration routes have been presented based on observations at main stopover sites (cf. Prange 2010, Leito *et al.* 2015) suggesting two main migration routes for Common Cranes breeding in Fennoscandia (Leito *et al.* 2015). In our study, we have merged Fennoscandian colour-ringing data to provide an overview of migration routes in relation to the earlier described Western European and Central European flyways of Common Cranes. By merging the data we were also able to describe possible differences in migration patterns of cranes from different Fennoscandian regions.

Material and methods

CAPTURING AND COLOUR-RINGING

In total 1,473 juvenile Common Cranes were equipped with colour-rings in their breeding territories in Finland (n=821, 1988–2014), Sweden (n=512, 1990–2013) and Norway (n=112, 1996–2013; Figure 1–2). All colour-ringed cranes were also equipped with a metal-ring provided from the national ringing schemes. By colour-ringing juveniles, the movements of the entire family group (i.e. parents and one or occasionally two siblings) are mirrored by the resightings of the juveniles until the separation occurring mainly at wintering sites during the first winter but occasionally also during spring migration (Alonso *et al.* 1984, Alonso & Alonso 1993).

The cranes were ringed at an approximate age of 6–9 weeks (for details about the capture procedure, see Månsson *et al.* 2013). Initially a minor number of alphanumeric colour-rings on the tibia were used, but since 1990, a 3+3 colour-ring system was used in all three countries to create unique individual combinations. The rings (width 2 cm and height 3 cm) enable readings by binoculars or telescopes at a distance.

DATA PROCESSING

The data used in this study is based on readings of the colour-rings of banded cranes outside their breeding regions. The vast majority of the resightings were reported by volunteers. The reports, nowadays often supported with photos, were evaluated for accuracy and accepted by the regional coordinators of the national crane working groups in Norway, Sweden and Finland. The three data sets were merged, totalling 15,378 resightings in order to construct distribution maps and descriptions of migration routes and flyways (Figure 3, Appendix 1–2).

For each resighting, we achieved information of colour-ring combination, the date of the sighting, the geographical coordinates (according to WGS84) and the name of the observer. An explicit aim of the study was to investigate movements between stopover sites, hence all reports with sufficient spatial resolution to identify stopover sites were included. In cases where multiple observations were made during a coherent period within a stopover site, the observations were merged together into a single data point (i.e. one resighting can include one or several observations). If both siblings were colour-ringed in a family group, only resightings from one of the siblings were included, as long as they did not separate from each other. Data maps presented were created in ArcMap (ver. 10.7).

In order to investigate possible differences in migration patterns dependent on the origin of the birds, we divided the studied population into five sub-groups based on breeding regions along a longitudinal gradient: NOR (longitude E 7.5–13.5), SWE-W (E 13.1–16.5), SWE-E (E 17.2–21.3), FIN-W (E 21.2–25.5), FIN-E (E 26.0–30.2; Figure 1).

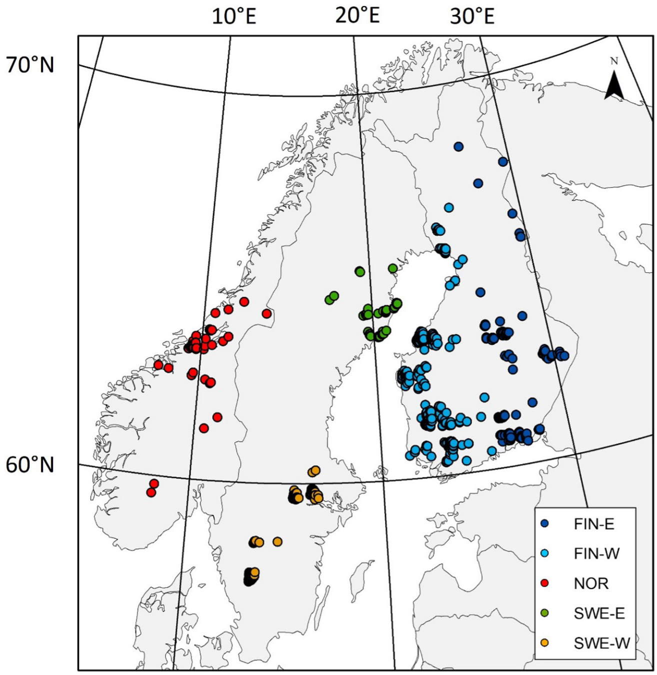

FIGURE 1. Breeding and ringing sites for the colour-ringed Common Cranes *Grus grus* (n=1,473) included in the study, in five non-overlapping Fennoscandian regions along a longitudinal gradient.
— *Platser där tranorna* Grus grus *i studien häckat och märkts med färgringar (n = 1 473). I studien ingår tranor från fem icke-överlappande regioner längs en öst-västlig gradient i Fennoskandia.*

To achieve more information about variation in used routes we also illustrate resightings of individuals that have been recovered at two or more stopover sites during the same migration season, hereafter called 'consecutive connections'. These consecutive connections were only explored for adult birds, as these individuals have amassed experience from several migration periods and should have a higher ability of orientation (Thorup *et al.* 2003). Colour-ringed juveniles (first calendar year [CY]) cover the movement of their adult parents during the first autumn migration while observations of individuals of an age between 2CY–5CY do not, and the latter observations were hence excluded.

Results

Common Cranes origin in Fennoscandia were resighted in 24 different countries (Appendix 1). Nearly all of the resightings (15,320) were made in Europe, with only small numbers in Israel (43) and Africa (15 resighted, from Ethiopia, Algeria and Tunisia; Appendix 2, Figure 4). The number of resightings per colour-ringed individual varied between 1 and 79 (median=6.0). Largest numbers of resightings per crane was observed in birds from Norway (NOR, median=22.5), followed by Sweden (SWE-W, median=14.5; SWE-E, median=15.5) and Finland (FIN-W, median=3.0; FIN-E median=3.0) (Appendix 2).

During spring (March–April) the majority of resighted are reported from the northern range of the flyway, but still 13% of resightings stem from France, Hungary, Israel and Spain (Figure 5). Also, during summer (May–August), 7% of the resightings are reported from outside Fennoscandia. In the autumn (September–November), most cranes originating in Norway and Sweden are reported from Germany, whereas the cranes originating in Finland are mainly recovered in Finland and Hungary. During winter (December–January), almost all (99.8%) of resightings were made in France (19%, mainly in Lac du Der and Arjuanx), Germany (27%, mainly in Lange Lohe), Hungary (8%, mainly in Hortobagy), Israel (0.6%, mainly in Hula valley) and

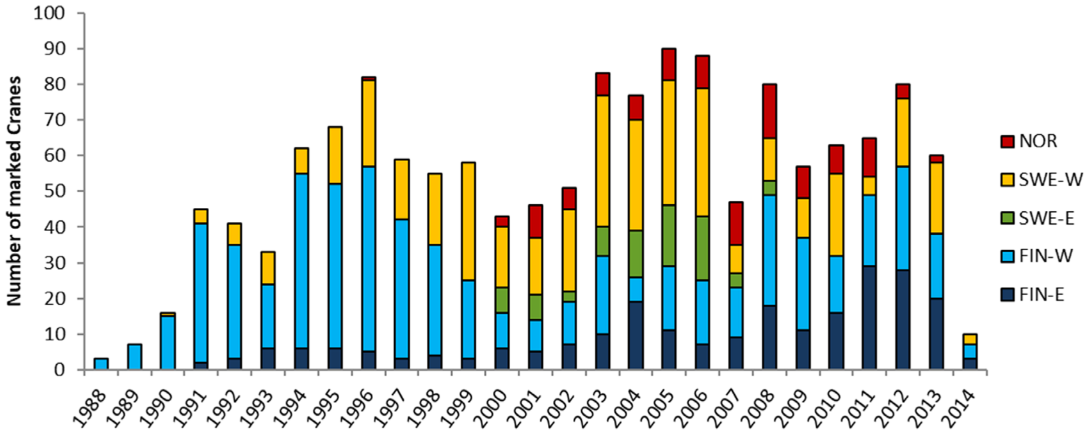

FIGURE 2. Yearly numbers (1988–2014) of colour-ringed Common Cranes *Grus grus*, in five different regions along a longitudinal gradient in Fennoscandia.
— *Årligt antal tranor* Grus grus *som har märkts med färgringar 1988–2014 i fem olika regioner längs en öst-västlig gradient i Fennoskandia.*

Spain (45%, mainly in Gallocanta and Extremadura) (Figure 4–6 for locations of sites mentioned).

The major difference between the Fennoscandian breeding regions was that cranes originating in Finland (FIN-W and FIN-E) show a more easterly migration with more variable total migration distances and a higher complexity in migration pattern than cranes with origin in Norway and Sweden (Figure 4–5). Some cranes originating in Finland followed the Western European flyway while others took a more pronounced easterly route (Figure 4–5). Resightings showed that the latter birds migrated both along the Central European flyway (passing Matsalu, Estonia and Hortobagy, Hungary) and along the eastern

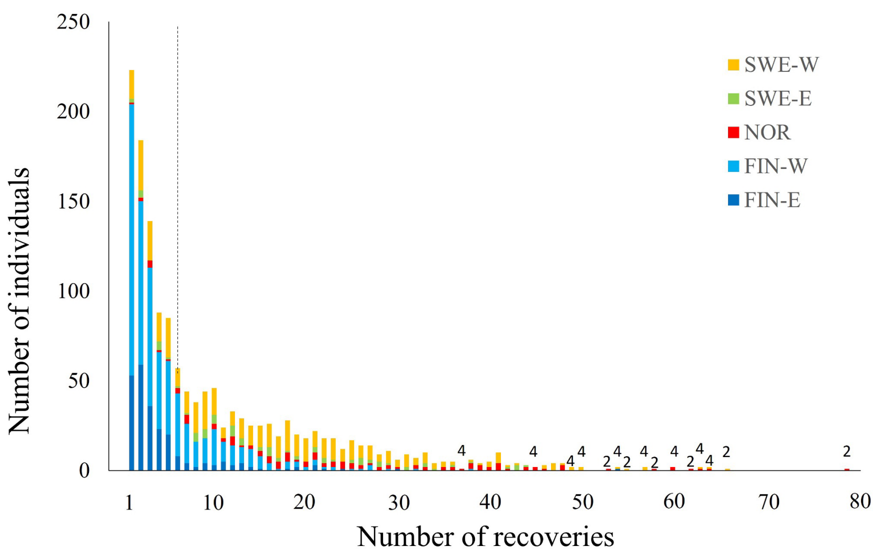

FIGURE 3. Number of resightings per individual of colour-ringed Common Cranes *Grus grus* in Fennoscandia (cases in which number of individuals <5 with labels with the total number for easier reading). The median number of resightings per individual was six (dashed line). Individuals that were never recovered outside breeding territories were excluded.
— *Antalet återfynd per individ av färgmärkta tranor* Grus grus *med ursprung i fem olika regioner i Fennoskandia. Siffror visar fåglar med mindre än fem fynd. Medianantalet återfynd per individ var sex (streckad linje). Individer som aldrig återfanns utanför häckningsreviren har uteslutits.*

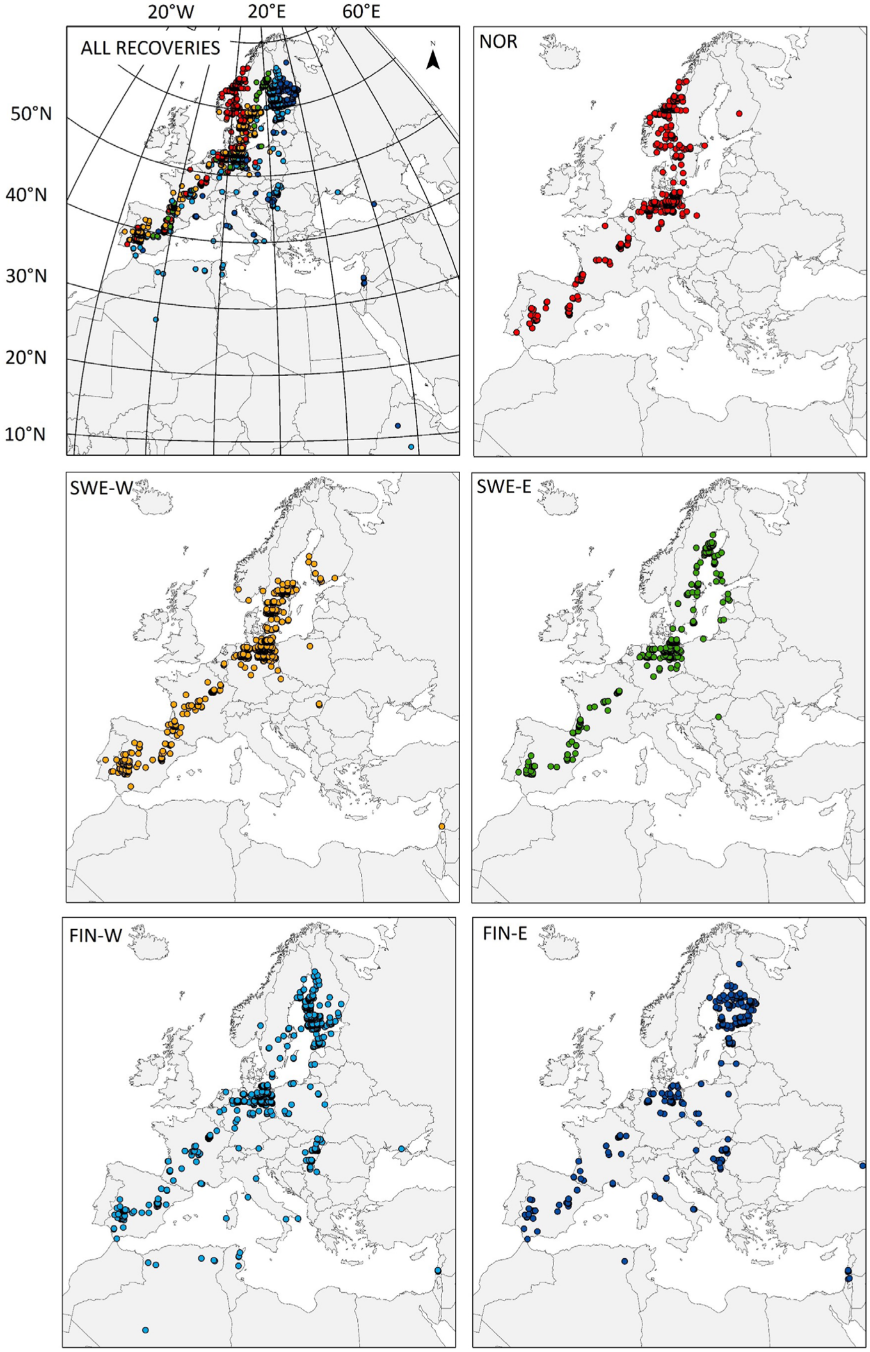

FIGURE 4. Resightings (n=15,378) of all colour-ringed Common Cranes *Grus grus* in Fennoscandia (top left panel) and separately for each of the five studied regions along a longitudinal gradient. The top left panel also shows resightings of Finnish cranes in Ethiopia.
— *Samtliga 15 378 återfynd (övre vänstra kartan) av de tranor* Grus grus *som färgmärkts och som häckar i västra Finland (Fin-W), östra Finland (Fin-E), Norge, nordöstra Sverige (Swe-E) och sydvästra Sverige (Swe-W) samt separata kartor för var och en av de fem studerade regionerna. I den övre vänstra kartan visas även de fynd som gjorts av finska tranor i Etiopien.*

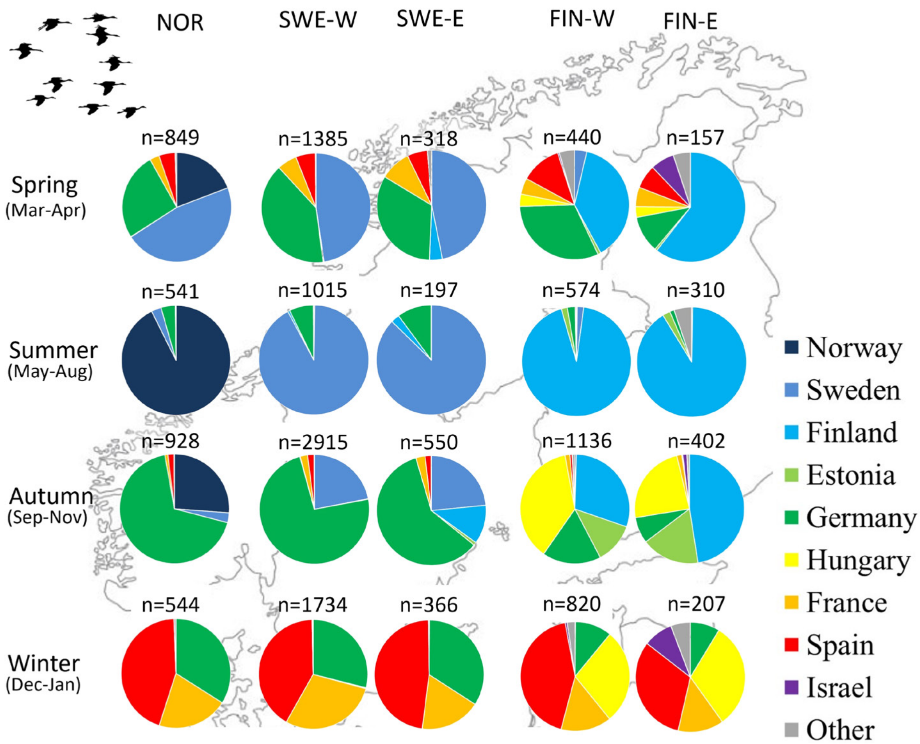

FIGURE 5. Number and proportion of resightings per season (spring, summer, autumn and winter) and countries for Common Cranes *Grus grus* origin in five different regions in Fennoscandia. Resightings are made from the country of origin southwards through Europe and sometimes even further south. The category 'other' includes countries with less than 2% resightings (Algeria, Austria, Czech Republic, Denmark, Estonia, Ethiopia, Georgia, Italy, Latvia, Netherlands, Poland, Portugal, Serbia, Slovakia, Tunisia and Ukraine; see Appendix 1).
— *Antal och andel återfynd per säsong (vår, sommar, höst och vinter) uppdelat per ursprungsland och region för tranor* Grus grus *som häckar i de fem fennoskandiska regionerna. Återfynd rapporteras från ursprungsländerna och söderut genom Europa och ibland även i Israel och Afrika. Kategorin "övriga" inkluderar länder med mindre än 2% återfynd (Algeriet, Österrike, Tjeckien, Danmark, Estland, Etiopien, Georgien, Italien, Lettland, Nederländerna, Polen, Portugal, Serbien, Slovakien, Tunisien och Ukraina; se Appendix 1).*

European flyway (passing Israel and the Black Sea; Figure 3, 5). Only a very small fraction (five resightings or 0.4‰) of the Scandinavian cranes were observed east of longitude 20°E and south of 35°N (Figure 4). Moreover, some cranes originating in Finland, unlike the cranes with Scandinavian origin, were also observed in Africa, in Algeria, Tunisia and Ethiopia. Cranes from NOR, SWE-E and SWE-W differed in that the main part of resightings of NOR and SWE-W cranes was in the central and western part of southern Sweden while the main part of resightings of SWE-E was from the eastern part of Sweden (Figure 4). A substantial portion of cranes originating in northeastern Sweden (SWE-E) crossed the Gulf of Bothnia at Norra Kvarken and migrated along the Finnish coast both during autumn and spring.

CRANES ORIGINATING FROM NORWAY (NOR) AND SOUTHCENTRAL SWEDEN (SWE-W)

Common Cranes with origin in Norway (NOR) and southcentral Sweden (SWE-W) showed many similarities in migration patterns. During autumn, they were using stopover sites close to their breeding areas before heading south to Germany. For instance, 92% of cranes with more easterly origin in SWE-W (in the province of Västmanland) made a first autumn stop at the lake Kvismaren. The NOR cranes were mainly observed in the western parts of Sweden (Figure 4) and the main site for resightings in Sweden was the lake Hornborgasjön (89% in spring and 56% in autumn, respectively). During spring, the main stopover sites, for migrating NOR and SWE-W cranes were the lakes Pulken, Hornborgasjön and Kvismaren.

FIGURE 6. Locations of areas and sites mentioned by name in the text: (1) Norra Kvarken, (2) Söderfjärden, (3) Tierp, (4) Kvismaren, (5) Matsalu, (6) Vättern, (7) Hornborgasjön, (8) Öland, (9) Pulken, (10) Rügen-Bock, (11) Lange Lohe, (12) Lac du Der, (13) Hortobagy, (14) Arjuanx, (15) Gallocanta, (16) Extremadura, and (17) Hula.
— Platser som nämns vid namn i texten: (1) Norra Kvarken, (2) Söderfjärden, (3) Tierp, (4) Kvismaren, (5) Matsalu, (6) Vättern, (7) Hornborgasjön, (8) Öland, (9) Pulken, (10) Rügen-Bock, (11) Lange Lohe, (12) Lac du Der, (13) Hortobagy, (14) Arjuanx, (15) Gallocanta, (16) Extremadura och (17) Hula.

From the resightings of SWE-W and NOR cranes, it seems to be one western and one central route through southcentral Sweden where the second largest lake in Sweden (Vättern) act as a divider, where relatively few cranes originating from Norway are reported from Kvismaren and few of SWE-W cranes are reported from Hornborgasjön. South of Sweden, from the Rügen-Bock area in Germany and southwards, the cranes origin in NOR and SWE-W use the same staging sites located on the Western European flyway. Out of 366 consecutive connections during the peak autumn migration (i.e. September–October) 93% were from Germany.

CRANES ORIGINATING FROM NORTH-EAST SWEDEN (SWE-E)

Common Cranes breeding in north-eastern Sweden (SWE-E) (provinces of Västerbotten and Norrbotten) showed a divergent pattern in the north part of the migration route. A substantial portion of the cranes crossed the sea Norra Kvarken and migrated along the Finnish west coast while some cranes followed the Swedish east coast, but along a significantly more easterly route than the NOR and SWE-W cranes in southern Sweden (Figure 4–5). Consecutive connections confirm the sea passage of SWE-E via Finland; in autumn (37 of 72 connections) as well as in spring (6 of

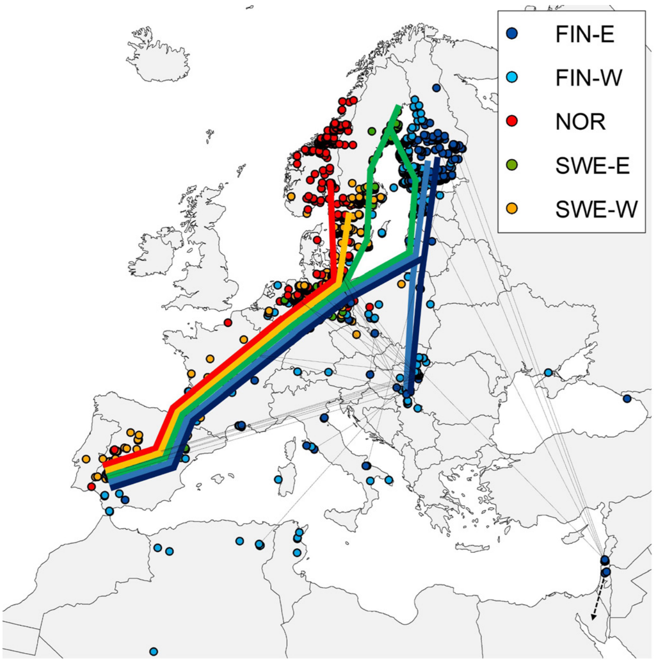

FIGURE 7. Generalised migration routes for Fennoscandian Common Cranes *Grus grus* based on resightings of colour-ringed cranes (n=15,378) and consecutive connections (same individual reported several times during the same migration season). Thin straight lines indicate consecutive connections but with less than 20 resightings and consecutive connections supporting the route. The dashed arrow, pointing south from Israel, indicates that two resightings have been reported further south in Ethiopia, see Figure 4.
— *En generaliserad karta över flyttvägar för de tranor* Grus grus *som häckar i västra Finland (Fin-W), östra Finland (Fin-E), Norge (NOR), nordöstra Sverige (Swe-E) och sydvästra Sverige (Swe-W) baserat på observationer av mer än 15 000 färgmärkta tranor. Tunna raka linjer indikerar fall där vi fått rapporter från en och samma trana under samma år men där vi totalt har mindre än 20 observationer som stöder rutten. Den streckade pilen, som pekar söderut från Israel, indikerar att två observationer har rapporterats längre söderut i Etiopien.*

31 connections). In addition, consecutive connections showed that SWE-E cranes, migrating via Finland, also were connected to the Rügen-Bock area (30 of 42 connections). South of the northern Germany staging sites, the SWE-E cranes use the same flyway as the NOR, SWE-W and parts of the cranes with origin in Finland. During autumn the easterly route through Sweden show connectivity of SWE-E cranes with the island of Öland situated in the southeast of Sweden, were 41% of all resightings from SWE-E were reported. Another stopover site with many resighted along the easterly route in Sweden was Tierp (44%). Most of the resightings of the SWE-E cranes (80% during autumn and 40% during spring) made in Finland were reported from Söderfjärden, (province of Österbotten). The SWE-E cranes taking the route via Finland then migrated east of the Baltic Sea, and all (>99%) resightings (except one in Hungary) were then made along the Western European flyway from Germany and southwards. A larger proportion of the SWE-E resightings were made in Finland during autumn (60%) than in spring (20%).

CRANES ORIGINATING FROM FINLAND (FIN-W AND FIN-E)

Common Cranes breeding in Finland migrated southwards over the Finnish Bay to Estonia, from where 21% of resightings outside Finland during autumn stem. The main stopover site in autumn is Matsalu, Estonia (Figure 4–5). However, during spring, only 2% of the resightings are reported in the Baltics (Estonia 5 and Latvia 2 resightings, respectively). Less than 3% of cranes marked in Finland were recovered in Sweden. In contrast, 86% of all 1cy-birds originating from Finland were reported in Estonia during September.

Seventy percent of the Finnish resightings were reported along the Central European flyway, while the remaining 30% were reported along the Western

European flyway, i.e. same route, from Germany and southward, as cranes originating from NOR, SWE-W and SWE-E. As much as 53% of all FIN-E and FIN-W resightings outside Finland during autumn stemmed from Hortobagy, Hungary, compared to 9% in spring. A substantial part of the Finnish cranes were recovered further southeast, especially in Israel, where they were staging or wintering (Appendix 1). A larger proportion of resightings in Israel were made for FIN-E than for FIN-W (79 and 21%, respectively). There were also a few resightings showing that some Finnish cranes use an even more easterly route crossing or flying east of the Black Sea (Figure 4–5). A larger proportion of resightings in Israel were made for FIN-E than for FIN-W (79 and 21%, respectively). Some cranes with origin in Finland were also observed in East Africa (i.e. Ethiopia), more than 6,000 km from their breeding area (Figure 4–5).

In total 98 consecutive connections of cranes originating from Finland were made in Hungary. Out of the 21 consecutive connections of cranes passing Hungary, the majority (13 or 62%) migrated westwards to Italy (1), France (4), Spain (6), Tunisia (1) or Algeria (1) (Figure 4–5). Three consecutive connections south of Hungary were made in Serbia and one in Israel. Besides, four consecutive connections were made northwards to Germany. There were no consecutive connections supporting that cranes migrating to Ethiopia actually have been staging in Israel, but one FIN-W crane recovered in Ethiopia January 16, 2010 was later recovered in Israel 8 March 2011.

Discussion

The present study confirms that the migration pattern of Fennoscandian Common Cranes differ depending on breeding regions. Finnish cranes show larger variation in migration distance and diversity of flyways, with a generally more easterly migration pattern and with some individuals migrating to northern Africa, which is not the case for cranes from Sweden and Norway. The migration of Fennoscandian cranes mainly coincide with two major and diverging flyways; the Western and the Central flyways through Europe (Figure 4, 7), as previously described (Lundin 2005, Prange 2010, Saurola *et al.* 2013, Leito *et al.* 2015). However, some cranes with origin in Finland use an even more easterly route, east of the Black Sea (Figure 4, 7). None of the observed cranes with origin in NOR, SWE-W and FIN-E crossed the Baltic Sea, while cranes originating from SWE-E and FIN-W were observed on both sides of the Baltic Sea.

In contrast to cranes originating from Scandinavia (NOR, SWE-W and SWE-E), the cranes with origin in Finland (FIN-W and FIN-W) use both the Central European and the Western European flyways through Europe. It is noteworthy that only a single resighting, out of all cranes colour-ringed west of the Baltic Sea, was made outside Europe (i.e. Israel) whereas cranes breeding in Finland have been observed in both NW Africa and in east sub-Saharan Africa. The multiple-route pattern has been described from other studies of cranes breeding in the Baltic countries (Saurola *et al.* 2013, Leito *et al.* 2015, Ojaste *et al.* 2020). The cranes originating from Finland show migration routes much in common with the cranes breeding in Estonia that migrate both along the Western, Central (including Africa) and the Eastern European flyways (Leito *et al.* 2011, 2015, Saurola *et al.* 2013). Our study show that some cranes with origin in Finland also use the Eastern European flyway as supported by a recent study (Ojaste *et al.* 2020). Moreover, the consecutive connections between Hortobagy in Hungary and staging places in Italy, France and Spain (Figure 7) indicate that cranes with origin in Finland in some cases may switch flyways during their southward migration (from the Central to Western European flyway). This hypothesis is also supported by Mingozzi *et al.* (2013) who, based on visual observations of cranes, suggested a migration route crossing northern Italy. There are no consecutive connections in the opposite direction (from Western to Central) but we cannot rule out that it occurs. The pattern in our study may suggest a loop migration, for some individuals, but further studies are needed to verify and quantify how common this pattern is.

Consecutive connections confirmed that a substantial part of the cranes originating in northeast Sweden migrate via Finland. Skyllberg *et al.* (2014) reported that cranes crossed Norra Kvarken based on both visual and surveillance radar observations and estimated that 15,000 cranes crossed the sea during autumn migration. A recent analysis of >40,000 crane migration observations in Fennoscandia confirmed this pattern but also identified Norra Kvarken as a very important site for several migrating soaring bird species when crossing the sea, i.e. a 'thermal bottleneck' (Hansson 2019). Even though a lower proportion of consecutive connections showed a passage over Norra Kvarken during spring, yearly counts still support that several thousand cranes arrive to northern Sweden by crossing this 'thermal bottleneck site' (Skyllberg *et al.* 2014, Hansson 2019).

Our study shows that the resighting rate of colour-ringed cranes in Europe can be very high. As an example, approximately 80% of the cranes with origin in Sweden were observed outside their breeding area compared to a resighting rate of 7% for ordinary metal-ring resightings of cranes in Sweden (Fransson *et al.* 2008). This clearly illustrates the power of colour-ringing to study the large scale migratory movements of cranes. The colour-ringing method also has the advantage, compared to conventional ringing, of producing multiple resightings of individual cranes (Figure 3), in our case up to 18 years after capture of the individual. However, the method relies on voluntary reports from the public and long-term data collection to achieve large numbers of resightings (Fiedler 2009, Thorup *et al.* 2014). Because the method is dependent on public reports, differences in reporting rates between areas may depend on possibilities and willingness to observe and report colour-ringed cranes. In our case it is for example likely that colour-ringed cranes are less reported along the central and eastern flyway compared to the western flyway as it can be assumed that the number of potential aware observers with necessary equipment are fewer in Africa compared to Europe. Therefore, direct comparison of number and proportion of resightings between different flyways and sites should be made with caution. Tagging cranes with biologgers that record GPS positions can be a reliable complement to colour-ringing in areas where detection rates are low.

One should be aware of that there may still be more variation hidden in our data as we have chosen to study quite large regions of crane origin and only an east-west gradient. Moreover Common Cranes have not been extensively colour-ringed in all parts of Fennoscandia. Recent studies have shown that there is also variation in migration patterns within the regions in our study, including along a south–north gradient (Ojaste *et al.* 2020). Moreover, our study focuses on describing the main flyways of cranes originating in Fennoscandia, without attempt to study seasonal differences, phenology or to link underlying mechanisms behind the patterns found. Therefore, more studies are needed to understand factors affecting the migration patterns of Common Cranes and how this knowledge can be used to facilitate future conservation and management efforts.

Migration patterns of birds play an essential role for understanding spatiotemporal distribution and environmental conditions affecting individual fitness and hence also to facilitate decisions regarding management, land use and conservation issues. For example, the knowledge about flyways are important for coordinated managememt actions, e.g. monitoring (Bacon *et al.* 2019, Månsson *et al.* 2022) and suitable placement of the current and rapidly expanding offshore windfarms (Krapu *et al.* 2014, Skov *et al.* 2016, Thaker *et al.* 2018, Hansson 2019).

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Svensk sammanfattning

För att lyckas med bevarande- och förvaltningsmål och för att förstå var och när fåglar vistas på olika platser under året är ingående kunskaper om fåglarnas flyttmönster avgörande.

I föreliggande studie analyserade vi >15 000 återfynd (avläsningar) av 1 473 färgmärkta tranor *Grus grus* från Sverige, Finland och Norge (Fennoskandia) för att kunna beskriva populationens övergripande flyttmönster. Tranan är en art med stort utbredningsområde och där en stor del av den europeiska populationen häckar i Fennoskandia. Tranan är en termikflyttare där individerna uppvisar betydande variation i hur långt de flyttar. Längs flyttrutterna kan tranorna samlas i stora antal då populationen har ökat mycket de senaste 40–50 åren.

Data i den här studien har samlats in under flera decenniers idogt arbete, där både märkning, avläsningar och datahantering skett genom volontärer från Fennoskandia i norr till Israel och Afrika i söder. Studien är den första i sitt slag där ett så omfattande material analyseras. En mycket stor andel av de färgmärkta tranorna återfanns långt utanför sina häckningsrevir.

Analysen av återfynden ger vid handen att fennoskandiska tranor följer två tidigare definierade flyttleder ('flyways') genom Europa till sina övervintringsområden.

Antingen följer de en *västeuropeisk* rutt med vinterområden i Spanien/Frankrike eller en *centraleuropeisk* motsvarighet, där en stor andel rastar och övervintrar i Ungern eller Israel. Finska tranor uppvisar – i förhållande till svenska och norska populationer – ett mer mångfacetterat flyttmönster, avseende både riktning och tillryggalagt avstånd. Det är till exempel bara bland de finska tranorna som det finns återfynd i Nordafrika och söder om Sahara. Några av alla de finska tranorna som påbörjar flyttningen söderut via den centraleuropeiska flyttvägen väljer att avvika mot västsydväst söder om Alperna för att, under samma flyttsäsong, ansluta till den västeuropeiska flyttvägen i södra Frankrike eller norra Spanien. De förlänger ibland resan ända ned till Nordafrika. På våren kan vi se att dessa tranor huvudsakligen återvänder till Finland via den västeuropeiska rutten – något som därmed kan betraktas som en form av ögleflyttning ('loop migration').

Tranor med ursprung väster om Östersjön (Norge och Sverige) ses mycket sällan längs den centraleuropeiska flyttvägen till skillnad från tranor av mer östligt ursprung (Finland). Betydande andelar av de tranor som häckar i norra Sverige (Västerbotten/södra Norrbotten) korsar Östersjön via Norra Kvarken. Således flyttar de via Finland innan de ansluter till de andra skandinaviska populationerna i norra Tyskland. Detta mönster är något vanligare under höstflytten än på våren. Även här kan man alltså tala om ögleflyttning.

Våra resultat ger en översiktlig bild av de fennoskandiska tranornas flyttmönster och denna kunskap bör tillämpas i bevarande-, förvaltnings- och markanvändningsstrategier. Till exempel kan kunskapen vara till nytta för att koordinera inventeringar under olika årstider. Dessutom ger resultaten handgriplig ledning vid planering av vindkraftsanläggningar så att man undviker viktiga knutpunkter, och andra platser med stora koncentrationer av tranor. Tranan är tillsammans med de flesta rovfåglar och storkar så kallade 'termikflyttare'. De koncentreras därför till områden längs deras flyttningsrutt där avståndet över hav blir så kort som möjligt. Lokaler som ger goda förutsättningar för termikbildning på ömse sidor om det kalla vattnet i sådana havsområden är därför extra skyddsvärda för den här gruppen av fåglar. Geografiska områden av detta slag, som till exempel Norra Kvarken, benämns 'termikflaskhalsar'. Våra data ger visserligen en grov bild av viktiga flyttkorridorer och platser, men fördjupade lokala studier behövs för att med bättre precision kunna beskriva dem.

APPENDIX 1. Number of resightings of colour-ringed Common Cranes *Grus grus* per country (in alphabetical order) and five different regions along a longitudinal gradient in Fennoscandia. (NOR=Norway, SWE-W=west Sweden, SWE-E=east Sweden, FIN-W west Finland and FIN-E=east Finland).
— Antal återfynd av färgmärkta tranor Grus grus *per land (i alfabetisk ordning) och de fem olika regionerna längs en öst-västlig gradient i Fennoskandia. (NOR = Norge, SWE-W = sydvästra Sverige, SWE-E = nordöstra Sverige, FIN-W = västra Finland och FIN-E = östra Finland.)*

Country/Region	FIN-E	FIN-W	NOR	SWE-E	SWE-W	Total
Algeria	1	7	0	0	0	8
Austria	1	0	0	0	0	1
Czech republic	0	0	0	0	1	1
Denmark	0	0	3	0	3	6
Estonia	77	151	0	5	0	233
Ethiopia	1	1	0	0	0	2
Finland	566	1,028	1	80	14	1,689

Country/Region	FIN-E	FIN-W	NOR	SWE-E	SWE-W	Total
France	43	160	146	150	455	954
Georgia	1	0	0	0	0	1
Germany	70	438	1,060	559	3,366	5,493
Hungary	168	689	0	1	3	861
Israel	34	8	0	0	1	43
Italy	6	5	0	0	0	11
Latvia	2	2	0	2	0	6
Netherlands	0	1	3	1	4	9
Norway	0	1	907	0	3	911
Poland	6	13	1	1	1	22
Portugal	0	0	2	1	2	5
Serbia	8	9	0	0	0	17
Slovakia	1	5	0	0	0	6
Spain	78	413	300	181	965	1,937
Sweden	1	33	439	450	2,233	3,156
Tunisia	0	5	0	0	0	5
Ukraine	0	1	0	0	0	1
Total	1,064	2,970	2,862	1,431	7,051	15,378

APPENDIX 2. Number of resightings per region (NOR=Norway, SWE-W=west Sweden, SWE-E=east Sweden, FIN-W west Finland and FIN-E=east Finland) and age in calendar year (CY). Note that 1CY birds also represent adult birds as juveniles follow their parents during the first southward migration.
— Antal återfynd av per region (NOR = Norge, SWE-W = sydvästra Sverige, SWE-E = nordöstra Sverige, FIN-W = västra Finland och FIN-E = östra Finland) och ålder i kalenderår. Notera att 1K-fåglar även representerar adulta fåglar då årsungarna följer sina föräldrar under den första sydflytten.

Age (CY)	NOR	SWE-W	SWE-E	FIN-W	FIN-E	Total
1	323	820	188	349	186	1,866
2	339	1,161	253	558	209	2,520
3	450	1,232	247	553	194	2,676
4	435	933	182	387	113	2,050
5	349	750	139	294	86	1,618
6	241	597	118	220	45	1,221
7	208	456	110	173	49	996
8	146	349	75	115	43	728
9	125	236	58	93	37	549
10	92	178	30	80	31	411

Age (CY)	NOR	SWE-W	SWE-E	FIN-W	FIN-E	Total
11	63	139	19	45	25	291
12	35	89	2	36	20	182
13	22	54	5	19	13	113
14	18	24	4	18	6	70
15	14	20	1	17	5	57
16	2	11	0	8	2	23
17	0	2	0	3	0	5
18	0	0	0	2	0	2
Total	2,862	7,051	1,431	2,970	1,064	15,378

BirdLife Sverige

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