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From northern Europe to Ethiopia: long-distance migration of Common Cranes (*Grus grus*)

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The majority of Common Cranes (*Grus grus*) breeding in northern Europe are short- to medium-distance migrants that overwinter in southern Europe, northern Africa, and the Middle East. However, some individuals migrate longer distances to as far as Ethiopia. Using data from 18 satellite-tracked juvenile Common Cranes, we assessed (1) the length and landscape composition of the migratory routes used and (2) the behaviour of neighbouring Finnish and Estonian (500 km apart in the north-south direction) sub-populations. Our results show that Common Cranes mainly use the East European flyway to reach the wintering grounds in Ethiopia, yet some individual cranes may alternatively use the Baltic-Hungarian migration route. Neither duration nor the number of stopovers used influenced the flight distances of the cranes. Further, 7–19 days of refuelling enabled the cranes to cover long flight distances, from 2,420 to 5,110 km in 6–15 days, without the need for settling down at potential stopovers on the route. Contrary to our expectations, the main refuelling sites of the Finnish breeding population were further south (in southern Ukraine) than those of the Estonian population (in Belarus). Despite the longer flight distances, Finnish cranes used three main migration stages, while cranes breeding at more southern sites generally used mainly four stages. Our findings demonstrate that large-sized social migrants such as the Common Crane may have spatially segregated, flexible migration patterns that involve only a few carefully selected stopovers during long-distance migration.

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1. Introduction

Many bird species that breed in the northern latitudes migrate between their breeding and southern wintering grounds in response to seasonal resource fluctuations and weather conditions. The timing and spatial use of different habitats during migration are crucial for survival and reproduction (Alerstam *et al*. 2003, Alerstam 2011, Bauer *et al*. 2011). Bird migration begins with active fuel deposition for the first migration flight (Alerstam & Lindström 1990, Lindström 2003). Active fuel deposition in the breeding area before the first migratory flight can result in large energy reserves, reducing the need for longer stopovers later during migration (Nilsson *et al*. 2013). A stopover area's location depends on the availability of landscape features that enable effective fuel deposition and safe roosting (Albanese & Davis 2015, Leito *et al.* 2015, Väli & Sellis 2016). Migration itself typically includes several stopover-flight periods, and the duration of the stopovers determines the total migration time (Alerstam *et al.* 2003, Nilsson *et al.* 2013, Kölzsch *et al.* 2016).

The Common Crane (*Grus grus*) is a symbol of wetland conservation. Over the past three decades, the species has undergone a rapid population recovery in Europe (Leito *et al.* 2006, Alonso *et al*. 2016, Prange 2016). The species is easy to observe visually and is relatively well studied (Keskpaik *et al.* 1986, Prange 1995, Prange *et al*. 1999, Nowald *et al.* 2013, Saurola *et al*. 2013, Prange 2016). However, there are still gaps in our knowledge about the migration strategies and patterns along some migration routes, especially for populations breeding in north-eastern Europe.

In the northern part of its breeding range, the Common Crane is a medium- to long-distance migrant (Berthold 2001, Saurola *et al*. 2013, Leito *et al*. 2015), whereas in the southern regions of its distribution, they are short-distance migrants or residents (Alonso *et al*. 2008, Prowse 2013). The autumn migration of cranes starts with the gathering of families and non-breeding floaters at certain staging areas, where fuel deposition begins in preparation for the first migratory flight. If suitable staging sites are lacking in the vicinity of the natal territory, the crane families search nearby for available foraging areas, where they join other small foraging flocks. The cranes commence migration when energy reserves are sufficient and weather conditions favourable. After the first flight, they settle at a second suitable staging area for refuelling. This stage is repeated until the cranes arrive at their wintering grounds (Cramp & Simmons 1980, Leito *et al*. 2015, Prange 2016).

In European populations of the Common Crane, four main migration routes have been identified: the West European, Baltic-Hungarian, East European, and Volga-Caucasian routes (Leito *et al*. 2015, Redchuk *et al*. 2015, Prange 2016). The migration along the first two routes is well documented (Leito *et al.* 2015, Végvári 2015, Alonso *et al.* 2016, Salvi 2016, Žydelis *et al.* 2016). However, less information is available for the latter two routes (Gorlov 1998, Pekarsky *et al.* 2015, Redchuk *et al*. 2015, Grinchenko *et al*. 2018). Each migration route includes a number of potential staging areas, usually located 100–800 km apart. The distance between minor staging areas (gatherings of up to 1,000 individual cranes) is shorter than that between main staging sites (used by ≥ 10,000 cranes; Prange 2016). This network of staging areas allows for finding suitable refuelling sites during migration to reach even the farthest wintering grounds in Ethiopia.

We used satellite telemetry data from platform transmitter terminal (PTT) units deployed in Finland and Estonia to investigate the migration pattern of the Common Crane in relation to the primary landscape features along the migratory routes leading to the southernmost wintering grounds in Ethiopia. Our main objectives were to describe the routes and key migration characteristics (i.e. the number of migration stages, the timing and speed of migration, daily flight distances, and the stopover durations) for two nearby sub-populations of the Common Crane.

2. Material and methods

2.1. Satellite tracking

Marking one juvenile crane per family, 17 juvenile cranes in Finland (2006–2013) and 28 juvenile cranes in Estonia (2009–2017) were individually marked with a unique combination of colour-bands on their tibiae and a regular metal-ring on the tarsus, then tagged with PTT units. For this analysis, we selected 18 young cranes, 16 of which migrated along the traditional East European route to wintering grounds in Ethiopia. The remaining two juveniles, one from Finland and one from Estonia, switched from the Baltic-Hungarian to the East European flyway during their second migration stage. For the 18 juveniles selected, 7 were fitted with PTT units in eastern Finland from 2009–2012, and 11 in eastern Estonia from 2009–2017. Common Cranes were captured, ringed, and fitted with PTT units in Finland with the permission of the North Karelian Centre for Economic Development, Transport and the Environment, and in Estonia with the permission of the Estonian Environmental Board.

The PTT units were mounted on the juveniles prior to fledging, with the distance between the tagging sites in Finland and Estonia being approximately 500 km. The PTT units deployed in Finland were manufactured by North Star Science and Technology, LLC (King George, VA, USA), whereas those deployed in Estonia were from Microwave Telemetry, Inc. (Columbia, MD, USA) and Ornitela, UAB (Vilnius, Lithuania). The weights of the PTTs ranged from 22 to 105 g, which is up to 3.3% of the body mass of a bird. According to basic bio-telemetry studies (Keskpaik & Leht 1983), the weight of a radio transmitter should be less than 5% of the bird's body mass to minimize negative effects such as an elevated heart rate during flight. The Finnish and Estonian breeding sub-populations should be considered a part of the same population of Common Cranes, with the main differing characteristic being their breeding latitude. For convenience, we will refer to the two sub-populations as "Finnish" and "Estonian" populations comparisons, but it should be remembered that breeding latitude is the primary difference between them.

The accuracy of the PTT geographical locations using Global Positioning System (GPS) units was ±18 m. In the case of the traditional PTT units mounted on 6 Finnish cranes in 2009–2011, rigorous field-testing prior to deploying the units found the median location error of the Doppler fixes varied from 182 to 3,822 m. This was fairly small relative to the spatial scale of the migration, and we can assume that location error related to Doppler fixes did not influence the results of this study to any significant degree.

To analyse the autumn migration pattern, we used only the data between the time when the crane families joined the migratory flocks and their arrival on the wintering grounds (or until the end of data transmission). For the Finnish sub-population, a total of 1,505 Doppler locations (144–414 locations per individual) for six birds and 164 GPS locations for one bird were analysed. For the 11 Estonian juveniles, a total of 876 GPS locations (63–127 locations per individual) were included in the analyses. The migration status, i.e. in flight "1" or staging "0", was annotated for each location.

2.2. Characterising the migration patterns

To characterize the migration routes, positional data from the PTT units ($N = 2545$ locations) was visualized using Google Earth (US Dept. of State Geographer, 2015 AutoNavi, Data SIO, NOAA, US Navy, NGA, GEBCO, Image Landsat). Accordingly, the migration trajectories (lines between geographical locations) and landscape features along the route were annotated as landscape that was either suitable (continental mainland) or unsuitable (seas, mountains, and deserts) for staging.

The main flyway characteristics measured at the population level were (1) the length of the flyway for the Finnish and Estonian populations, (2) the locations of the stopover sites, (3) the locations and widths of the ecological barriers (unsuitable landscapes), and (4) the locations of the wintering grounds. The length of the migration routes and distances between potential stopovers were measured by straight lines between the stopovers, beginning from the breeding areas until arrival at Lake Tana in Ethiopia. The migration pattern of the Common Cranes was described at the individual and population levels by (1) the number of migration stages along the route, (2) the timing and duration of the migratory stages, (3) the stopover duration as a function of migration progression, (4) the flight distance between stopover sites, and (5) the migration speed.

A "migration stage" consisted of a staging period for fuelling at a stopover site followed by a migratory flight to the next stopover area or the wintering grounds. The duration of the first stopover was calculated from the date when the crane

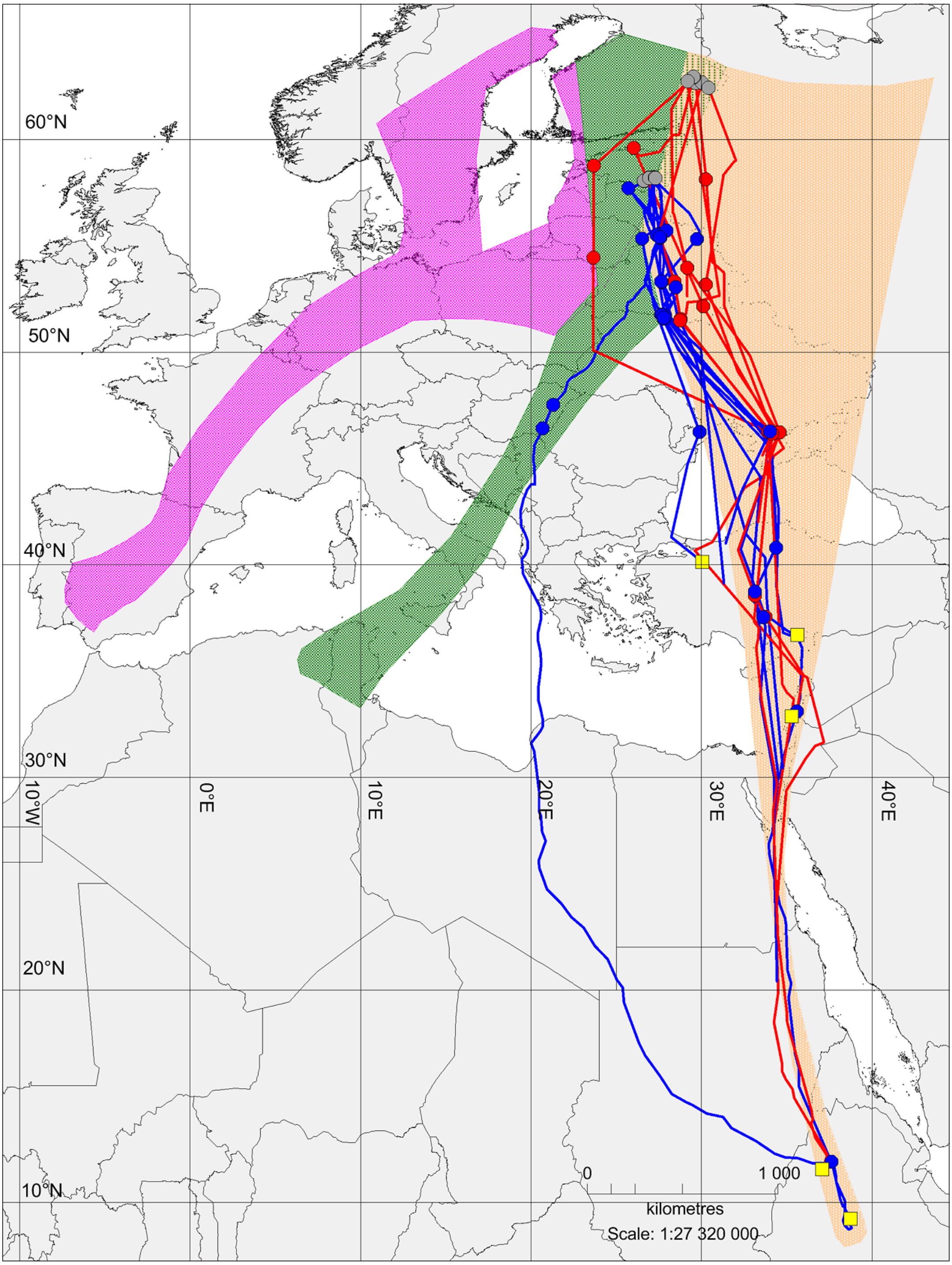

Fig. 1. Migratory routes of the Common Cranes studied along the East European flyway. Grey circles denote the tagging sites in Finland and Estonia, and yellow squares indicate the overwintering areas. Red and blue lines and circles indicate the flight tracks and staging sites of the Finnish and Estonian cranes, respectively. The West European, Baltic-Hungarian and East European flyways are shown with different colours according to Leito *et al.* (2015).

family joined other foraging cranes to the date of departure. For individuals that perished during the migration, the migration distance was calculated using the location of the first potential wintering grounds at Lake Tana (Ethiopia) only if the location data showed that they had skipped the last potential stopover area in Israel. A "stopover area for refuelling" was defined as a location on the migration route where the crane stayed for a minimum of 4 days. Feeding at stopovers was determined using Google Earth images, when daytime fixes from cultivated fields located up to 30 km away from a wetland night roost (Leito *et al.* 2015) were accompanied with return flights back to the night roosts.

The short 1- and 2-day stops ($N = 5$ for 3 individuals; no 3-day stops were recorded) during migration were included as a part of the migration flight duration, as birds cannot usually find food sources for efficient fuelling immediately after arrival at a new stopover site (Hedenström 2008). Those short stopovers were made in Belarus, Ukraine, or Turkey. On one occasion, the probable reason for the 1-day stop was a headwind over the Black Sea; the reasons for the other cases remain unknown. Total migration duration and overall migration speed were calculated according to formulas described by Alerstam (2003).

2.3. Statistical analyses

Depending on the data distribution, we used a *t*-test or Mann-Whitney *U*-test to determine potential differences in the behavioural characteristics of the Finnish and Estonian crane populations. We used two-way analyses of variance (ANOVA) and Tukey post-hoc tests to examine the links between the different factors. The Spearman's rank correlation was used to find the correlation between overall migration speed and the progression of migration. The 95% confidence intervals were calculated throughout to describe the variation in the mean values. The statistical analyses were conducted using the software R (Version 3.0.1; R Core Team 2013).

3. Results

Of the 18 satellite-tracked cranes, seven (3 from Finland and 4 from Estonia) reached wintering grounds in either Turkey, Israel, or Ethiopia. The cranes from Finland wintered in the Hula Valley in Israel (1 ind.) or in the Lake Tana region in Ethiopia (2 ind.), while those from Estonia wintered in the Kayabelen region or at the Yumurtalik lagoon in Turkey (2 ind.) or in the Sululta region of Ethiopia (2 ind.; Fig. 1). The other 11 birds either perished whilst migrating, or their PTT units had technical problems.

3.1. Main features of the migratory routes

The cranes that reached the wintering grounds farthest away in Ethiopia typically flew along the East European route, but two individuals partly followed the Baltic-Hungarian route (Fig. 1). Depending on where the birds wintered, the length of the East European migration route ranged from 3,400–5,870 km for the Finnish crane sub-population and from 2,040–5,350 km for the Estonian sub-population. The total distance flown varied from 3,520–6,527 km and 2,177–5,862 km for the Finnish and Estonian cranes, respectively. For both populations, the differences between the measured flyway length and the total distance flown to the northernmost wintering sites in Turkey or Israel varied from 3.5% to 6.7% ($N = 3$ ind.), while those to Ethiopia varied from 8.2% to 10.6% ($N = 3$). For the Estonian cranes using the Baltic-Hungarian flyway, the route length increases up to 5,860 km and the total distance flown up to 6,876 km, resulting in the flyway length increasing by 10.6% and the total distance flown by 17.3% compared to the East European flyway.

The extent of the ecological barriers along the East European route is approximately 2,800 km (47% to 52% of the total route). The first ecological barrier (for the Finnish cranes) is the up to 100 km-wide Gulf of Finland (if the route over Estonia is used), and the second barrier is the 300 km-wide Black Sea. The third and widest ecological barrier is a 2,400 km-wide belt that includes the Taurus Mountains, Mediterranean Sea, Negev Desert, Red Sea, and Sahara Desert. Along the Baltic-Hungarian route, the extent of the ecological barri-

Table 1. Location of Common Crane stopover sites (4-day minimum) along the East European flyway. Staging areas are ordered according to their coordinates from north to south. Numbers on the first row of each country are the totals. The stopover sites used along the Baltic-Hungarian flyway are marked by an asterisk. Parentheses indicate wintering at a stopover.

Country and name of stopover area		Staging site coordinates	Cranes from Finland (*N* = 7)		Cranes from Estonia (*N* = 11)	
			No. of staging cases	Total time (days)	No. of staging cases	Total time (days)
Estonia			1	5	–	–
	Lobi	59°37 N, 25°59 E	1	5	–	–
Russia			1	5	–	–
	Soltsy	58°05 N, 30°16 E	1	5	–	–
Latvia			–	–	2	38
	Seda	57°42 N, 25°43 E	–	–	2	38
Lithuania			1	9	–	–
	Žuvintas*	54°28 N, 23°37 E	1	9	–	–
Belarus			5	60	18	247
	Vidzy	55°20 N, 26°30 E	–	–	1	13
	Yelnya	55°33 N, 27°48 E	–	–	4	67
	Kurjanovo	55°17 N, 27°39 E	–	–	1	17
	Sloboda	55°18 N, 30°01 E	–	–	1	8
	Kukarava	53°53 N, 29°11 E	1	12	–	–
	Krõvaja Grada	53°20 N, 27°35 E	–	–	3	42
	Talka	53°22 N, 28°15 E	1	11	–	–
	Tatarka	53°13 N, 28°48 E	–	–	1	7
	Kisteni	53°08 N, 30°17 E	1	9	–	–
	Pervomaisk	52°05 N, 30°03 E	1	15	–	–
	Karma	51°40 N, 27°41 E	–	–	7	93
	Grishi	51°34 N, 28°40 E	1	13	–	–
Hungary			–	–	2	51
	Hortobagy*	47°32 N, 21°16 E	–	–	1	35
	Feher-to*	46°28 N, 20°37 E	–	–	1	16
Ukraine			6	98	2	24
	Uspenivka	46°10 N, 29°53 E	–	–	1	13
	Askania-Nova	46°28 N, 33°51 E	2	58	–	–
	Sivash	46°05 N, 34°05 E	4	40	1	11
Turkey			–	–	2	18
	Lake Tuz	38°50 N, 33°11 E	–	–	1	12
	Akgol	37°31 N, 33°43 E	–	–	1	6
Israel			(1)	–	1	17
	Agamon Hula	33° 6 N, 35°36 E	(1)	–	1	17
Ethiopia			(2)	–	2	34
	Lake Tana	11°55 N, 37°37 E	(2)	–	2	34

Table 2. Summary of the autumn migration of Common Cranes from Finland (*N* = 7) and Estonia (*N* = 11) on the East European flyway. Parentheses indicate individuals that partly followed the Baltic-Hungarian flyway. Number after the name of the bird refers to the transmitter tagging year. Abbreviations: FIN – Finland, EST – Estonia, * – individuals that completed migration.

Country code	Individual	Total migration duration (D+E, days)	Total flight period (days)	Total refuelling time (days)	No. of stopovers for refuelling	Total distance flown (km)	Mean daily distance covered over total flight period (G/D, km/24 h)	Overall migration speed (G/C, km/24 h)
A	B	C	D	E	F	G	H	I
FIN	Upetto-09	44	4	40	3	1,909	477.3	43.4
FIN	Einari-10	45	3	42	3	1,763	587.7	39.2
FIN	(Goljatti-10)	47	9	38	3	4,487	498.6	95.5
FIN	Sipriina-10	93	7	86	3	2,479	354.1	26.7
FIN	Outo-11*	66	13	53	3	6,178	475.2	93.6
FIN	Ruvas-11*	58	17	41	3	6,527	383.9	112.5
FIN	Mansikka-12*	83	10	73	3	3,520	352.0	42.4
EST	Tom-09	63	12	51	4	4,430	369.2	70.3
EST	Rasina-10*	65	9	56	3	2,177	241.9	33.5
EST	Ahja2-11*	80	11	69	4	2,747	249.7	34.3
EST	Lootvina-11	73	9	64	2	4,027	447.4	55.2
EST	Ahja3-12	82	4	78	3	1,388	347.0	16.9
EST	Hauka1-12	80	12	68	4	3,672	306.0	45.9
EST	Kadaja-12	88	5	83	3	2,278	455.6	25.9
EST	Hauka2-13	57	6	51	4	2,337	389.5	41.0
EST	Ahja4-13*	83	19	64	5	5,862	308.5	70.6
EST	(Ahja5-16*)	127	21	106	4	6674	317.8	52.6
EST	Mustakurmu-17	79	10	69	2	3,620	362.0	45.8

ers is approximately 3,850 km (58% of the total route) and consists of the 100 km wide-Carpathian Mountains, the 300 km-wide Dinaric Alps, the 850 km across the Mediterranean Sea, and the 2,600 km-wide Sahara Desert.

A total of 22 stopover sites were identified along the East European route, 12 of which were in Belarus. Three additional stopovers were used along the Baltic-Hungarian route (Fig. 1, Table 1). For the Finnish cranes, the shortest distance to the first stopover site in northern Estonia or Russia was 410–500 km, whereas for the Estonian cranes, the shortest distance from southern Estonia or northern Latvia to a stopover site in northern Belarus was 280 km. The distance between the stopover sites in northern and central Belarus was 250 km, and from there to the border area between Belarus and Ukraine, 190 km. Further south, refuelling sites are available in southern Ukraine (730–780 km from Belarus), central and southern Turkey (810–960 km from Ukraine), Israel (520–670 km from Turkey), and Ethiopia (2,420 km from Israel; see Fig. 1).

The selection of stopover sites and total time spent at stopovers differed between the Finnish and Estonian populations (Table 1). The Finnish birds did not concentrate at certain stopovers until reaching southern Ukraine. Instead, they preferred to stop shortly the first time for refuelling in central or southern Belarus, approximately 970–1,240 km from their natal area. The Askania-Nova and Sivash areas proved to be the most favoured stopover sites along the East European route for the cranes breeding in Finland (Table 1). The Belarusian stopovers used by the foraging Estonian cranes did not overlap with those of the Finnish cranes. In southern Ukraine, the birds from Estonia made only an overnight stop or stayed for a longer period only to avoid headwinds when flying across the Black Sea. Long stopovers were also infrequent in Turkey for both populations (Table 1). Only two cranes followed the coastline

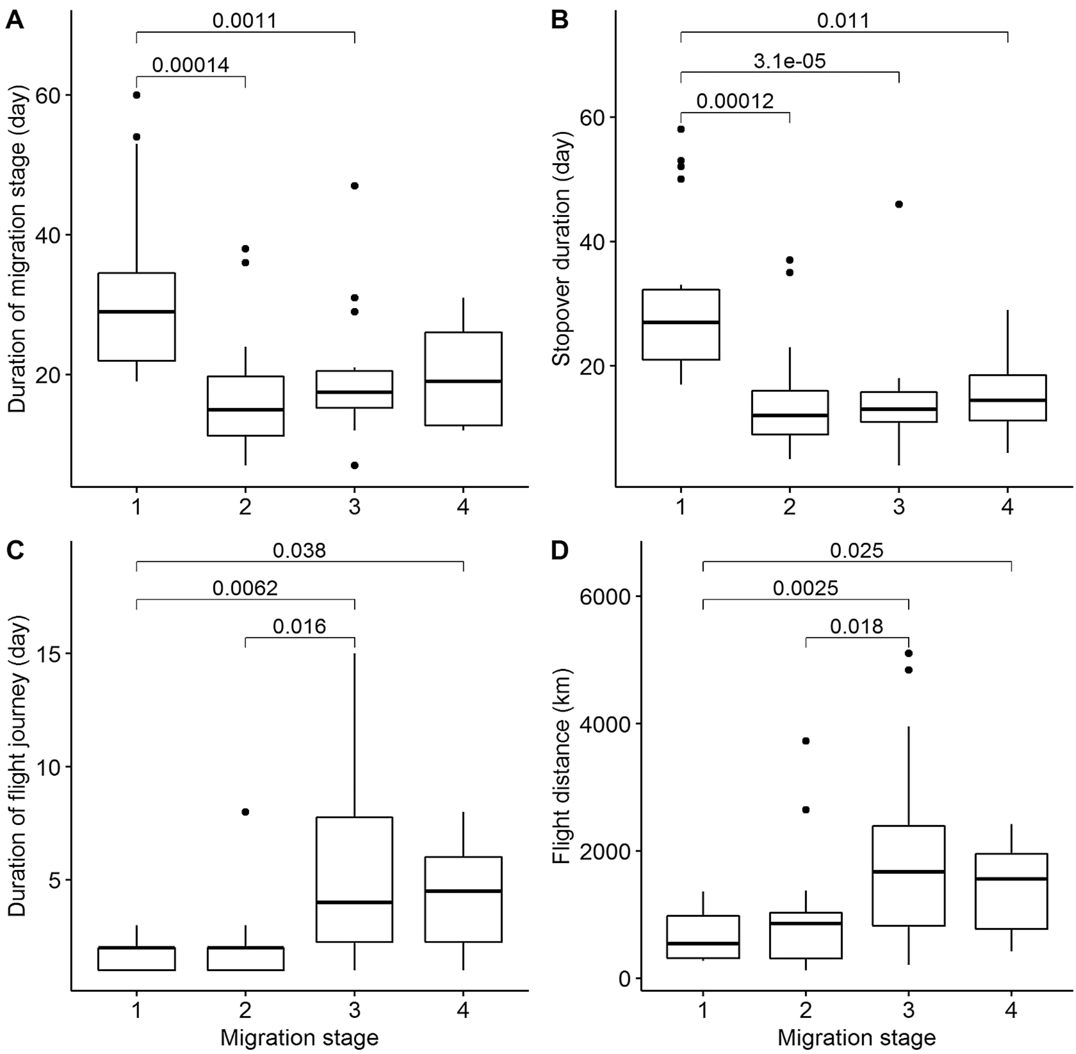

Fig. 2. The effect of migration stage on the duration of the (A) migration stage, (B), stopover period, (C) flight duration, and (D) flight distance. Bold horizontal lines indicate the medians, boxes shows the quartiles, and whiskers (vertical lines) indicate the extreme data points not exceeding 1.5× the interquartile range from the quartile boundaries. The adjusted significance levels of the mean group differences (*U*-test) are indicated above the boxes for those that are significant.

of Turkey and the Middle East to reach a stopover or wintering site in Israel. The maximum potential number of stopovers available *en route* was seven for the Finnish cranes and six for the Estonian birds. None of the cranes used all the stopover sites along the East European route. The Finnish individuals utilized two stopovers, corresponding to 29% of those available, while the Estonian cranes used from one to four stopovers, corresponding to from 17% to 67% of those available.

Both populations avoided the last potential stopover in Israel (used by only one individual) prior to the 2,420 km-long flight across the vast desert areas to Ethiopia. The majority of cranes (N = 7) preferred to set off to Ethiopia directly from more northerly stopover sites in Turkey, Ukraine, or even Belarus, facing distances of 3,030–5,060 km. After successfully crossing the Sahara Desert, all cranes from both populations made a stopover in Lake Tana in Ethiopia. Traversing the longest distances between refuelling sites (2,420–5,110 km from Belarus/Hungary/Ukraine/Israel to Ethi-

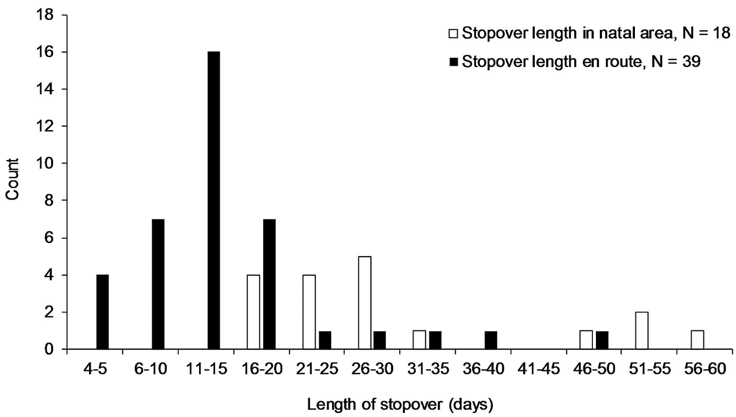

Fig. 3. Distribution of stopover lengths during the long-distance migration (N = 57).

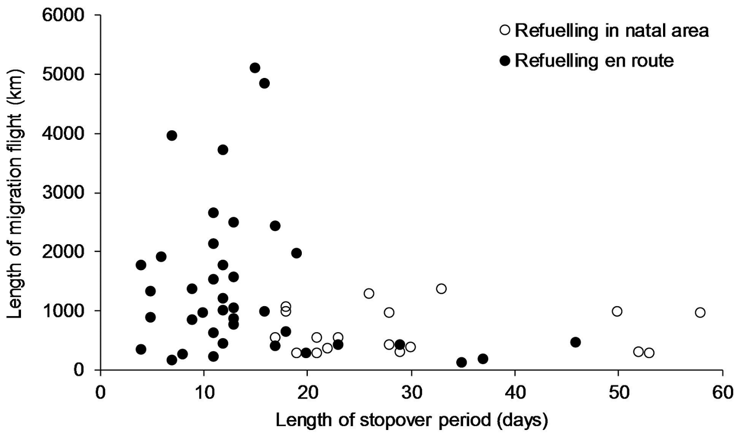

Fig. 4. Relationship between stopover length and the following flight distance.

opia) took 6–15 days, with the cranes making only overnight stops. Crossing the 1,600–2,600 km-wide desert area over Sinai peninsula and in north-east Africa took 4–11 days, lending support to the idea that only daytime flights occurred. The longest non-stop flight was by the young crane "Ahja 5" and lasted 36 h 30 min, allowing for the coverage of 1,727 km, from Serbia to Libya. During the following days, the crane continued the migration with daytime flights until reaching Lake Tana in Ethiopia.

3.2. Quantitative analysis of the migration patterns

The satellite-tracked cranes joined with migratory crane groups in Finland on 1st September ± 9 days (N = 7) and in Estonia on 26th August ± 7.2 days (N = 11). The dates did not significantly differ between the populations (t-test: t = –1.382, df = 13.995, p = 0.188). The mean departure date for the Finnish cranes was 29th September ± 6.9 days (N = 7, range 19th September to 10th October), while for the Estonian cranes, it was 26th September ± 7.5 days (N = 11, range 9th September to 14th October). Again, there was no significant difference between the populations (t-test: t = –0.678, df = 15.914, p = 0.507).

All the Finnish cranes used three migration stages, while the Estonian cranes used from two to five stages (Table 2). The East European migration route involved a minimum of two migration stages, i.e. the crane family made only one stop *en route* for energy deposition after departing from Estonia (Table 2). The first migration stage lasted significantly longer (32.2 ± 6.7 days, N = 18) than the second (16.8 ± 4.4 days, N = 18; U-test: W = 282.5, p < 0.001) and third (20.2 ± 5.8 days, N = 14; U-test: W = 213, p < 0.001) stages (Fig. 2A). This resulted in a significant difference between the first (30 ± 10.8 days, N = 7) and second (11.6 ±

3.2 days, $N = 7$) stages among the Finnish cranes (Tukey post-hoc test: $p = 0.05$), and between the first (33.6 ± 10 days, $N = 11$) and third (17.7 ± 5 days, $N = 9$) stages among the Estonian cranes (Tukey post-hoc test: $p = 0.04$).

Most stopovers lasted 11–20 days, which is 47.4% ($N = 27$) of all stopovers (Fig. 3), indicating this period is sufficient for restoring fuel reserves for a subsequent long-distance migratory flight (Fig. 4). The mean stopover duration *en route* was 12.8 ± 6.9 days ($N = 12$) for the Finnish cranes and 15.1 ± 3.2 days ($N = 27$) for the Estonian cranes, with the difference being marginally insignificant (U-test: $W = 102.5$, $p = 0.07$). The duration of the first stopover (30.3 ± 6.7 days, $N = 18$) was significantly longer for the first migration stage compared to those of the second (14.4 ± 4.5 days, $N = 18$; U-test: $W = 284$, $p < 0.001$), third (14.3 ± 5 days, $N = 16$; U-test: $W = 272$, $p < 0.001$), and fourth (15.7 ± 8.4 days, $N = 6$; U-test: $W = 92.5$, $p = 0.01$) stages (Fig. 2B). The mean first stopover periods close to the natal sites (Finland, 28 ± 10.4 days, $N = 7$; Estonia, 31.8 ± 10.1 days, $N = 11$) did not differ between the two populations (U-test: $W = 32.5$, $p = 0.617$). The second stopover of the Finnish cranes in Belarus (9.1 ± 2.9 days, $N = 7$) was significantly shorter (t-test: $t = –2.59$, $df = 12.78$, $p = 0.02$) than that of the Estonian cranes (17.7 ± 6.9 days, $N = 11$).

The durations of the first (1.8 ± 0.4 days, $N = 18$) and second (2.3 ± 1.1 days, $N = 18$) flights did not differ. A statistically significant difference was detected between the durations of the first and third flights (5.4 ± 2.6 days, $N = 14$, U-test: $W = 55.5$, $p = 0.006$), the first and fourth flights (4.3 ± 2.8 days, $N = 6$, U-test: $W = 24$, $p = 0.038$), and the second and third flights (U-test: $W = 64$, $p = 0.016$; Fig. 2C). In addition, there were similar relationships between the mean flight distance and migration stages (Fig. 2D). The Finnish cranes covered significantly (U-test: $W = 64$, $p = 0.02$) longer distances during the first flight (905.2 ± 293.9 km, $N = 7$) than the cranes from the Estonian population (504.1 ± 222.4 km, $N = 11$).

The overall migration speeds of the Finnish and Estonian cranes were 64.7 ± 31.8 km/day ($N = 7$) and 44.7 ± 11.3 km/day ($N = 11$), respectively, and did not significantly differ between the populations (t-test: $t = 1.430$, $df = 7.879$, $p = 0.19$; Table 2). The overall migration speed correlated positively with the progression of migration (Spearman's rank correlation test: $S = 14{,}030$, $p < 0.001$, $rho = 0.52$), i.e. the migration speed of the cranes increased as they moved south. The mean daily flight distances significantly differed (U-test: $W = 3404$, $p < 0.001$) between the Finnish and Estonian populations (563.7 ± 72.4 km/day, $N = 47$ and 364.5 ± 45.9 km/day, $N = 100$, respectively). The maximum daily flight distances (above mean values) for the Finnish and Estonian cranes varied from 652–1,130 km and 412–977 km, respectively. The total time spent at stopovers did not differ between the populations, 85.2 ± 7.6% ($N = 7$) among the Finnish cranes and 86.6 ± 3.5% ($N = 11$) among the Estonian cranes (Table 2). Having set off from the natal area and following the traditional East European route, it took 32–37 days for the Finnish cranes ($N = 3$ ind.) to reach wintering grounds and 55–65 days for the Estonian cranes ($N = 3$ ind.) to arrive. The arrival of the Finnish cranes to the wintering grounds in Israel or Ethiopia (a difference in distance of 2,420 km) and the Estonian cranes in Turkey or Ethiopia (a difference in distance of 2,830 km) took nearly the same time.

4. Discussion

Herein, we show that the long-distance autumn migration strategy differed between two neighbouring sub-populations of the Common Crane. These differences included the density and location of stopovers, daily flight distances, and the total migration duration. However, other aspects of the migration such as the date when the juveniles joined the migratory flocks prior to the first migration stage, the date of departure, the length of time spent at stopovers, and the overall migration speed did not differ between the sub-populations. In addition, our data suggests that the speed of migration was positively associated with the phase of migration due to the scarcity of potential stopovers outside Europe. In addition to the East European flyway, cranes can also reach wintering sites in Ethiopia via the Baltic-Hungarian flyway, although this involves a 1,010 km detour and significantly wider ecological barriers. Both migration routes are complex due to the locations of the main stopover sites in the European part of the routes, as well as to the extent of the ecological barriers south of Ukraine and Hungary. Our data indicates some flexibility in the Common Crane regarding route selection, which could be due to either genetically programmed orientation (Liedvogel *et al*. 2011, Väli *et al.* 2018) or, more likely, social transmission (Pulido 2007, Mueller *et al*. 2013).

Our satellite-tracked cranes either used (1) one refuelling area in Belarus or southern Ukraine or (2) used two to three stopovers in Belarus or Hungary prior to setting off on the subsequent demanding long-distance flight. The different refuelling areas used by the two sub-populations may be explained by the Finnish cranes accumulating more extensive energy reserves in the natal area. A similar observation was found for the West European migration route, where cranes from northern Sweden had an average 10-day shorter stopover in northern Germany than the cranes from southern Sweden (Nowald 2010).

The second strategy involves short flight distances between the stopovers associated with smaller fuel reserves (Hedenström 2008). Refuelling at *en route* stopovers lasted 13–15 days on average, 50% less than the mean preparation time for the first flight from the natal area. Our results on the span of the mean refuelling time agree with previous findings for the West European route (Alonso *et al*. 2008, Nowald 2010) and Volga-Caucasian flyway (Pekarsky 2015). Neither the geographical location of the birds nor the location of the ecological barriers had an effect on the duration of refuelling at stopovers.

The satellite-tracked cranes frequently covered 1.2- to 2.1-fold longer flight distances than the shortest available (2,420 km between Israel and Ethiopia), which supports the idea that the cranes selected particular weather conditions for migratory flights. The selection of days with weather conditions supporting flight is a well-known phenomenon in birds (Alerstam 1978, 1979, Alonso *et al.* 1990), although the selection of the time window for departure can differ among species (cf. Leito 1996). The effective use of large-scale anticyclones with a moderate and stable tailwind in combination with thermals (Richardson 1978, 1990) facilitates economical flight (Alerstam 1979, Hedenström 1993, Liechti *et al.* 1994). During long-distance migrations, cranes need to change their flight mode from flapping flight in vee-formation flocks to soaring and gliding flight in response to the landscape composition and time of day (Pennycuick *et al*. 1979). Both flight modes help to reduce the amount of energy required for flight and increase migratory range (Lissaman & Shollenberger 1970, Weimerskirch *et al*. 2001, Hedenström 2003). Increased body mass after fuel deposition can potentially increase cross-country performance for soaring birds by allowing faster gliding speeds under strong thermal conditions (Alerstam & Hedenström 1998). Our data suggests that the autumn migration of Common Cranes has elements of both a time and energy minimization strategy (Alerstam & Hedenström 1998).

The overall migration speed of the Finnish cranes was 1.4-fold faster than that of the Estonian cranes, mainly due to fewer stopovers, longer flight distances between stopovers, and 1.3-fold longer daily flights. Interestingly, the shortest migration time of 32 days covering 6,178 km on the East European migration route was only four days longer than the longest migration (28 days covering 1,800 km) from northern Germany to northern Spain by cranes using the West European route (Alonso *et al*. 2008). Overall migration speed varied highly between cranes within the same population (Finnish: 26.7–112.5 km/day; Estonian: 16.9–70.6 km/day), which might be explained by different weather conditions along the route between migration years.

Newton (2010) highlighted the time available for migration as an important factor regulating migration speed between different populations. The higher mean daily migration speed of the Finnish population suggests that, in general, compared with populations in southern latitudes, it was more selective with respect to migration conditions to facilitate completing their longer migration on time. The seasonal variations in migration speed may indicate that external weather factors play an important role in determining migration speed in species that rely on winds and thermals for their migratory flights.

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Pohjois-Euroopasta Etiopiaan: kurjen (*Grus grus*) pitkän matkan muuton kulku

Valtaosa Pohjois-Euroopassa pesivistä kurjista (*Grus grus*) kuuluu lyhyen tai keskipitkän matkan muuttajiin, jotka talvehtivat Etelä-Euroopassa, Pohjois-Afrikassa ja Lähi-Idässä. Jotkut kurjet ovat kuitenkin kaukomuuttajia, talvehtien Etiopiassa. Selvitimme 18 satelliittilähettimillä seuratun nuoren kurjen paikannustietojen avulla (1) kurjen syysmuuttoreittien pituutta ja maiseman rakennetta muuttoreitillä ja (2) vertailimme 500 km pohjoisempana olevaa Suomen osapopulaatiota Viron osapopulaatioon.

Tulostemme mukaan Etiopiassa talvehtivat kurjet käyttävät pääosin Itä-Euroopan kautta kulkevaa muuttoreittiä. Jotkut yksittäiset kurjet voivat kuitenkin vaihtoehtoisesti käyttää Baltiasta Unkariin suuntautuvaa reittiä. Muutonaikaisten etappien välisten levähdys- ja tankkaustaukojen määrä ja kesto eivät olleet yhteydessä muuttoetappien pituuteen. Pituudeltaan 7–19 vuorokautta kestävät levähdystauot mahdollistivat riittävien energiavarastojen tankkaamisen, joiden avulla muuttavat kurjet pystyivät lentämään pitkiä, 3 950–5 360 km muuttoetappeja ilman tarvetta pysähtyä etappien varrella oleville potentiaalisille tankkaus- ja levähdyspaikoille.

Toisin kuin oletimme, suomalaiset kurjet pysähtyivät tankkaamaan muutollaan etelämpänä (Etelä-Ukrainassa) kuin virolaiset (Valko-Venäjällä). Pidemmästä muuttomatkasta huolimatta Suomen osapopulaation kurjet jakoivat syysmuuttonsa kolmeen muuttovaiheeseen, kun taas Viron osapopulaation kurjet jakoivat muuttonsa neljään muuttovaiheeseen. Tuloksemme osoittavat, että suurikokoisilla ja sosiaalisilla muuttolinnuilla, kuten kurjella, voi olla alueellisesti erilaistunut ja joustava muuttokäyttäytyminen, jossa käytetään vain harvoja, tarkkaan valittuja levähdys- ja tankkauspaikkoja pitkän muuttomatkan aikana.

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