Eesti Maaülikool
Estonian University of Life Sciences

BREEDING AND MIGRATION ECOLOGY OF COMMON CRANE (*GRUS GRUS*)

SOOKURE (*GRUS GRUS*) PESITSUS- JA RÄNDEÖKOLOOGIA

IVAR OJASTE

A Thesis
for applying for the degree of Doctor of Philosophy in Applied Biology

Väitekiri
filosoofiadoktori kraadi taotlemiseks rakendusbioloogia erialal

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The thesis is dedicated to the memory of my supervisor
Dr. Aivar Leito

Tartu 2019

Institute of Agricultural and Environmental Sciences
Estonian University of Life Sciences

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The present thesis is based on the following research papers, which are referred to by their Roman numerals (I-V in the text).

I Leito, A., Truu, J., Leivits, A., **Ojaste, I.** 2003. Changes in distribution and numbers of the breeding population of the Common Crane Grus grus in Estonia. Ornis Fennica 80: 159–171.

II Leito, A., **Ojaste, I.**, Truu, J., Palo, A. 2005. Nest site selection of the Eurasian Crane Grus grus in Estonia: an analysis of nest record cards. Ornis Fennica 82: 44–54.

III Leito, A., Truu, J., Õunsaar, M., Sepp, K., Kaasik, A., **Ojaste, I.**, Mägi, E. 2008. The impact of agriculture on autumn staging Eurasian Cranes (Grus grus) in Estonia. Agricultural and Food Science 17: 53–62.

IV Leito, A., Bunce, R.G.H., Külvik, M., **Ojaste, I.**, Raet, J., Villoslada, M., Leivits, M., Kull, A., Kuusemets, V., Kull, T., Metzger, M.J., Sepp, K. 2015. The potential impacts of changes in ecological networks, land use and climate on the Eurasian crane population in Estonia. Landscape Ecology 30: 887–904.

V **Ojaste, I.**, Leito, A.†, Suorsa, P., Hedenström, A., Sepp, K., Leivits, M., Truu, J., Sellis, U., Väli, Ü. 2020. From northern Europe to Ethiopia: long-distance migration pattern of Common Cranes (Grus grus). Ornis Fennica xxx–xxx [Accepted].

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Author's contributions to the articles:

	Article				
	I	II	III	IV	V
Idea and study design					*
Data collection	*	*	*	*	*
Data analysis		*		*	*
Manuscript preparation	*	*	*	*	*

ABBREVIATIONS

CLC – Corine land cover

EnS – environmental stratum/strata

EnZ – environmental zone/zones

NAO – North-Atlantic Oscillation

UTM – Universal Transverse Mercator

1. INTRODUCTION

Understanding the basic ecology of a bird species starts from its distribution, at least from nearest history until nowadays, does the distribution broaden or tighten, what is the population trend, what is the habitat requirement and availability of potential nesting habitat for the species, clutch and brood size, sex and survival rate at different ages. It is important to understand the features of high-quality nesting sites while the production of the offspring that eventually recruited into the breeding population is related to territory quality (Sergio *et al*. 2009). And finally, is the species sedentary, or a short-, medium or long-distance migrant. If the species is migratory, what is the migration strategy, where are the main stopover sites and wintering grounds and what factors limit their quality. For example, long-lived species breeding in northern regions are directly dependent on the quality (availability of food) of stopovers as body reserves are being depleted for egg formation before arrival at the breeding ground (ref. Sénéchal *et al.* 2011, Glahder *et al.* 2006). Knowledge about threats to the distribution and population trends are a basic necessity for development of species conservation measures.

The Common or Eurasian Crane (*Grus grus*) has over the last four decades been a symbol of wetlands, a target species for conservation and one of the species showing rapid population recovery in Europe (Prange 2016a). The Common Crane can be characterized as a typical long-lived species with low mortality, delayed maturity and low fecundity. The species is a solitary breeder during the reproduction period but becoming highly gregarious during migration and wintering, as well as during the immature stage.

The first recorded observations of Common Cranes were made in Estonia in 1866. Most observations made since then until end of 1970s were traditional ornithophenological observations including visual migration sights (Leito *et al.* 2006). The first overview of the migration of Common Crane based on the data provided by the ornithophenological observation network of the Estonian Naturalists' Society, was published in 1955 (Tamm 1955) and the second one in 1971 (Veroman 1971).

The Common Crane was numerous in Estonian mires and grasslands in the 18th and 19th centuries but was rare by the middle of the 20th century

(Kumari 1954, 1958). While there are no studies for Common Cranes from that period, the reasons for low population remain unknown. The first numerical total breeding population size estimate (150–200 pairs) in Estonia was made in 1970. The second estimation was 350 pairs, based on the first Estonian Bird Atlas (period 1977–1982) (Renno 1993).

A new phase in the study of the Common Crane visual migration began in 1980 under the project "Grus", headed by Dr. Jüri Keskpaik. The study focussed on migratory assemblies and was at the cutting edge of research in that particular field in the Soviet Union at the time. A complex research methodology for studying the migration of the Common Crane was developed and published in 5 methodological articles, followed by more than 20 scientific and popular scientific articles. Besides the visual study of migration, Dr. Keskpaik concentrated also on intensive study of the moult and associated migration at the end of the 1980s and during the first half of the 1990s. This work yielded significant results in the description of the complete moult cycle of the Common Crane in its natural habitat (ref. Leito *et al.* 2006, Keskpaik 2011).

Modern research of Common Crane's local breeding population and its reproduction, home range of breeding pairs and migration ecology was developed by Dr. Aivar Leito in the later 1990s. He was the first to use radio- and satellite tracking in studies of bird ecology and migration in Estonia. By intensive marking with coloured leg rings, radio- and satellite tracking and with international cooperation, Dr. Leito managed to determine three migration directions of Common Cranes breeding in Estonia and their wintering grounds, especially in Ethiopia.

This thesis presents the current state of knowledge of the ecology of Common Cranes breeding in Estonia, the result of more than 20 years co-operation between Dr. Aivar Leito and the author.

Paper **I** details the development of understanding of the distribution of the species since the 1970s and of changes in population size. The densities of crane populations in different habitats and landscape regions are discussed. Paper **II** is based on analysis of nest cards and reports the proportions of the breeding population in the seven principal habitats in Estonia. The nesting site and breeding phenology are described. Paper **III** explores the influence of changes in agricultural land use on the local numbers and distribution of autumn staging cranes in Estonia.

The objectives of paper **IV** were to examine the stability of the habitat network used by cranes in Estonia and then compare this with potential shifts in land use and climate elsewhere in Europe. Finally, paper **V** analyses in detail the long-distance migration pattern of Common Crane.

2. REVIEW OF THE LITERATURE

2.1. Population patterns of long-lived bird species

Body size is one of the main features of birds determining their life history: the larger the species (1) the longer it tends to live; (2) the later the age at which it begins breeding; (3) the longer the annual breeding cycle, and (4) the fewer the young produced at each attempt. Therefore, long-lived species are typical slow- or *K*-strategy breeders, showing a trade-off between quantity and quality of offspring (Newton 2013). There are exceptions: ostrich (long lifespan but large clutch), common swift and hummingbirds (long lifespan, small body and clutch). However, the main life-history features among birds are correlated, so that long life, low annual mortality, delayed maturity, long breeding cycles and small broods usually go together, as do short life, high annual mortality, early maturity, short breeding cycles and large broods (*r*-strategy breeders; Newton 2013).

The distribution patterns of species are related either to the spatial structure of the environment and the habitat requirements of species, or to spatial aspects of population dynamics (Hanski 1999). Availability of appropriate unoccupied nesting patches of the species gives potential for population increase during following years if reproduction and/or immigration rates exceed mortality and/or emigration. Increasing population density may result in density-dependent decrease of reproduction (Larsson & Forslund 1994, Pöysä & Pöysä 2002, Nummi & Saari 2003). Density-dependence is more frequent in long-lived species than in shorter lived species, which have greater annual population variability than long-lived bird species (Holyoak & Baillie 1996). Interactions between different types of limiting factors such as food, nest sites and predators may be important in limiting breeding density and reproductive output (Newton 1998). Considering reproduction output, there is a need to consider how different events in annual cycle interact with subsequent events at the individual and population level, for both resident and migratory species (Webster *et al.* 2002). For migratory species the quality of wintering habitat influences reproductive success thousands of kilometres away on the breeding grounds i.e. loss of high-quality winter habitat may have a negative carry-over effect on individuals during the following season (Norris *et al.* 2004, Gunnarson *et al.* 2006).

Habitat selection is a complex process having two main phases: (1) finding a region that is suitable for an animal and (2) locating a small space within appropriate habitat that may be a territory (a defended area) or home range (which is not defended; ref. Piper 2011). Three kinds of cues seem to be important for habitat selection by pre-breeders: (1) direct assessment during searching for environmental cues associated with likelihood of reproductive success, (2) public information through conspecific attraction and use of cues indicating successful reproduction and (3) imprinting upon their natal site leading to choice of a habitat in adulthood that resembles the natal one (Piper 2011). Habitat preferences may vary between populations of the same species that breed in different geographical areas (Väli *et al.* 2004) or among different landscape types within a compact region (Skuja *et al.* 2019). There may even be shifts in habitat preferences in an expanding (Bai *et al.* 2009; Treinys *et al.* 2016) or stable (Grašytė *et al.*, 2016; Rumbutis *et al.* 2017) population.

The breeding attempt is an energy demanding process when tactics for food resources use have important consequences for fitness (Jönsson 1997). The availability of endogenous and exogenous resources to breeding organisms can influence several key life-history traits such as timing of breeding, number and quality of offspring and degree of parental care, as well as reproductive investment and lifespan (ref. Sénéchal *et al.* 2011). Long-lived species, especially those breeding in northern regions, show both capital- and income-based breeding tactics (Drent & Daan 1980, Stearns 1992) for resource compensation: (1) previously stored body energy reserves and (2) energy acquired during the reproductive period (Gauthier *et al.* 2003, Nolet 2006, Gorman *et al.* 2008, Sénéchal *et al.* 2011, Drent *et al.* 2007).

The fitness of territorial species (mating success, breeding performance, survival and recruitment) is determined mainly by site quality (Newton 1989, Pärt 2001, Laaksonen *et al.* 2004, Krüger 2005, Hakkarainen *et al.* 2008). It is also known that the best individuals monopolize the best territories and relegate lower quality individuals to lower quality sites (Rodenhouse *et al.* 1997, Sergio & Newton 2003), generating covariation between individual and territory quality (Newton 1991, Marra 2000, Candolin & Voight 2001, Sergio *et al.* 2009). Sergio & Newton (2003) suggested that the mean occupancy could be used as the measure of overall habitat quality and population performance, with (1) high-occupancy territories being occupied earlier in spring, (2) the occupation rate being related positively to food availability and negatively to mortality risk and (3) mean occupancy being positively correlated with spatial variation in mean productivity.

Predictions from life history theory are that breeding animals should achieve a balance between their investment in recruitment and securing their own future survival and reproduction performance (Williams 1966). Reproductive performance itself should increase with age among long-lived species and therefore the proportion of high-quality individuals should increase through age classes (Forslund & Pärt 1995, Angelier *et al.* 2007). In response to female body mass (indicative of prospects of survival), quality of breeding season and potential fitness of the brood, during poor breeding conditions most birds should either not breed or should abandon their eggs or chicks (Weimerskirch 1992, Chastel *et al.* 1995, Erikstad *et al.* 1998). This means that recruitment rate depends on birth-year conditions, with effects on offspring development (growth rate, age of reaching sexual maturity, individual conditions etc.). The offspring of favourable years reach maturity earlier and start to breed at a younger age (Cam *et al.* 2003, Rattiste & Tartes 2005).

The population turnover rate of long-lived birds is generally slow (Lõhmus 2001, Walters *et al.* 2010, Gil-Weir *et al.* 2012), with relatively more overlap between generations and a more stable age structure, both of which tend to dampen short-term fluctuations in numbers (Newton 2013). Such species are sensitive to changes in adult mortality but are relatively insensitive to changes in reproduction and recruitment to the breeding sector (Stearns 1992, Weimerskirch 1992, Caswell 2001). Even if no recruitment occurred for a period of years, breeding numbers would decline only at the rate of the annual mortality (5-15% in most long-lived species). In such long-lived species, there also tends to be a large non-breeding sector, consisting mainly of younger birds (Village 1983, Sandvik *et al.* 2008, Muths *et al.* 2010). These birds can to some extent buffer the breeding population against decline, because after large mortality events vacant breeding sites can be rapidly taken over by young birds, which then start to breed at an earlier age than they otherwise could. Declining production of young does not necessarily lead to population decline, because it may be offset by improved survival. Neither does decline in survival, because it may be offset by improved reproduction (Newton 2013).

2.2. Migration strategies of birds

Bird migration is a response to seasonal changes in food supplies, governed by seasonality in climate. Such changes include the four seasons at the higher latitudes and wet–dry seasons in the tropics. Migratory birds fly between breeding and non-breeding areas, either on a broad front through the landscape or via clearly defined, and sometimes narrow, routes (Kirby *et al.* 2008, Newton 2008). The total geographic area used by a migratory bird species (or groups of related species or distinct populations of a single species) throughout its annual cycle from the breeding grounds to non-breeding areas, including intermediate resting and feeding places as well as the area within which the birds migrate is termed a flyway (Boere & Stroud 2006). Birds wintering in tropical areas are long-distance migrants. Among medium- and short-distance migrants the migration features vary greatly as migration routes, migratory periods and wintering grounds may differ between age and sex (Berthold 2001, Newton 2008). While most migratory bird species move for the winter to lower latitudes in the same hemisphere, some travel longer distances to the opposite hemisphere (Newton 2008). Because the seasons are reversed between the northern and southern hemispheres, with the northern winter coinciding with the southern summer, such species gain the advantage of summer conditions year-round (Newton 2013). Long-distance trans-equatorial migrants show a strong positive effect of latitude on energy accumulation rate, most probably related to primary productivity and available daily foraging time (Aharon-Rotman *et al.* 2016).

Migration timing is integrated into the annual cycle in a manner that minimizes overlap with breeding and moult, for nutritional reasons (Newton 2008). While the extrinsic factor controlling the annual cycles of birds is the seasonality of the environment, the primary intrinsic factor is apparently an endogenous rhythm within the bird (Newton 2008). This self-sustaining rhythm tends to ensure that the major processes of migration, breeding and moult occur in the correct sequence each year, and at roughly the right times (Berthold 1974, Berthold & Terrill 1991).

Migratory behaviour may be determined either genetically (young birds migrate alone and after the parents) or culturally (extended parental care as the young migrate with their parents; the offspring of non-migrating adults, do not migrate; Sutherland 1998). Migration has a genetic basis relating to (1) timing and duration of movement in the temporal/circannual program of the organism, (2) physiological adaptations for energy deposition and metabolism, (3) behavioural adaptations for responding to the variable conditions (weather, wind, currents) during the journey and (4) control of orientation and navigation (Berthold 2001, Liedvogel *et al.* 2011, Väli *et al.* 2018). Within the population, phenotypic variation in migratory behaviour and variation in experience and condition, may also be important. Migratory flocks of long-lived species (geese, storks, cranes) are guided by the oldest, most experienced individuals. In these species, the genetic component, although still present, seems to play only a minor role in determining variation in migration. This cultural transmission of migration may facilitate very rapid changes in migratory behaviour (Sutherland 1998, Pulido 2007, Mueller *et al.* 2013, Kölzsch *et al.* 2016).

Migration involves two main alternating phases: stopover for energy accumulation (concluding when energy reserves have been restored) and locomotion between stopovers along migratory route (when distance is covered, and energy is partly or completely consumed). Migration starts with energy deposition already before the bird departs on its first migration segment (Alerstam & Lindström 1990, Jenni-Eiermann & Jenni 2003, Lindström 2003, Alerstam & Bäckman 2018). Active energy deposition in the breeding area before the first migratory flight can provide large energy reserves, reducing the need for longer stopovers later during migration (Nilsson *et al.* 2013). Location of a stopover area depends on the availability of landscape features that enable effective energy deposition and safe roosting (Albanese & Davis 2015, Väli & Sellis 2016). Migration itself typically includes several stopover-flight phases. While many birds have to spend the main part of migration on accumulating energy before and after the costly flights, the total duration of the stopovers determines the total migration time (Hedenström & Alerstam 1997, Alerstam *et al.* 2003, Nilsson *et al.* 2013, Kölzsch *et al.* 2016, Alerstam & Bäckman 2018).

Among migratory birds there are two main migration strategies, time and energy minimization strategies (Alerstam & Hedenström 1998; Hedenström 1993, 2008; Hedenström & Alerstam 1997). The time minimization strategy is characterized by maximizing the speed of migration (i.e. minimizing the time of migration) which requires large energy stores while the energy consumption rate during flight is high.

The optimal strategy for a time minimizer if the energy accumulation is possible along the flight route is to soar while thermals are available and continue with powered flight until depletion of energy (Hedenström 1993). The energy minimization strategy is to cover short flight distances between stopover sites with low energy load and low energy consumption rate using thermals for soaring/gliding flight. If the energy accumulation along the flight route is not possible but there are strong thermals, for large birds using soaring flight mode, the optimal strategy for migration is to exploit the approximately 8 hours of daylight when thermals are available and not to fly at night (Hedenström 1993). During long flights when birds become lighter due to the consumption of energy stores their flight speed should decrease (Pennycuick 1978; Hedenström 2003). However, strength and frequency of thermals have the opposite effect on the flight speed. Increasing rate of climb in thermals will increase both the cross-country speed and the glide speed between thermals while the rate of energy expenditure is constant during flight. This strategy depends on a sufficiency of thermals (Hedenström 1993, 2003, Horvitz *et al.* 2014).

2.3. Ecology of family *Gruidae*

Cranes (15 species) are cosmopolitan in their distribution, occurring from the North American and Asian tundra to Southern North America and Asian, Australian and African tropics. (Archibald & Meine 1996). Of the 15 species, 11 are listed as threatened under the IUCN 2019 Red List: one Critically Endangered (Siberian Crane), three Endangered (Grey Crowned, Red Crowned, and Whooping Cranes), and seven vulnerable (Black-Crowned, Black-Necked, Blue, Hooded, Sarus, Wattled, and White-Naped Cranes); the other four are listed as Least Concern (Brolga, Demoiselle, Common, and Sandhill Cranes). North America has two species of cranes, including the rarest and the most abundant. Asia has eight species of cranes, two Endangered, three Vulnerable, and three with widespread distribution of Least Concern. Europe has one species of Least Concern. The two species of southeast Asia/Australia include one Vulnerable and one of Least Concern. All four species of cranes resident in Africa are threatened (one Endangered and three Vulnerable) (Mirande & Harris 2019).

Space and solitude are especially important requirements during the breeding season. Most cranes are associated with wetlands, especially for nesting and roosting. The degree to which cranes use and require wetlands varies widely among, and within, species. Two species, the Cuban race *nesiotes* of the Sandhill Crane and Demoiselle Crane live mainly in pine and palm savannas and in arid grassland (even in true deserts, as long as water is available), respectively (Archibald & Meine 1996, Aquilera *et al.* 2000). Other Sandhill Cranes, and the Sarus, Brolga, White-Naped, Common and Black-Necked Cranes nest and roost in wetlands but forage in surrounding uplands (Baker *et al.* 1995, Archibald & Meine 1996, Higuchi *et al.* 2004, Leito *et al.* 2006, Wu *et al.* 2009). Wattled Cranes breed in the extensive floodplains of Central Africa when water levels peak during the annual floods but remain in the wetlands for much of the year. In the montane wetlands of South Africa, Zimbabwe and Ethiopia the same species nests at the end of dry season on small wetlands bordered by grassland (Archibald & Meine 1996, McCann & Benn 2009, Motsumi *et al.* 2009). The large white cranes, the Siberian, Whooping and Red-Crowned, remain in wetlands throughout the nesting and rearing periods, as may the Hooded Crane, which nests in isolated larch (*Larix*) swamps (Archibald & Meine 1996, Jiao *et al.* 2014).

Cranes generally try to maintain a distance of at least several kilometres between themselves and areas of human activity. Thus, Sarus Cranes in India have adapted to the high human population density in the country, and commonly nest and roost in small village ponds (Archibald & Meine 1996). The recovering populations of Common Cranes in Europe and Sandhill Cranes in North America have in recent decades taken to using smaller, less isolated, and lower quality wetlands that are closer to human settlements (Archibald & Meine 1996, Budrys 1999, Lumpe & Tichackova 2018). In parts of Kazakhstan and the Ukraine, the Demoiselle Crane has been able to continue breeding in steppes that have been converted to agriculture, as long as farming operations are timed so as to minimize disturbance (Archibald & Meine 1996).

Generally, cranes first breed between the ages of four and eight years (Archibald & Meine 1996, Prange 2016a). Cranes almost invariably lay two eggs. The exceptions are the crowned cranes, which regularly lay three and sometimes four eggs, and the Wattled Crane, which usually lays only one (Littlefield 1987, Archibald & Meine 1996, Leito *et al.* 2006).

In terms of their movements, cranes can be divided into two groups: migratory and non-migratory. Non-migratory cranes move distances of varying lengths between their breeding and non-breeding areas, typical of the lower latitude species, the crowned cranes, the Blue, Wattled and Sarus Cranes, and the Brolga of Australia and New Guinea. In most cases their movements, are related with the duration and intensity of the local rainy seasons (Archibald & Meine 1996, Allan 1997). The migration routes of northern cranes are thousands of kilometres long, during which the cranes must confront ecological barriers like deserts, high mountain ranges and sea (Archibald & Meine 1996, Petrula & Rothe 2005, Leito *et al.* 2006, Prange 2016a).

2.4. Common Crane: status, ecology and migration

The Common Crane is one of the flagship bird species of Europe. The European Crane Working Group having been established in 1983 (Salvi 2013). Regular conferences have been organized since then in several countries. The former Crane Working Group of the USSR was reinstated in 2000 as the Crane Working Group of Eurasia. There have been always tight contacts between researchers and organizations. Therefore, the distribution and population trends, breeding biology, behaviour and visual migration as well as wintering have been thoroughly studied in many regions (Prange 2016a). Two methods have contributed greatly to behavioural knowledge of the Common Crane. These have been colour-banding and radio-tagging since 1988 (Alonso *et al.* 1995) and satellite telemetry since 1998 (Alon *et al.* 2003). More recently, the stable isotope technique has been used to study migratory connectivity in birds inhabiting poorly studied areas (Pekarsky 2015).

The whole population of Common Crane was about 690,000 individuals in 2013/2014 (Prange 2016b). The Western European population (Scandinavia, Central Europe, Finland, the Baltic countries, and western part of Russia and Belarus) is about 490,000. The Eastern European population (Belarus, Russia, the Ukraine, north-western Kazakhstan) is about 80,000, the Western Siberian population (east of the Ural Mountain in West Siberia, North and Central Kazakhstan about 100,000 and the Central and Far East Asian populations (East Siberia, North China) about 20,000. The Western European population, at least, is genetically largely homogeneous probably reflecting the its rapid, recent growth and range expansion (Haase *et al.* 2019).

The Common Crane was a rare breeding species in Europe in the middle of last century. The recovery of breeding population started in 1970s, continued with a rapid increase in 1990s but a much lower rate since then (Lundgren 1999, 2013, Leito *et al.* 2006, Bolt 2016, Prange 2016a, 2016b, Tichackova & Lumpe 2016). Due to population growth the breeding range has widened. In Germany, compared with 1975, it has expanded 410 km to the south, 280 km to the west and 160 km to the northwest (Lehrman & Mewes 2018). The Common Crane started to breed in the Czech Republic in 1989 and the size and distribution of the breeding population started to increase since beginning of the millennium (Tichackova & Lumpe 2016). Cranes have started to breed in Hungary in the last few years indicating ongoing range expansion in southern regions (Végvári 2018).

Accompanying population growth, breeding density has increased. In Germany it was 0.8 pairs/100 km^2 in 1967 (Bolt 2016). In core areas the density is as high as 9.3–18.7 pairs/100 km^2 (Lehrman & Mewes 2018) but on the border areas of breeding range it is about 2 pairs/100 km^2 (Mewes *et al.* 2013). The highest densities in Germany reach 33–60 pairs/100 km^2 or even more (Mewes *et al.* 2013). In Sweden, the breeding density was 3.7 pairs/100 km^2 in 1980 and 9 pairs/100 km^2 in 1994–1995 (Lundgren 1999). In southwest Poland the breeding density was 5.0–5.6 pairs/100 km^2 but in high concentration areas up to 32–62.5 pairs/100 km^2 during 1997–1998 (Konieczny 2003).

Cranes form their first partnership within a group of cranes when they are 2 years old. They occupy their own territory in the fourth or fifth year and start to reproduce. Breeding success depends strongly on an individual crane's fitness (Blahy & Henne 2018) but is also positively related with quality of breeding territory (Avotins 1999) and on the water level in the breeding habitat, i.e. on the level of precipitation (Lundgren 1999).

The breeding habitat of the Common Crane is always associated with some type (natural or artificial) of wetland. The primary breeding habitats for cranes in core areas of the breeding range always used to be bogs, transitional mires or fens (Renno 1993, Alhainen 1999, Vaverins 2003, Leito *et al.* 2006). In Latvia, Vaverins (2003) noticed that cranes had started to occupy territories in new habitats (wet forest, swampy meadows and areas near lakes and sites flooded by beavers) in the 1980s.

In Germany, the border area of breeding range, the breeding sites were predominantly located near current or former lakes and in forest (alder swamps) in 1960s and 1970s (Mewes 2017). In the following two decades, cranes started to occupy small wet patches in open land (fields and grasslands) for nesting. Over the 50-year study period, crane breeding habitat types increased from four in the 1960s up to 14 in nowadays (Schwarz & Boldt 2014, Mewes 2017). At the beginning of millennium cranes in the Czech Republic inhabited large wetlands but now they have also spread to small artificial ponds (Lumpe & Tichackova 2018); half of crane pairs bred in reedbeds of eutrophic lakes and one third in wetlands where taller sedge species are widespread (Tichackova & Lumpe 2016). Alhainen (1999) describes an optimal habitat of Common Cranes as a wetland many hectares in size with peaceful surroundings where the nest itself is located in a wet area at least a few metres across, with sufficient food and good hiding places. Rich and diverse vegetation provides hiding possibilities but for cranes, it must be possible to watch the main areas of the habitat all the time.

The moulting of the Common Crane was first described in detail by Oskar and Magdalena Heinroth (1928). Every 2- or 4-years Common Cranes underwent a complete moult, and in intervening years, a partial moult. During the complete moult the entire plumage is replaced, with the primary feathers all being lost at once (Heinroth & Heinroth 1928). Three peaks of the dropping of the flight feathers occur between early May and the end of July (Keskpaik & Ojaste 2003). The flightless period for an individual crane is 36–38 days (Leito *et al.* 2006, Keskpaik 2011). During the partial moult the body feathers and some of the wing feathers are replaced, i.e. the crane retains its flight capability during moult (Heinroth & Heinroth 1928). Moulting rhythm of the Common Crane is the same throughout their distribution area (Keskpaik & Kashentseva 1995). Depending on moulting rhythm of the breeding partners, one or both partners may be flightless at the time when the chicks are being reared (Blotzheim *et al.* 1973, Andronov 1989). A few direct observations from Germany demonstrates that pairs successfully reared chicks during the female complete moult phase but were unsuccessful during the moulting of the male (Henne & Blahy-Henne 2013). The complete moult phase of immature cranes occurs in different wetlands with good hiding possibilities connected to summer staging areas (Leivits 1989, Keskpaik & Kashentseva 1995, Avotins 1999, Keskpaik & Ojaste 2003, Leito *et al.* 2006). Moulting sites in Teichi bog were characterized as the most distant from bog borders, with dense pine growth (Avotins 1999). Restoration of flight ability was recorded from the middle of June until the middle of August (Keskpaik & Ojaste 2003). Therefore, the flightless phase is situated between the spring and autumn migration (Leito *et al.* 2016, Keskpaik 2011).

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.* 2006, 2013, Redchuk *et al.* 2015, Prange 2016a, 2016b). 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 1000 individual cranes) is shorter than that between main staging sites (used by at least 10,000 cranes; Prange 2016a).

The number of cranes passing along the West European migration route in autumn increased from 50,000 to 340,000 birds between 1985 and 2013/2014 (7% per year). The Baltic-Hungarian migration route was used by about 150,000 cranes in 2014 with increase of 5% per year since 1990 when 40,000 cranes were counted in Hungary (Fintha 1999, Prange 2016b). The East European migration route was used by at least 80,000 cranes in 2013 (Prange 2016b). In connection with the rapid development of the crane population there are found new connections along the Alps mountains (northern and southern alpine route) between Baltic-Hungarian migration route and West European route, as well as in the eastern parts of France. Also, a new wintering ground in Camargue (France) was established in 1999 (Mingozzi *et al.* 2013, Hansbauer *et al.* 2016, Salvi 2016).

Considering migration routes of Common Cranes in Europe the shortest distances between breeding site to wintering site have the cranes breeding in Germany and the longest route have the cranes from eastern Finland (Alonso *et al.* 2008, Nowald 2010; Saurola *et al.* 2013). The cranes breeding in south-eastern United Kingdom are sedentary (Prowse 2013). Therefore, based on the location and length of migration route the Common Cranes from different populations can be resident, short- or medium-distance migrants and/or long-distance migrants as defined by Berthold (2001). Cranes can change their migration routes and wintering sites in different years or use loop-migration strategy (Leito *et al.* 2006, Saurola *et al.* 2013).

The availability of restored or artificial wetlands and the extensive cultivation of maize along the West European flyway, as well as milder winters explain the changes observed in migration and wintering strategies (Alonso *et al.* 2008, Nowald *et al.* 2013). Along West European flyway the northward shift of wintering areas started in the 1980s when the number of wintering cranes in Spain and Portugal started a steady increase (Alonso *et al.* 1994, Alonso *et al.* 2008, Salvi 2013, 2016, Alonso *et al.* 2016). This process is illustrated also through decreased median migration distance of the German crane population, from 2088 km (1997) to 320 km (2007; Nowald *et al.* 2013), and an increasing number of cranes spend the winter in Germany. Some remain most of the winter, close to their breeding territories (Nowald *et al*. 2018). Also, cranes breeding in Czech Republic have started to spend the winter close to breeding sites (Lumpe & Tichackova 2018). The number of cranes wintering in Hungary has also increased (Végvári 2018). Selection for lower migratory activity is predicted to result in the evolution of residency in exclusively migratory populations of birds (Pulido & Berthold 2010, Lumpe & Tichackova 2018, Nowald *et al*. 2018, Zsolt 2018).

3. HYPOTHESES AND AIMS OF THE STUDY

In order to study breeding and migration ecology of Common Cranes breeding in Estonia, detailed objectives of this thesis were:

- to analyse population trends and distribution of the breeding population of the Common Cranes in Estonia (**I**) and availability of potential breeding habitat (**IV**).

  Hypothesis 1: *During recent decades the population of Common Cranes has increased which is connected to the wider distribution and higher population density of the Common Crane resulting from the substantial availability of potential breeding habitat.*

- to describe in detail nesting habitats of the Common Cranes in Estonia and explore relationships between different habitat characteristics, and the timing and success of nesting (**II**).

  Hypothesis 2: *The favoured nesting habitats are wetlands of various types that are similar in structure. Timing and nesting success are associated with habitat characteristics.*

- to explore the relation between the local numbers and distribution of autumn staging Common Cranes and agricultural land use during recent decades in Estonia (**III**).

  Hypothesis 3: *Arable land used for growing cereals has a great influence on the local numbers and distribution of staging Common Cranes.*

- to examine the stability of the habitat network used by Common Cranes in Estonia and elsewhere in Europe (**IV**).

  Hypothesis 4: *Existing habitat networks support and mitigate the impact of climate change on the Common Crane population breeding in Estonia.*

- to study the long-distance migration pattern of Common Cranes (**V**).

  Hypothesis 5: *The main migration characteristics (number of migration phases, timing and speed of migration, daily flight distances, location of energy acquisition sites, duration of stopovers and total migration period) are similar between the populations that breed in proximity.*

4. MATERIALS AND METHODS

4.1. Increasing population and potential nesting sites (I, IV)

The historical overview for distribution and population size of the Common Crane in Estonia is based on 11 components of the relevant literature together with unpublished data. For estimation the contemporary distribution and breeding population size three methods were used, (1) bird atlas (periods 1977–1982 and 1997–2001), (2) regular mapping of territorial calls (since 1997) and (3) single-visit mapping of territorial pairs in mires (since 1986). From 1986 to 2001, all three census methods were used on 120 plots covering 3089 km^2, or 7% of the total area of Estonia.

The calculation of the population size of the breeding Common Crane in Estonia in 1997–2001 was based on the method of stratified means (Krebs 1999). For this, the territory of Estonia was divided up into three strata (Fig. 1) to provide representative samples and to take into consideration the regional differences in the distribution of the Common Crane.

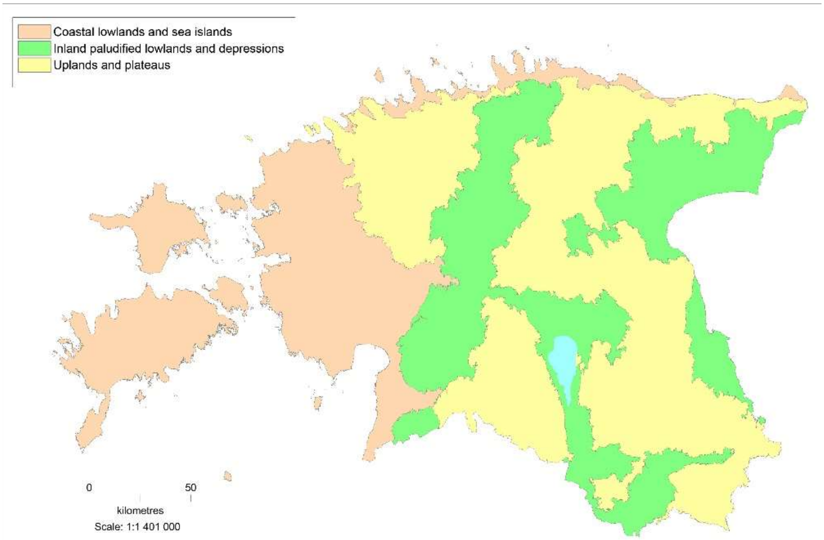

Figure 1. Distribution map of Estonian landscape types (according to Arold 2001).

The geographic distribution of potential nesting habitats of the Common Crane (**IV**) was analysed using an approach termed species distribution models. For modelling the potential distribution of crane nesting sites, the original Common Crane nest record cards (Leito *et al.* 2006), data from Estonian Breeding Bird Atlas (Elts *et al.* 2018) and breeding bird survey program of mire birds in the National Environmental Monitoring Programme (Leivits 2013) were used. The raster layers used for the environmental variables were the classes of the CLC map, soil type (Estonian Soil Map from the Estonian Land Board) and Landsat-7 Enhanced Thematic Mapper Plus (ETM+) multispectral bands. Green (2), red (3) and near-infrared (4, 5) channels were used. Different spectral bands enable the identification of finer scale patterns in the vegetation.

4.2. Nest site selection (II)

Analysis of nest site selection of the Common Crane in Estonia is based on 161 reported nest finds between 1880 and 2001. Most of the data originate from the middle and end of the 20th century (61%) and from the years 2000 and 2001 (27%). The nest finds cover almost the whole of Estonia; the largest number of nests ($N = 95$) have been found in the western part of country.

Seven different nesting habitats were provided (raised bog, transitional mire, fen, river plain, brackish-water or fresh-water coastal lagoon, inland lake and forest). Each habitat is characterized by a vegetation type and micro-relief. Original description of the structure of habitat, demonstrating the ecological variability of habitats, has been provided on the basis of the classification of Estonian vegetation types (Paal 1997) and land cover types (Meiner 1999).

The area of the “nesting site” is defined as a circle of 5 metre radius centred on the nest. “Nesting site characteristics” comprise the location of a nest within the nesting site in terms of its proximity to trees, the composition of plant species and the vegetation type estimated by geobotanical analysis, the openness of the nesting site and its micro-relief. Additionally, features relevant to nest site selection including water regime in the nesting site, landscape around the nest, disturbing factors and nesting success, were tabulated.

4.3. Impact of changes of agricultural land use for cranes (III)

The autumn staging of the Common Crane has been monitored in the Matsalu area since 1961, on Hiiumaa Island since 1982 and throughout Estonia since 1983. In Matsalu and Hiiumaa, censuses have been carried out almost every year. Total crane counts in Estonia were conducted in the years 1983, 1994, 1999, 2000 and 2003. Censuses were performed using the standard method developed in Estonia.

The data on area and yields of winter rye, winter wheat, summer wheat, barley, oats, potato and hay, and for the total area of cereals and for all crops together in Hiiumaa and Läänemaa Counties and for the whole of Estonia from 1965–2005 were collected from the archive of the Estonian Farmers' Union and from the Statistical Office of Estonia (2006). In Hiiumaa County (area 1019 km^2), the cultivated areas of crops coincide with the feeding area of cranes, since the birds feed on all fields throughout the island. The crane staging population of the Matsalu region is spread over about 2000 km^2, which makes up about 84% of the territory of Läänemaa County (area 2394 km^2). The total land area of Estonia without Lake Peipsi and Lake Võrtsjärv is 43,428 km^2 (Maansoo 2001), and agricultural land currently makes up about 20.5% (8890 km^2) of this (Statistical Office of Estonia 2002).

4.4. Function of the ecological network (IV)

Each Common Crane migration route consists of a network of stopover sites which are needed for energy loading during the migration period. Stopover and wintering sites for cranes have two important components, an overnight location on a wetland, for example marshes, lagoons and shallow lakes, and a feeding area on adjacent agricultural land. The average distance between overnight resting places and feeding areas, both on stopover and wintering sites on flyways, was estimated to be 30 ± 9.8 km (± 95% CI). The locations of the crane stopover sites were overlaid on the CLC map (version 16; 2006) in order to determine their land cover composition. The land cover composition at the migration and wintering sites was calculated as the proportion of each CLC class within every buffer polygon (30 km radius circles), through polygon clipping and area measurement procedures performed in ArcMap v. 10.1.

In addition, in order to provide a comparison between the sites occupied by cranes and the wider landscape, CLC was analysed at control points 60 km south from the initial location. These sites acted as controls to show differences in land cover between the staging and wintering sites and independent locations. The average percentage of each land cover class at the Estonian sites and all other locations was calculated. Similarly, the average values for the Estonian sites were compared with all other sites aggregated by stopover sites only, by wintering and stopover areas, or by wintering areas.

The nature conservation layer was composed of areas of four types of protected sites that have actual conservation measures in place. These include GIS layers according to the Nature Conservation Act as follows: (1) protected areas; (2) limited conservation areas; (3) single protected natural features; and (4) species protection sites.

The analysis climate scenario impact for the Common Crane population bases on the European environmental stratification, where 84 EnS were joined hierarchically into 13 EnZ (Metzger *et al.* 2005). In order to assess how the main European environments would shift under different climate change scenarios, climate functions were fitted to the EnS. The TYN SC 1.0 dataset has a resolution of 10 arcmin longitude-latitude and contains 20,400 monthly grids of observed climate, for the period 2001–2100 (Mitchell *et al.* 2004). It comprises five climatic variables, namely: cloud cover, diurnal temperature range, precipitation, temperature, and vapour pressure. For analysis the climate impact the climate variables contained in the CRU TS 1.2 and TYN SC 1.0 datasets were used. Fisher's Discriminant Functions were calculated for each EnS stratum and used in ArcGIS to determine the future distribution of the 84 strata from the monthly climate variables. Separate maps were created for the three time slices (2020, 2050 and 2080). For simplicity, only the most likely scenario was used in the present study, namely the CGCM2 Circulation Model-A2 emissions scenario.

Patterns of shift of EnZ at the crane migration sites were analysed based on the projected climate change at the time steps 1990, 2050 and 2080. The assessment of the proportion of the EnSs in mainland Europe was derived by overlay, clip and area measurement operations in ArcMap 10.1. The EnSs were then grouped into the EnZs, and the average geographic coverage of each Zone obtained for each migration site type: staging, migration, and wintering.

4.5. Long-distance migration pattern of Common Cranes (V)

For the analysis of long-distance migration patterns of Common Cranes, the sample consists of 18 birds who selected the East European migration route towards Ethiopia – 7 from eastern Finland (tagged in 2009–2012) and 11 from eastern Estonia (2009–2017). The distance between the tagging sites in Finland and Estonia is approximately 500 km. The Finnish and Estonian breeding sub-populations should be considered as components of the same population of Common Cranes, with the main difference being their breeding latitudes. For convenience, here the two sub-populations are referred as 'Finnish' and 'Estonian' populations during comparisons, but it should be remembered that breeding latitude is the primary difference between them.

On juveniles, satellite transmitters were deployed immediately prior to fledging. For analysing the migration pattern, the data between time when crane families joined with the migratory flocks and arrival at the wintering area (or until the end of data transmission) were used. It was possible to analyse a total of 2545 locations. The migration status (in flight "1" or staging "0") was annotated for each location.

The main flyway characteristics measured on and above population level were: (1) flyway length from Finnish and Estonian subpopulations to wintering sites, (2) location and distance between stopover sites, (3) location and width of ecological barriers, and (4) location of wintering areas. The migration pattern of Common Cranes on individual and population level was described by (1) a number of migration phases along route, (2) timing and duration of migratory phases, (3) stopover duration dependence on migration phases, (4) flight distance between stopover sites, and (5) overall migration speed.

4.6. Statistical analysis (I–V)

Statistical and data analyses were performed using MS Excel 7.0 (**II**), Statistica 6.0 **(I, II, III**), Statgraphics (**II**) and R (Version 3.0.1, R Development CoreTeam 2013) (**V**). The MAXENT program version 3.3.3k was utilized in the R environment (Hijmans *et al.* 2013; R Core

Team 2013) for calculation the distribution of potential breeding habitats for Common Crane. The suitability map of the potential nesting sites of cranes in Estonia was calculated from the predicted probability map using the 32% threshold value. The land use composition of nature protection areas was calculated by overlay analysis separately for the suitable nesting sites of cranes (probability over 32%) and for the areas where nesting is unsuitable (probability up to 32%) (**IV**). For geographic information system (GIS) analysis the programs ArcGIS 10.1 and MapInfo 15.0 were used (**IV, V**).

Basic statistical methods, Pearson's correlation, Spearman rank correlation coefficient (r_s), Mann-Whitney non-parametric U-test, Student t-test, Kruskall-Wallis non-parametric test and Chi-squared tests were used to determine the relationships between crane numbers and cropping area in the same year, and the potential differences between the behavioural characteristics, in papers **II**, **III** and **V**.

The Mann-Kendall non-parametric test (*MK*) was used to detect trends in time series (**I**, **II**, **III**). The relationship between the population density and biotope area was fitted by the inverse first order model using non-linear regression with the Marquardt-Levenberg algorithm (**I**). Locally weighted regression (LOWESS) was used to illustrate trends in the time series data of crane numbers (**III**). The coefficient of variation (*CV*) was calculated in order to demonstrate the temporal variation of crane number and cropping area (**III**). For examining links between different factors, the two-way ANOVA test, Tukey post-hoc test was used (**V**).

Principal component analysis (*PCA*) was used for ordination of cropping areas of different crops according to year in Hiiumaa, Matsalu and in Estonia as a whole (**III**).

5. RESULTS

5.1. Breeding ecology of Common Crane

5.1.1. Increasing process of Common Crane population (I, IV)

The Common Crane broadened its distribution between the first bird atlas period (1977–1982) and period 1997–2001 with a speed of 9.2 UTM atlas squares per year. This means that the proportion of occupied squares increased 2.3% per year with a time lag of 19 years (between 1982 and 2001), i.e. from 323 (57% of atlas squares) to 498 (88%) of atlas squares (Fig. 2). During that time lag the Common Cranes, which had previously occupied for breeding only large natural wetlands (bogs and fens) (Renno 1993), started to breed in agricultural landscapes (small wetlands with high vegetation in middle of fields), in abandoned quarries, in small wetlands on islands and on territory of towns. Most of the crane nests that were located in different forest types have been found since 1984. Broadened distribution of the Common Crane has been favoured by the good availability of potential nesting sites all over Estonia (Fig. 3).

The population of the Common Crane increased significantly from 300 breeding pairs (corrected population size) in 1970 up to 5800 pairs in 1999 (Fig. 4) which is in good correlation with expanded breeding distribution. The breeding population mean increase was 8.8% per year between 1971 and 1980, 11.2% per year between 1981 and 1992, 9.8% between 1993 and 1997 and 20.2% between 1998 and 1999.

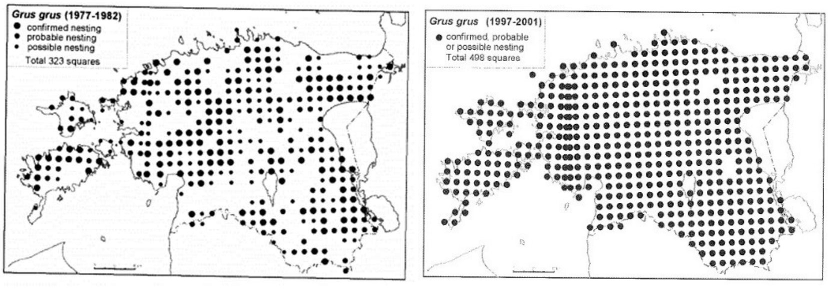

Figure 2. Expansion of the distribution of the Common Crane breeding population in Estonia over 15 years (1977–1982 and 1997–2001).

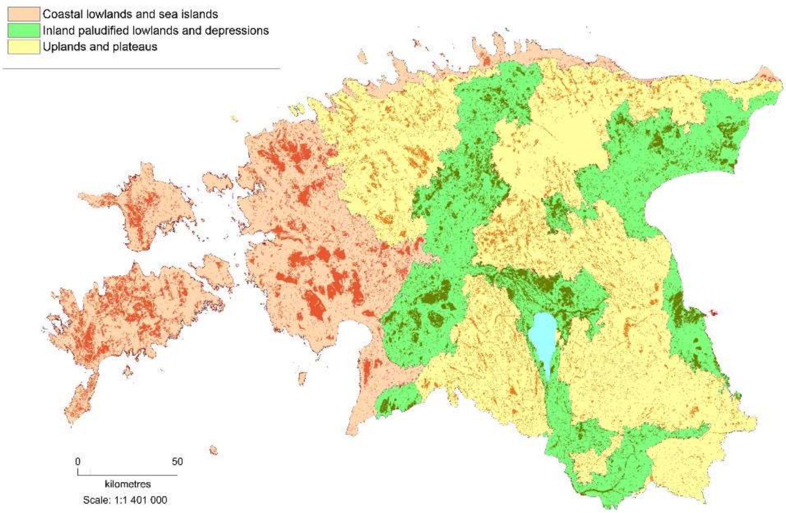

Figure 3. Suitability map of potential nesting sites (dark patches) of the Common Crane in Estonia calculated from the predicted probability map using the 32% threshold value.

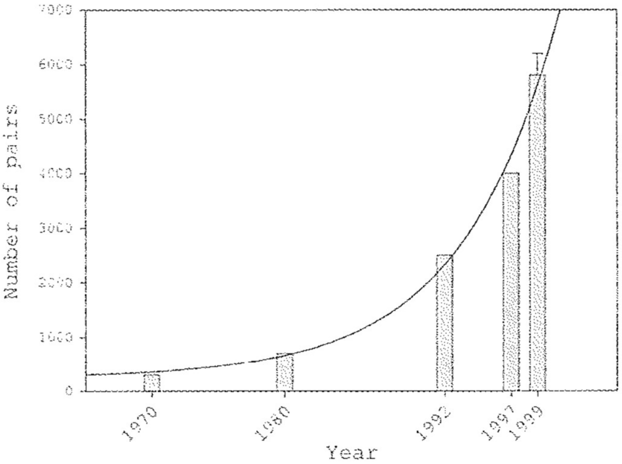

Figure. 4. Estimated population size of the breeding Common Crane in Estonia in 1970–1999. The exponential growth curve was fitted to the data ($R^2 = 98.2$, $P < 0.01$). A 95% confidence interval for the estimated population mean is shown for 1999.

According to the statistically reliable results provided by the stratified random sampling approach, 4200±1700 pairs (±95% CI) had territory in fens and 700±200 pairs in raised bogs. Breeding pairs in transitional mires number about 400 and in all other habitats about 500. The relationship between population density of the Common Crane and the breeding habitat (non-linear regression with the Marquardt-Levenberg algorithm; for fens: $P < 0.001$, $N = 16$, transitional mires: $P < 0.001$, $N = 9$ and raised bogs: $P < 0.001$, $N = 28$) was statistically significant being highest in smaller habitat patches, i.e. population density correlates negatively with size of nesting habitat. Mean population density increased from 2.2 pairs/100 km^2 in 1980 to 17.4 pairs/100 km^2 in 1999 without significant differences between the landscape regions occupied. Comparing core habitats, the mean population density varied from 15.9 pairs/100 km^2 in raised bogs to 38.3 pairs/100 km^2 in transitional mires and 41.3 pairs/100 km^2 in fens.

5.1.2. Nest site selection and nesting success (II)

In Estonia, about 72% of the local breeding population of Common Crane breed in different types of mires which together constitute about 20% of the territory of Estonia. The most important breeding habitat for Common Crane are fens, especially treeless quagmire or paludified grassland with the sedge-reedbed mosaic community and wooded or open hollow-pool-ridge bog site types with different herb and dwarf shrub complexes (Table 1). Nearly 10% of the crane population breeding on inland lakes where treeless shore quagmire with herb or moss community was most frequently used by cranes for nesting and deciduous forest with a majority of birch or alder is the most frequent nesting site for cranes. In terms of water regime, the majority of nests (75%) were located in rich paludified forests or wooded meadows. The habitat size differs significantly between the different habitat types (Kruskal-Wallis non-parametric test, $P < 0.001$, $N = 159$). On the average, the largest nesting habitat is the raised bog, compared to fen, coastal lagoon, inland lake and forest. No statistically significant correlation between openness and other single characteristics, other than the combined nesting site characteristic, both openness and hummock type ($r = -0.27$, $P < 0.01$, $N = 154$) was found. In terms of micro-relief and hummock type, most of the nests were located on a grass hummock (88 nests), followed by nests on level ground (46 nests) ($N = 146$). Most nests (97 nests, 64%) were located in sites where the depth of water at the nest was only 0–15 cm, followed by those with water depth of 16–30 cm (29 nests) ($N = 151$).

Table 1. Nesting habitats of the Common Crane in Estonia and distribution according to habitat of the nests found. Total land area of Estonia without Lake Peipsi and Lake Võrtsjärv is 43,428 km^2.

Biotope category	Total area (km^2)	Share of habitats of the total area of Estonia (%)	Share of nests of nesting habitats (%)	Number of nests in a habitat type	Distribution of nests in relation to habitats (%)
Raised bog	2,780	6.4	23.6	43	27.0
Transitional mire	1,140	2.6	9.7	9	5.7
Fen	5,150	11.4	43.8	63	39.6
Riverplain	276	0.6	2.3	6	3.8
Coastal lagoon	15	0.03	0.1	7	4.4
Inland lake	243	0.6	2.1	15	9.4
Forest[1]	2,152	5.0	18.3	16	10.1
Total	11,756	27.1	99.9	159	100.0

[1] Seven forest site types: *Filipendula ulmaria*, drained swamp, grass swamp, *Equisetum*, *Molina caerulea*, *Molina caerulea-Filipendula ulmaria*, *Carex* and *Carex-Filipendula ulmaria*.

The most common nest-to-neighbouring nest distance (65 nests) was > 1 km, while for 41 nests, the distance was 0.5–1 km. The smallest distance measured between two occupied neighbouring crane nests is 120 metres in Estonia. Mean brood size (1.65 nestlings, $N = 20$) was in cases where the distance between neighbouring nests was 0.5–1.0 km significantly larger than in cases where the distance was more than 1 km (1.16 nestlings, $N = 32$) (Student t-test, $P < 0.05$, and the Mann-Whitney U-test, $P < 0.05$, $N = 52$).

Most crane nests were located in the zone of weak human disturbance (a distance of more than 0.5 km to the nearest building or settlement, main road or path from the nest more than 0.5 km: 104 nests), followed by nests in areas with medium human disturbance (distance 0.1–0.5 km: 45 nests) and in the zone with strong disturbance (distance less than 0.1 km: 6 nests) ($N = 155$). The mean number of juveniles in the nests subject to weak human disturbance was significantly larger than in the nests located in the zone of medium human disturbance. (Student's t-test, $P < 0.01$ and Mann-Whitney U-test, $P < 0.01$, $N = 67$).

5.1.3. Breeding phenology of Common Crane (II)

According to the nest record cards, the date of the beginning of egg laying of the Common Crane in Estonia ranges between 11 April and 6 June, with a mean value of 22 April ± 10 days (± SD; $N = 93$). We found that in the West Estonian Archipelago, cranes start laying eggs at a significantly, i.e. 12 days earlier date than on the mainland (Student t-test, $P < 0.05$, $N = 93$). The average date of the beginning of egg laying on Saaremaa is 18 April ± 9 days ($N = 23$), and 30 April ± 11 days ($N = 70$) on the mainland. There is also a significant correlation between the size of the nesting habitat and the beginning of egg laying (Kruskal-Wallis non-parametric test, $P < 0.01$, $N = 91$). Variation in the beginning of egg laying is greatest in the habitat size category of 11–100 ha (Fig. 5). An analysis of the variation of the beginning of egg laying by cranes over time indicates a significant trend of advancement in Estonia over the whole 1901–2001 period (Fig. 6). The average change for a ten-year period is almost two days.

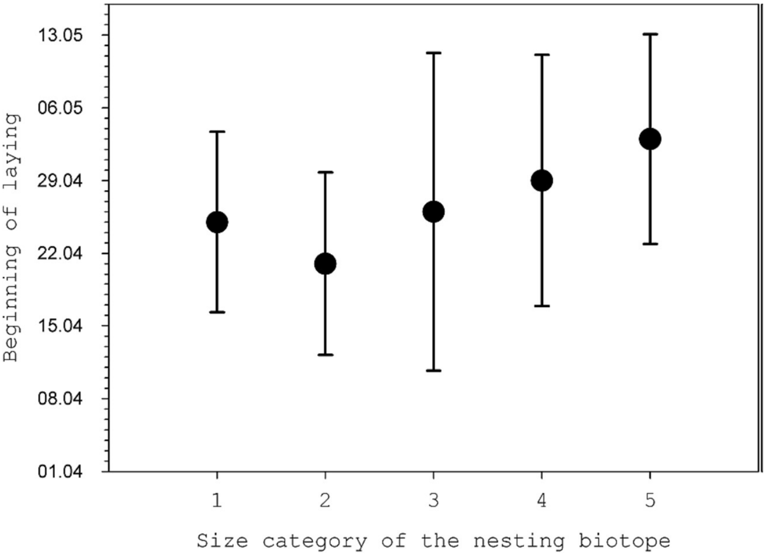

Figure 5. Relationship between the beginning of egg laying (mean annual date ± SD) and the size of the nesting habitat of the Common Crane in Estonia. Habitat size categories: 1 = less than 1 ha; 2 = 1–10 ha, 3 = 11–100 ha, 4 = 101–1,000 ha, 5 = more than 1,000 ha.

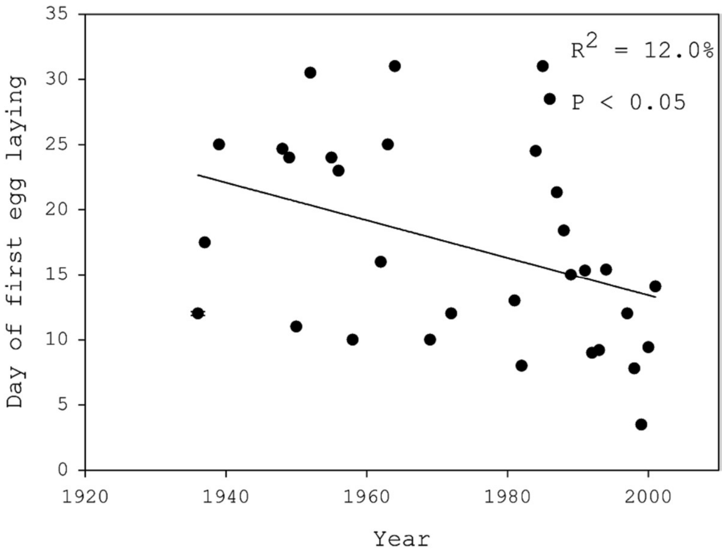

Fig. 6. Relationship between the annual mean date of the laying of the first egg and the year, for the Common Crane in Estonia, 1901–2001. Annual mean dates of the laying the of first egg are displayed in days. Cranes started to lay earlier in more recent years ($r = –0.43$, $P < 0.01$, $N = 93$).

5.2. Migration ecology of Common Crane

5.2.1. Impact of changes of agricultural land use for cranes (III)

Total counts during the period 1983–2003 indicate the number of autumn staging Common Cranes in Estonia has varied between 18,000 in 1997 and 30,000 in 1994 ($CV = 0.51$, $N = 5$ years). The total number of cranes has fluctuated without any visible trend. A total of 51 crane staging sites in 8 concentration areas were established in the 1980s, and 61 staging sites in 10 concentration areas in the 1990s. The most important gathering area of Common Crane has been Western Estonia, including the islands of Hiiumaa and Saaremaa, where, in different years between 1983 and 2003, 72% and 87% ($N = 5$) of all cranes were counted. The relative share of all staging cranes in Matsalu has been 48–71% ($N = 5$) during the period 1983–2003. There is a significant positive correlation between the number of cranes staging in Hiiumaa and in Matsalu ($r_s = 0.47$, $p < 0.05$, $N = 21$).

In the Matsalu area three periods of population change were characterized as follows: (1) substantial population growth from 1965–1983; (2) a period with fluctuating numbers at a level of about 10,000 cranes, and (3) a new growth period during the last decade since 1995. There is a significant positive trend in staging crane abundance over the whole study period 1961–2005 ($MK = 2.66$, $p < 0.01$, $N = 30$ years; Fig. 7a). On Hiiumaa Island four periods were distinguished: (1) relatively stable numbers at a low level in the 1980s; (2) population growth with a peak numbers at the beginning of the 1990s; (3) a rapid decrease in numbers until 1998, and (4) relatively stable numbers from 1999-2005, remaining at the same level as in the 1980s (Fig. 7b).

During the period 1965–2004, the total area of cropland in Estonia has decreased to 259,248 ha in 2002 from 444,223 ha in 1980 ($CV = 0.55$, $N = 40$). The dynamics of the total area of cropland in Läänemaa County, Hiiumaa County and in the whole Estonia has been similar (Fig. 5 in **III**). Five main periods in the total area of field crops can be distinguished for Estonia: (1) the growth in total area in the period 1965–1976, (2) a relatively stable total area in the period 1977–1992, (3) a rapid decrease in the period 1993–1996, (4) a new increase and stabilization on a lower level at the end of the 1990s, and (5) stabilization in total area of field crops at a new level close to that of the 1960s.

In Estonia there were great changes in the relative shares of different field crops in the period 1965–1990: the share of oats and potato had decreased, and the share of cultivated grassland had increased (Fig. 6a in **III**). For all cereals together, except for summer wheat, the total cropping area of has decreased since the 1990s.

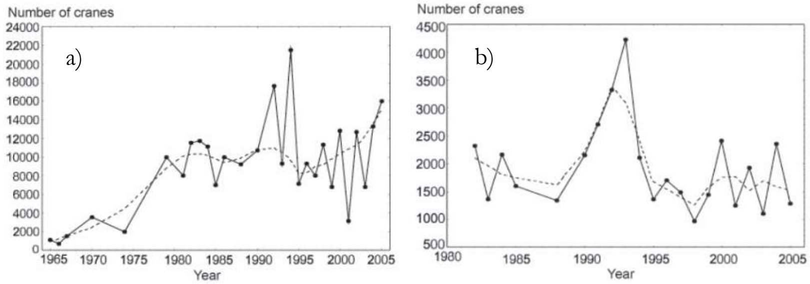

Figure 7. Temporal dynamics of crane numbers in Matsalu area (a) and on the island of Hiiumaa (b). The solid line represents the actual counted crane number and the dashed line reflects robust locally weighted regressions (LOWESS) over time.

In Matsalu the relative share of different field crops has been stable during the period 1965–1990 and has changed substantially in the period 1991–1995, when the cropping area of all cereals together decreased. Since 1996 the area of cultivated grassland and summer wheat has decreased (Figure 6b in **III**). On Hiiumaa the changes have been similar to Matsalu during the period 1965–1990, but in the period 2001–2004 the structure of cropland on Hiiumaa has been more stable (Figure 6c in **III**).

The significant positive correlation between the number of staging cranes and the cropping area of winter rye, winter wheat, summer wheat and all cereals combined, and a negative correlation between crane numbers and the cropping area of potato were found. The correlation was strongest with the cropping area of winter rye ($r_s = 0.58$, $P < 0.05$, $N = 21$) and winter wheat ($r_s = 0.58$, $P < 0.05$, $N = 21$) on Hiiumaa, and with the cropping area of all cereals combined in Matsalu ($r_s = 0.56$, $P < 0.05$, $N = 28$). No statistically significant correlation between crane numbers and the area of cultivated grasslands was found in either Matsalu or Hiiumaa.

5.2.2. Viable ecological network of cranes (IV, V)

Migratory network. Majority of the cranes from Estonian population use the West European and the Baltic-Hungarian Flyways, in smaller numbers the East European Flyway (Fig. 8; **IV, V**). Approximately 90% of the Estonian crane population overwinter in southern Europe, and the remainder in Africa (**IV**). The wintering ground can be reached also using partly other migration route (**V**). The most northern irregular wintering areas of Common Cranes are in northern Germany (south from latitude 53°). Starting from the latitude 48° and further south the stopover sites along flyways overlap with regular wintering sites. The most southern wintering areas of Estonian cranes are on latitude 9° in Ethiopia (**IV**, **V**). Each flyway links the network of stopover sites for energy acquisition during the migration period (**IV**, **V**). The geographical location of stopover sites is nearly equally distributed along West European Flyway while in the Baltic-Hungarian Flyway the main stopover sites lie in middle of route. On the East European Flyway, the energy acquisition sites are clearly concentrated in the first quarter of the distance of the flyway (**IV**, **V**).

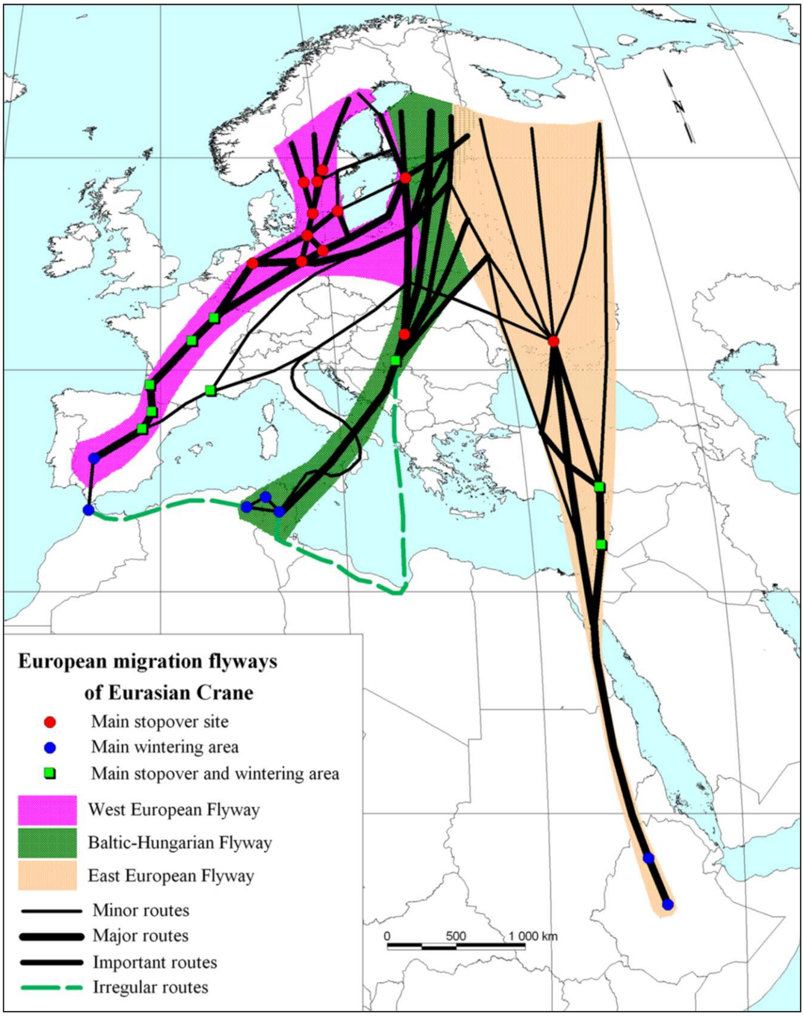

Figure 8. Generalized map of the European Flyways (migration routes) of the Common Crane. The main stopover areas, stopover and regular wintering sites, and wintering areas are shown on the key, as well as different types of routes followed.

Land cover in stopover and wintering sites. Almost all stopover sites used by Common Cranes along migration routes have more land cover associated with water than the controls, confirming the primary requirement of cranes for roosting sites (Figure 4 in **IV**). The areas of water are small, which may in part be due to the minimal patch size of 25 ha in CLC, but it also suggests that the cranes can manage where wetlands form a relatively small part of the landscape. However, the surrounding network shows contrasting patterns between the northern Zones, where forest dominates and cereals occupy only a small area, and the southern Zones. The latter have a much higher proportion of agricultural land, varying from cereals in the Continental Zone to irrigated arable land and other types in the Mediterranean Zones. Cranes are therefore sufficiently flexible to find feeding places within a range of different landscapes, confirmed by their ability to fly up to 30 km to locate suitable foraging areas. Therefore, these results also highlight the flexibility of cranes in adapting to a range of habitat networks, providing that the primary requirement of wetland for roosting is available (**IV**).

The stopover sites are in the Nemoral, Continental, Atlantic North, Atlantic Central and Pannonian Zones, as defined by Metzger *et al.* (2005). According to the mean values of the individual classes, none of the sites will be frozen at the time of winter migration. The Boreal and Nemoral Zones are deeply frozen throughout the winter months but only one continental class is frozen, which shows why the cranes stopover in the continental zone in favourable winters (**IV**).

Impact of climate change. The likely impact of climate change scenario is minimal for cranes because the core area of wintering sites in the Mediterranean is predicted to remain superficially the same. By 2080, the Lusitanian site becomes Mediterranean North, which will have minimal impact on cranes. The shift in Estonia is from Boreal to Nemoral in 2050, and then to Atlantic North in 2080. Figure 5 (**IV**) shows the regions where winter temperatures in 2080 will be above freezing. In Central Europe this map is coincident with the current area where irregular stopovers occur. However, the most striking feature of the map is the potential shift in Western Estonia towards non-freezing conditions. This suggests the possibility of cranes being able to overwinter in the country by 2080. However, overall, the data confirm the potential for further expansion of cranes in Europe, because conditions are likely to become more favourable for the species. In contrast, the sites in the Atlantic Central and Pannonian Zones are expected to be stable. Another major influence on crane migration patterns is likely to be the shift within the Mediterranean Zone to hotter and drier classes, which could lead to drying out of shallower wetlands (**IV**).

5.2.3. Long-distance migration pattern of Common Crane (V)

Long-distance autumn migration strategies of the Common Crane differed between northern and southern sub-populations in relation to the number and location of stopovers, daily flight distances, and the total migration duration. The number of stopover sites used along migration route, their geographical locations and importance (total time spent in stopovers) for energy acquisition can vary greatly between neighbourhood populations breeding in different latitudes. Cranes from Finnish subpopulation used two stopovers (29% of available) while Estonian cranes used one to four stopovers (17%–67%) for this purpose along East European migration route. Cranes from Finland preferred more southern stopovers (Askania-Nova and Sivash areas in Ukraine) then cranes from Estonia, which staged in Belarus. Hence, cranes can bypass most potential stopover sites. The East European migration route was covered with two migration cycles, i.e., the crane family made *en route* only one stop for energy acquisition after departing from Estonia. The most frequent stopovers in length of 11–20 days formed 47.4% ($N = 27$) of all stopovers *en route* indicating this period is sufficient for restoring energy reserves for a subsequent long-distance migratory flight (Fig. 4 in **V**). The mean stopover duration *en route* was 12.8 ± 6.9 days (± 95% CI; $N = 12$) for the northern cranes and 15.1 ± 3.2 days ($N = 27$) for the cranes breeding more south, with the difference being marginally insignificant (U-test: $W = 102.5$, $p = 0.07$). The total time spent on stopover sites during whole migration period was among northern cranes 85.2 ± 7.6% and among southern cranes 86.6 ± 3.5%.

Stopover duration influences the duration of migration stage along the flyway (Fig. 9A, B). The duration of flight journey and flight distances are short during first part of flyway, but the values of both features increase significantly towards the wintering areas (Fig. 9C, D). Although the total migration speed of northern cranes was 64.7 ± 31.8 km/day and of southern cranes 44.7 ± 11.3 km/day, this difference is not statistically significant ($t = 1.430$, $df = 7.879$, $P = 0.19$) (Table 2 in **V**). 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 differed between Finnish and Estonian subpopulations significantly (563.7 ± 72.4 km/day, $N = 47$ and 364.5 ± 45.9 km/day, $N = 100$, respectively; U-test: $W = 3404$, $p < 0.001$). Reaching the wintering ground after setting off from home area, took 32–37 days for northern cranes (Israel and Ethiopia) and 55–65 days for more southern cranes (Table 2 in **V**) following traditional East European migration route (southern Turkey and Ethiopia). Moreover, arrival of northern cranes to wintering ground in Israel or Ethiopia (difference 2400 km) or southern cranes to southern Turkey or Ethiopia (difference 2800 km) took nearly the same time (**V**).

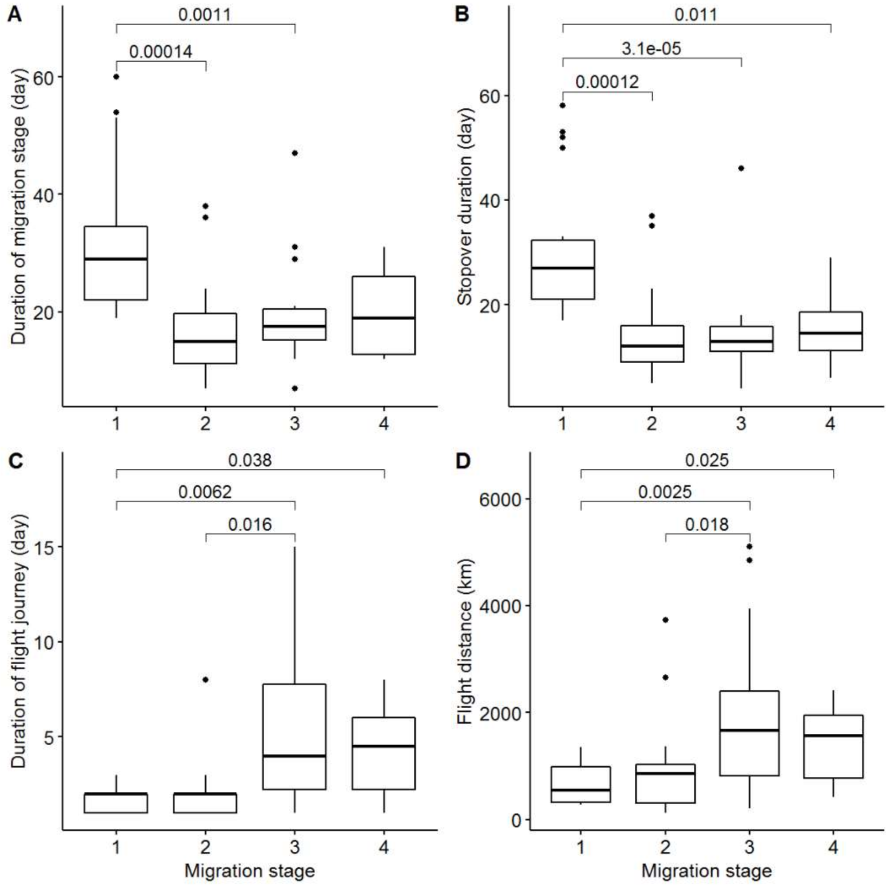

Figure 9. The effect of migration stage on the duration of the (A) migration stage, (B), stopover period, (C) flight duration, and (D) flight distance. Bold horizontal lines indicate the medians, boxes show the quartiles, and whiskers (vertical lines) indicate the extreme data points not exceeding 1.5× 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.

6. DISCUSSION

6.1. Development of the Common Crane population

The Common Crane was, in the mid-20th century, generally described as a widely distributed but not numerous breeding bird (Kumari 1954, 1958, Haartman *et al.* 1963). The main breeding habitats of Common Crane were then described as bogs and various mire and fen types in northern breeding regions (Kumari 1954, 1958, Haartman *et al.* 1963, Renno 1993) and eutrophic lakes overgrown with reed in the western range (Mewes 2017), which held the relatively small breeding population of the time. The population started to increase simultaneously all over Europe (Drobelis 1999, Lundgren 1999, 2013, Vaverins 1999, Bolt 2016, Prange 2016a, 2016b), as well as in Estonia (**I**). This process was reflected also in counts on wintering areas (Alonso *et al.* 2016). While the number of breeders increased, the density of pairs increased (Lundgren 1999, Konieczny 2003, Mewes *et al.* 2013, ref. Bolt 2016, Leito & Ojaste 2016), initially in core breeding areas/habitats (Prange 2016a, Mewes 2017). Subsequently new breeders started to occupy new habitats (for example small wetlands in forest, overgrown wetlands in old quarries, fields or grasslands and on marine islands), previously not used for breeding, throughout the breeding range (**I**, Vaverins 2003, Leito *et al.* 2006, Schwarz & Boldt 2014, Mewes 2017, A. Karlin pers. comm.). It is estimated that the reproduction rate of approximately 0.9 fledged young per breeding pair led to yearly population increases approximating 8% (Boldt 2016, Leito & Ojaste 2016, Prange 2016a). Therefore, the availability of potential unoccupied wetlands provided an excellent resource for population increase and enlargement (**IV**). This process led to the emigration and breeding range started widening especially in Germany (Bolt 2016, Prange 2016b, Lehrman & Mewes 2018) as well as in Czech Republic (Tichackova & Lumpe 2016) and in Hungary (Végvári 2018). Due to continuous population growth the reproductive rate has started to decrease (Leito & Ojaste 2016, Prange 2016a).

6.2. Selection of nesting site, nesting success and climate impact

The criteria for selecting suitable breeding habitat are in principle similar throughout the breeding range with only small modifications due to landscapes and wetland types available (Alhainen 1999, Avotins 1999, Prange 2016a, Tichackova & Lumpe 2016, Mewes 2017). Despite the fact that the Common Crane nests in different biotopes, all nesting sites include similar structural elements (vegetation types, plant species and communities and elements of microrelief). The study showed that in terms of plant communities, identical or similar reedbed and sedge communities occur in fens, river plains, as well as coastal lagoons and inland lakes. Different nesting sites are characterized by similar water regime – flooding or long-term floods in the fen, river plain, coastal and inland lake, and also in swamp and floodplain forests. Occurrence of hummocks is characteristic of all nesting habitats. Common Crane is well adapted to breed in different types of wetlands available in an area, but prefers mires and other swampy habitats and avoids, whenever possible, saline habitats on the seacoast (**II**).

The habitat quality is one of the reasons for the difference in nesting success and population density of cranes. The relationship between breeding success and distances between neighbouring nests suggests that habitat quality was probably higher when distances between nest were short (first time breeders follow information through conspecific attraction which indicates successful reproduction in new territories: Piper 2011). The lower breeding success associated with long distances between nests rather reflects lower quality of nesting habitat and/or unexperienced breeders in new habitat patch. However, it is also evident that nesting success decreases when the distance between nests becomes too short, because then competition between pairs and families with young increases substantially despite the original quality of a nesting site in terms of other important characteristics (food resources, predators, disturbance and hiding places) remaining unchanged (this concerns the same or very similar nesting habitats) (**II**). As occupancy of breeding territory reflects its quality (Sergio & Newton 2003), Avotins (1999) demonstrates that inside a large bog system which is typical breeding habitat for cranes, the territories have different quality and only quarter of them are occupied every or nearly each year.

The human activity had a significantly negative effect on the breeding success of cranes in Estonia. The mean brood size in nests close to roads or buildings was significantly smaller than in nests that were further away from human disturbance. Nevertheless, this result is not surprising, but it was important to prove that human activity really has a negative influence on the breeding success of cranes, confirming the earlier but often too generalized declarations to that effect (**II**). Despite this there are signs that cranes adopt human settlements closer to their nesting site as was the case some decades previously (Lumpe & Tichackova 2018).

The significant advancement of oviposition by cranes about 10 days over time is in good accordance with the mean earlier arrival of cranes to Estonia (Keskpaik *et al.* 1997). It is suggested that earlier arrival is strongly affected by North Atlantic cyclonic process in early springtime. NAO index in April and May, as well as air temperature on the wintering and on the breeding ground and precipitation and snow cover in Estonia were highly related to reproductive success (Palm *et al.* 2013). These findings are in good agreement with general processes associated with ongoing climate change: (1) species-specific response in timing of migration (increased migration speed, earlier arrival/departure to/from breeding/wintering area, shortening migration distance), (2) short-distance migrants respond more strongly to climate change than long-distance migrants in arrival to breeding ground, (3) food generalist species advance their arrival to a greater extent than food specialist species, (4) moulting strategies determine the response to the timing of spring migration and (5) earlier breeding, greater number of broods and reproductive success (Gordo 2007, Hedenström *et al.* 2007, Leech & Crick 2007, Alonso *et al.* 2008, Végvári *et al.* 2010, Dunn & Winkler 2010, Lehikoinen & Sparks 2010, Hansbauer *et al.* 2014). Generally, higher temperatures at the wintering areas and stopover sites during migration are favourable for this species due to increased food availability and therefore higher energy reserves and better physiological conditions for birds (Gordo 2007, Both 2010, Newton 2010).

6.3. Number of staging cranes correlates with availability of cereal fields

The total number of Common Cranes staging in Estonia during the autumn migration rose rapidly in the 1960s and 1970s and stabilized in the 1980s. The staging crane numbers were positively correlated with cropping area of cereals and negatively with the extent of potato fields. The strongest relationship was between crane numbers and the area of winter rye and wheat because, with these crops' cranes can feed on newly sown fields and on green crops for one autumn, and on germinated fields and stubbles during the next. Visually, rye and wheat fields seem to be much richer in additional food for cranes, if only because of the higher stand of the germinated crop and stubble compared to barley (**III**). Most probably, newly cultivated lands, especially large field systems, have been the most important factor for the rise and development of autumn staging crane assemblies in Estonia during the 1950s and 1960s (Leito *et al.* 2006). The study in wintering ground (Alonso *et al.* 1994) shows that number of locally staging cranes is limited by the carrying capacity of the area. They also suggest that this is leading factor of the northward shift of wintering range associated with increasing agricultural food resources. Moreover, this is probably the main factor causing the increase of staging sites in the most important stopover regions holding more than 10,000 cranes (Estonia, Hungary, Sweden, Germany, France; Fintha 1999, Végvári & Tar 2002, Lundin 2005, Leito *et al.* 2006, Salvi 2013, Prange 2016a, Végvári 2018).

6.4. Viable ecological network supporting Common Crane population

The capacity to select freely the migration route and therefore adapt to new feeding and environmental conditions clearly demonstrates the flexibility of the Common Crane and its responsiveness to endo- and exogenous factors, a combination of genetic background (Liedvogel *et al*. 2011, Väli *et al*. 2018) and on social transmission (Pulido 2007, Mueller *et al*. 2013). Migration flyways of Common Cranes form an ecological network (Mander *et al.* 2003, Ings *et al.* 2008) of staging and wintering areas while the individual cranes may change their migration routes and use different staging and wintering areas in different years (Leito *et al* 2006, Prange 2016a). The continued upward trend of the Common Crane population in Estonia suggests that, if there is no sudden change in land use, the existing ecological network of interrelated wetlands and fields will maintain the current status of the species, or even enable a population increase. The lack of change in the ecological network in Estonia has been an important factor influencing the continued success of the cranes; although this cannot be attributed to a positive environmental conservation policy, but rather to a lack of financial resources for the continued agricultural intensification that has taken place elsewhere in Western Europe. The analysis shows that protected site designation has played a relatively minor role in Estonia. Despite earlier ideas, that increase of crane population was supported by increase of protected areas (**I, III**), latter modelling showed that the success of the Common Crane is independent of site protection (**IV**). Therefore, if financial returns in the agriculture sector improve, it is possible that the current abundance of suitable sites may be threatened. However, the abandoned fields that were formally in agricultural use, although generally on soils of low fertility, are likely to be the first to be converted back into crops (Kukk *et al.* 2010).

Climate change may also lead to changes in agricultural crops, e.g. maize is likely to become more widespread and other crops could also change in their distribution patterns. As a result, longer staging periods are possible in the northern stopover sites of cranes, with more food resources may becoming available or even during wintering. Current knowledge about Common Cranes behavioural flexibility support idea that the cranes are likely to be able to modify their current flyways and overwintering sites (**IV**).

Considering knowledge about historical and current habitat preference and selection the nesting sites (**I**, **II**) of Common Cranes it seems, despite the modest contribution of nature conservation to the population increase (**IV**), that conservation efforts to protect and restore the natural water regime of peatlands (raised bogs, transitional mires, fens) (Kimmel *et al.* 2010, Fraixedas *et al.* 2017) play key roles in the conservation of the Common Crane in the longer term. Peatlands of a wide range of types have historically been important refuges for maintenance of viable populations in periods of minimal population level. While peatlands with natural water regime provide safe nesting and roosting sites with low human interference, good overview to the territory, still holding hiding opportunities and probably lower predation rate by mammal predators due to wetness, we can predict that in the case of a future population decrease, most of the breeders will persist in such habitats. Considering environmental and climatic changes, as well as species plasticity to habituate nesting in the proximity of human settlements, there could be changes in habitat quality as well in preferences which emphasize the importance of studies of this aspect of crane ecology.

6.5. Long-distance migration pattern

Our findings on the long-distance migration pattern of Common Crane produced some unexpected results: (1) maximum migratory flight range without additional energy accumulation is 2400 km up to 5100 km covered in 6 up to 15 days, (2) cranes are able to perform long non-stop flights for at least 36.5 hours, (3) stopover duration and location are not related with heading flight distance and ecological barriers, (4) cranes from northern population can cover nearly the same migratory distance as cranes from southern latitude in only half the time, and (5) cranes from northern and southern latitude arrived at their wintering grounds in a quite narrow time window (32–37 days and 55–65 days, respectively) despite a great difference in distance between wintering areas (2420 km and 2830 km, respectively) (**V**). These results suggest that cranes should select particular, broad-scale favourable weather conditions for migratory flights. In response to changing environmental conditions during long-distance migration, cranes should change the flight mode (flapping flight in vee-formation flocks or soaring/gliding flight) in response to certain circumstances (Pennycuick *et al.* 1979, Alerstam & Bäckman 2018). Both flight modes help to reduce the amount of energy required for flight and increase migratory range (Lissaman & Shollenberger 1970, Hedenström 1993).

During long-distance migration cranes used either (1) one refuelling area in Belarus or southern Ukraine or (2) two to three stopovers in Belarus or Hungary prior to setting off on the subsequent demanding long-distance flight. First strategy involves heavily increased body mass after energy accumulation which can potentially increase cross-country performance for soaring birds by allowing faster gliding speeds under strong thermal conditions (Alerstam & Hedenström 1998). The second strategy involves short flight distances between the stopovers associated with smaller energy reserves (Hedenström 2008). This finding suggests that the autumn long-distance migration of Common Cranes exhibits a combination of both time- and energy-minimization strategies (Alerstam & Hedenström 1998) (**V**).

The higher mean daily migration speed of the northern crane population suggests that, in general, compared with populations in southern latitudes, it was more selective with respect to migration conditions, thus facilitating completion of their longer migration on time (Newton

2010). The seasonal variations in overall 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 (**V**).

An understanding of crane migratory patterns and behaviour is critically important in assessing the conservation status and needs of the different species. The problems cranes face during migration often constitute weak links in the chain of conservation actions. Even if the cranes are secure in their breeding and wintering areas, they may be vulnerable to habitat changes at traditional staging and resting areas, and often face other dangers associated with human activity along the migration routes (Archibald & Meine 1996).

7. CONCLUSIONS

In the present thesis, the basic aspects in breeding and migration ecology of Common Cranes breeding in Estonia are examined. Based on the results the following conclusions can be drawn:

1. The distribution of Common Crane started broadening and population increased already in 1970s like elsewhere in Europe. The population growth was more rapid during 1980s and 1990s. The main nesting sites were related mainly with large wetlands in 1970s but while population and breeding density increased, cranes started to occupy new habitats (**I**). Moreover, all over Estonia there can be found potential nesting sites for cranes which strongly supported the increase of crane population (**IV**). This conclusion corroborates our **hypothesis 1**.

2. The results from article **II** confirm that Common Crane breeding in different wetlands where the main habitat characteristics and water regime are similar. The preferred habitats are various mires. Cranes rather keep their distance from human activities, thus reducing negative impact on breeding success. The timing of the start of egg laying was related to area of suitable habitat. These findings support our **hypothesis 2**.

3. The analysis of long-term monitoring data of staging cranes and changes in cropping area in article **III** confirm significant positive correlation between crane numbers and the cropping area of summer wheat, winter wheat, winter rye and all cereals together, and a negative correlation with the area of potatoes. It is predicted that changes in the local numbers and distribution of Common Cranes staging during their migration in Estonia and elsewhere will depend on changes in agricultural land use in staging areas. These findings corroborate our **hypothesis 3.**

4. Examination the stability of the habitat network used by Common Cranes (**IV**) emphasizes (1) the wide range of potential breeding habitats available in Estonia, (2) migration routes used by cranes form a widespread ecological network of staging and wintering areas. Individual cranes may change their migration routes, and this

clearly demonstrates the flexibility of the species towards different endo- and exogenous factors, the result of a combination of genetic background and social transmission, (3) the climate change scenario modelling suggests minimal impact on cranes and confirm the potential for further expansion of cranes in Europe. These findings support our **hypothesis 4.**

5. The analysis of satellite telemetry data (**V**) confirmed 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. These findings do not corroborate our **hypothesis 5**.

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SUMMARY IN ESTONIAN

Sookure (*Grus grus*) pesitsus- ja rändeökoloogia

Sissejuhatus

Maailmas hinnati sookurepopulatsiooni suuruseks 2013.–2014. aastal 690 000 isendit, kellest Lääne-Euroopas (Kesk-Euroopa, Skandinaavia, Soome, Baltimaad, Venemaa ja Valgevene läänepoolne osa) elas 490 000 isendit, Ida-Euroopas (idapoolne Valgevene ja Venemaa, Ukraina, Kasahstani loodepoole osa) 80 000 sookurge, Lääne-Siberis (Uuralite idapoolne osa Lääne-Siberis, Kasahstani põhja- ja keskosa) 100 000 lindu ning Kesk- ja Kaug-Idas Aasia populatsioonis (Ida-Siber ja Hiina põhjaosa) 20 000 sookurge. Uuringud on näidanud, et vähemalt Lääne-Euroopa sookurepopulatsioon on geneetiliselt homogeenne.

Sookurg oli 20. sajandi keskel Lääne-Euroopa areaalis laialt levinud, kuid väikesearvuline pesitseja. Populatsiooni suurenemine algas 1970. aastatel, millele järgnes kiire kasv alates 1990. aastatest ning see on jätkunud tänapäevani. Juurdekasv on aeglustunud alles viimastel aastatel. Populatsiooni suurenemisega kaasnes ka leviala laienemine, eeskätt Saksamaal, kus see võrreldes 1975. aastaga on liikunud 410 km lõuna-, 280 km lääne- ning 160 km loodesuunas. Tšehhimaal hakkasid sookured pesitsema 1989. aastal, Ungaris aga alles viimastel aastatel.

Sookure populatsiooni kasvuga kaasnes pesitsevate paaride asustustiheduse suurenemine. Kui 1967. aastal oli Saksamaal keskmine asustustihedus 0,8 paari 100 km^2 kohta, siis tänapäeval on see sealsel põhilevialal 9,3–18,7 paari 100 km^2 kohta, leviku piirialadel aga ligikaudu kaks paari 100 km^2 kohta. Rootsis oli keskmine asustustihedus 1980. aastal 3,7 paari 100 km^2 kohta, kuid aastatel 1994–1995 juba üheksa paari 100 km^2 kohta.

Sookure elupaigavalik on juba ajalooliselt seotud erinevate märgaladega. Liigi levila põhjapoolses osas olid populatsiooni madalseisu ajal eelmise sajandi keskel esmased elupaigad erinevad sootüübid, kuid läänepoolses osas (Saksamaa) eutroofsed, kinnikasvanud või roostikuga järved, aga ka väikesed märgalad sanglepikutes. Populatsiooni suurenemisega on kaasnenud ka uute sobilike elupaikade asustamine. Nii on Saksamaal asustatud elupaikade hulk suurenenud neljalt tüübilt 1960. aastatel 14 tüübini tänapäeval. Lätis hakkasid sookured 1980. aastatel pesitsema väikestel märgaladel keset metsi, liigniisketel niitudel, järvede ümbruses ja kobraste tekitatud märgaladel. Tšehhis asustasid nad alguses ulatuslikke märgalasid, kuid on nüüdseks levinud ka väikestele tehisjärvedele, kus leidub roostikku või kõrgekasvulist tarna.

Lindude rände lähtepunktiks loetakse aktiivse toitumise algust pesitsusalal enne esimest rändelendu selleks vajalike energiavarude kogumiseks. Ränne koosneb üldiselt toitumisest rändepeatuskohtades rändelennuks vajalike energiavarude taastamiseks ja sellele järgnevast rändelennust järgmisse peatuskohta. Need kaks rändeelementi moodustavad ühe rändefaasi. Ränne tervikuna koosneb üldjuhul mitmest järjestikusest rändefaasist talvitamisalale jõudmiseni. Rändelennu pikkuse järgi jagunevad linnud lühi- ja keskmaa- ning kaugränduriteks.

Euroopas on kirjeldatud sookurgede nelja rändeteed: Lääne-Euroopa, Balti-Ungari, Ida-Euroopa ja Volga-Kaukaasia. Iga rändetee koosneb rändepeatuskohtadest, mis paiknevad üksteisest tavaliselt 100–800 km kaugusel. Väikeste peatusalade (koondavad kuni tuhat isendit) vahemaa on lühem kui suurte (koondavad enam kui 10 000 sookurge) rändepeatuskohtade vahemaa. Lääne-Euroopa rändetee talvitamisalad paiknevad Saksamaast Marokoni (peamiselt aga Prantsusmaal ja Hispaanias), Balti-Ungari rändeteel talvitavad sookured Ungaris, Balkanimaades ja Põhja-Aafrikas. Ida-Euroopa ja Volga-Kaukaasia rändeteid kasutavate lindude talvitamisalad ühtivad, need asuvad Türgis, Iisraelis ning Etioopias. Pesitsusaegse levila põhjaosa sookured on keskmaa- ja kaugrändurid, lõunaosas aga lähirändurid. Sookurgedel on kirjeldatud ka silmusrännet.

Töö eesmärgid

Käesoleva doktoritöö eesmärk oli uurida järgmisi sookure pesitsus- ja rändeökoloogilisi aspekte:

1. Eestis pesitseva asurkonna suuruse ja leviku muutusi ning võimalike pesitsusalade levikut Eestis (**I, IV**);

2. Eesti asurkonna elupaiga valikut ning selle seost pesitsusedukuse ja -fenoloogiaga (**II**);

3. sügisrändel peatuvate sookurgede arvukuse muutusi seoses põllumajandusliku maakasutusega (**III**);
4. sookurgede kasutatava ökoloogilise võrgustiku stabiilsust Eestis ja Euroopas (**IV**);
5. sookurgede kaugrändestrateegiat (**V**).

Materjal ja metoodika

Eestis pesitseva sookure asurkonna muutuste kirjeldamiseks (**I**) töötati läbi olemasolev kirjandus ja kättesaadav, seni avaldamata andmestik. Liigi leviku ja asurkonna suuruse uurimiseks kasutati linnuatlase metoodikat, territooriumite kaardistamist püsialadel ja ühekordseid soolinnustiku loendusi. Arvestades pesitseva asurkonna suuruse arvutamisel sookure leviku regionaalseid iseärasusi, jagati Eesti maastikutüüpide levikukaardi kohaselt kolmeks piirkonnaks: (1) rannikumadalikud ja saared, (2) sisemaised soostunud madalikud ja nõod, ning (3) kõrgustikud ja lavamaad. Sookure võimalike pesitsusalade leviku analüüsimiseks kasutati liigi leviku statistilisi mudeleid, mis kirjeldavad, kuidas on keskkonna tunnused seotud liigi geograafilise levikuga. Mudeldamisel kasutati sookure pesakaartide, Eesti linnuatlase ja ühekordsete soolinnustiku loenduste andmestikku (**IV**).

Sookure Eesti asurkonna elupaigavaliku analüüs baseerus 161 pesaleiul ajavahemikust 1880–2001 (**II**). Elupaikade jaotuse kirjeldamiseks rühmitati pesaleiud seitsme elupaigatüübi (raba, siirdesoo, madalsoo, jõeluht, riim- ja mageveelised rannikulaguunid, sisemaa järved ning mets) vahel. Pesapaiga kirjeldus (5 m raadiuses ümber pesa) kajastab pesa asukohta asustatud elupaigas, veerežiimi, puude lähedust pesale, taimekooslust, pesa avatust ja selle ümbruse mikroreljeefi. Veel mõõdeti pesa kaugust pesitsust häirivatest teguritest (ehitised, inimasustus, maanteed, jalgrajad) ja analüüsil arvestati ka pesitsusedukust.

Põllumajandusliku maakasutuse muutuse mõju analüüsil sügisrändel peatuvate sookurgede arvukusele (**III**) kasutati statistikaametilt saadud andmeid erinevate põllukultuuride pindala ning saagikuse kohta Hiiumaal, Läänemaal ja Eestis tervikuna ajavahemikul 1965–2005. Sookurgede loendusandmed pärinesid Matsalu piirkonnast alates 1961. aastast, Hiiumaalt alates 1982. aastast ja kogu Eesti kohta alates 1983. aastast.

Sookurgede kasutatava ökoloogilise võrgustiku uuring (**IV**) sisaldas (1) rändeteede kaardistamist, (2) rändepeatuskohtade (30 km raadius ümber ööbimiskoha) ja kontrollalade (rändepeatuskohast 60 km lõuna poole asetsev piirkond) CORINE maakatte analüüsi, (3) sookurgede elualade kaitstuse analüüsi ning (4) kliimamuutuse mõju analüüsi sookure populatsioonile.

Sookure kaugrändestrateegia analüüs (**V**) tugines Soomes (2009–2012 märgistati seitse isendit) ja Eestis (2009–2017 märgistati 11 isendit) satelliitsaatjatega märgistatud Ida-Euroopa rändeteed kasutanud noorlindude andmetele (sookurgede noorlinnud rändavad sügisel koos vanematega). Soome ja Eesti sookure asurkondade märkimisväärne ökoloogiline erinevus on pesitsemine erinevatel laiuskraadidel, mida tuleb meeles pidada, kui räägitakse vastavatest asurkondadest. Märgistuspiirkondade vahemaa oli 500 km. Rändetee kohta mõõdeti järgmised parameetrid: (1) rändetee pikkus Soome ja Eesti sookurgedel, (2) rändepeatuskohtade asukohad ja vahemaad, (3) ökoloogiliste tõkete (meri, mäestik, kõrb) asukohad ja laiused ning (4) talvitamiskohtade paiknemine. Sookure kaugrändestrateegia kirjeldamiseks kasutati (1) rändefaaside arvu Soome ja Eesti asurkondadel, (2) rändefaasi ajastust ja kestust, (3) rändepeatuse kestuse sõltuvust rändefaasist, (4) rändelennu pikkuseid rändepeatuskohtade vahel ja (5) üldist rändekiirust.

Tulemused

Sookure populatsiooni kasv algas 1970. aastatel ühtaegu nii Eestis (**I**) kui ka kogu Euroopas, mis kajastus kohe ka talvitamisaladel tehtud loendustes. Pesitseva asurkonna suurenemisega Eestis (300 paari 1970. a ja 5800 paari 1999. a, keskmine kasvukiirus erinevatel ajaperioodidel oli vahemikus 8,8–20,2% aastas) kaasnes leviku üldine laienemine (323 asustatud UTM-i atlaseruutu 1977–1982 ning 498 atlaseruutu 1997–2001, keskmine atlaseruutude asustamise kiirus 2,3% aastas) ning keskmise asustustiheduse suurenemine (2,2 paari 100 km^2 kohta 1980. a kuni 17,4 paari 100 km^2 kohta 1999. a) (**I**). Sellega kaasnes uute, seni asustamata, kuid pesitsemiseks sobivate elupaikade (taimestikurikkad veekogud vanades karjäärides, väikesed märgalad meresaartel ja metsades) asustamine (**I**). Enamik sookurgi pesitses Eestis sajandivahetusel madalsoodes (4200 paari), millele järgnesid rabad (700 paari) ja siirdesood (400 paari). Ülejäänud elupaikades pesitses kokku 500 paari. Sookure populatsiooni suurenemisele ja lausalise leviku tekkimisele Eestis on oluline toetav tegur olnud võimalike elupaikade lausaline levik (**IV**). See protsess Euroopas tervikuna on viinud eeskätt noorlindude väljarändele ning pesitsusala laienemiseni. Hinnanguliselt tagas sigimisedukus 0,9 lennuvõimestunud noorlindu pesitseva paari kohta populatsiooni 8% juurdekasvu aastas. Populatsiooni jätkuva suurenemise tulemusena on sookurgede sigimisedukus hakanud vähenema.

Sookure pesitsusala valikukriteeriumid on üldiselt sarnased kogu pesitsusareaali ulatuses. Väikesed erinevuses selles tulenevad peamiselt maastikulistest ja märgalade tüübi erinevustest. Vaatamata lindude pesitsemisele erinevates elupaikades on kõikidel pesitsusaladel sarnane veerežiim, taimekooslus ja mikroreljeef. Kuigi sookured pesitsevad erinevatel märgaladel, eelistavad nad pesitseda rabades ja soodes (72% kogu populatsioonist) (**II**). Sookurgede pesitsusedukus on seotud elupaiga kvaliteediga (saadaoleva toidu hulk, varjepaikade olemasolu, kisklus, häiringud) ning kaugusega naaberpesadest. Pesakonna keskmine suurus (1,65 poega pesitseva paari kohta) oli palju suurem, kui naaberpesad olid üksteisest 0,5–1,0 km kaugusel, võrreldes pesakondadega (1,16 poega pesitseva paari kohta), kes paiknesid üksteisest enam kui 1 km kaugusel (**II**). Inimhäiringul (pesa kaugus ehitistest, inimasustusest, teedest ja jalgradadest) on pesitsustulemustele selgelt negatiivne mõju (**II**). Vaatamata sellele on täheldatud üha sagedamini sookurgede pesitsemist inimasustuse vahetus läheduses kui aastakümned tagasi. Sookurgede pesitsemine (munemise algus) on Eestis muutunud alates 20. sajandi keskpaigast iga dekaadiga keskmiselt kaks päeva varasemaks (**II**). Eestisiseselt erineb munemise algus märkimisväärselt (12 päeva) Lääne-Eesti saarestiku ja maismaa vahel, keskmised väärtused vastavalt 18. aprill ning 30. aprill. Muu hulgas sõltub munemise algus ka sookurgede elupaiga pindalast (**II**).

Sügisrändel peatuvate sookurgede arvukus on positiivselt seotud külvatud teravilja pindalaga ja negatiivselt kartulipõldude pindalaga (**III**). Tugevaim oli seos peatuvate sookurgede arvu ning talirukki ja -nisu pindalaga, sest sookured saavad orasepõllul toituda nii sügisel kui ka järgmisel kevadel ning sügisel nende kõrrepõldudel. Tõenäoliselt olid just 1950. ja 1960. aastatel Eestis rajatud suured põllumassiivid peamised sügiseste rändekogumite tekke ajendid. Leitud tulemus kinnitab, et sookurgede arvukus ja levik rändepeatuskohtades sõltub nii Eestis kui ka rändeteedel põllumajanduslikus maakasutuses toimuvatest muutustest (**III**).

Kõik rändeteed koos rändepeatus- ja talvitamisaladega moodustavad ühtse ökoloogilise võrgustiku, sest sookured võivad erinevatel aastatel oma rändeteed vahetada ning seega kasutada geograafiliselt ja keskkonnatingimuste poolest väga erinevaid peatus- ja talvitamisalasid (**IV**). Ökoloogilise võrgustiku püsivus ja liigi suutlikkus kohaneda erinevate keskkonnatingimustega on ilmselt olnud tähtis tegur, mis on taganud sookurepopulatsiooni püsiva kasvu. Analüüs näitas, et kaitstavate alade moodustamine mõjutab vähe populatsiooni juurdekasvu, mis on sellest pigem sõltumatu (**IV**). Kliimamuutused näivad mõjutavat sookurepopulatsiooni pigem positiivselt, sest sellega kaasnev kliima soojenemine põhjustab talvitamisalade ulatuslikumat nihet põhja suunas. See tähendab aga rände (suurima suremusega ajaperiood lindudel) lühenemist ja võimalikku, eriti noorlindude veelgi paranevat elumust. Kliimamudelid ennustavad Lääne-Eestis 2080. aastaks keskmise talvise temperatuuri tõusu üle 0 °C, millega võib kaasneda sookurgede talvitama jäämine (**IV**). Arvestades sookure varasemat ja tänapäevast elupaigavalikut ning vaatamata looduskaitse tagasihoidlikule mõjule populatsiooni arengule, on soode ja rabade kui liigile esmatähtsa elupaiga kaitse ning nende loodusliku veerežiimi taastamine sookure pikaajalises kaitsestrateegias kriitilise tähtsusega.

Sookure põhjapoolse asurkonna kaugrändestrateegia erineb märgatavalt lõuna pool pesitseva asurkonna kaugrändestrateegiast rändepeatuskohtade tiheduse ja paiknemise, päevase rändelennu pikkuse (vastavalt 563,7 ja 364,5 km päevas) ning kogu rändeperioodi pikkuse (vastavalt 32–37 päeva ja 55–65 päeva) poolest (**V**). Sookured Soome asurkonnast taastavad rändeks vajalikke energiavarusid peamiselt Askania-Nova ja Sivaši piirkonnas Lõuna-Ukrainas. Eesti asurkonna lindude peamised energiavarude taastamise piirkonnad paiknevad aga Valgevenes. Keskmine rändepeatus kestab 12,8 päeva ja sookured veedavad rändepeatuskohtades 85,2–86,6% kogu rändeajast. Sookured kasutasid kaugrändel kahte strateegiat: (1) rändeks vajalike energiavarude taastamine ühes rändepeatuskohas Valgevenes või Ukrainas, millele järgneb lend talvitamisalale (rändeaja minimeerimise strateegia), või (2) kaks kuni kolm rändepeatust Valgevenes või Ungaris enne otselendu talvitusalale (energia minimeerimise strateegia). Arvestades maksimaalset rändelennu ulatust (2400–5100 km 5–15 päevaga) energiavarude täiendava taastamiseta (**V**), peavad sookured valima rändeks ideaalselt sobivad ilmatingimused (taganttuul, ulatuslik kõrgrõhkkond) ning vahetama rändeteel vahelduvate tingimuste tõttu lennuviisi (sõudelend rände kolmnurgas või tõusev/laskuv lennuviis). Põhja pool pesitsevate sookurgede keskmisest kiirema päevalennu ja ligikaudu poole lühema rändeperioodi põhjal võib oletada, et võrreldes lõuna pool pesitsevate lindudega olid nad rändetingimuste suhtes oma rände õigeaegseks lõpetamiseks rohkem valivamad (**V**).

Kurgede rändemustri ja käitumise mõistmine on kriitilise tähtsusega nende kaitsestaatuse ning erinevate liikide vajaduste hindamiseks. Isegi kui kured on nende pesitsus- ja talvitamisalal kaitstud, võivad neid ohustada rändeteel toimuvad elupaigamuutused traditsioonilistes rändepeatus- ja puhkepaikades.

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I

ORIGINAL PUBLICATIONS

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Changes in distribution and numbers of the breeding population of the Common Crane *Grus grus* in Estonia

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The aim of this study is to analyse population trends and distribution of the breeding population of the Common Crane in Estonia. The population size and density of the Common Crane in Estonia has increased several times over the last 30 years (1970–2001). According to the most recent population estimate, about 5800 pairs were breeding in Estonia in 1999. The mean population density of the Common Crane in Estonia was 17.4 pairs/100 km^2. Most of the Common Cranes are nesting in mires (5300 pairs, 91%), primarily in fens (4200 pairs, 72%). The mean population density in fens, transition mires and raised bogs was 41.3, 38.3 and 15.9 pairs/100 km^2, respectively. Several factors have probably contributed to the recent increase in the Common Crane breeding population in Estonia, e.g. the emergence of new nesting sites connected to human activity, locally higher spring temperatures and conservation activities.

1. Introduction

The Common Crane is a breeding species and passage migrant of wide distribution in Europe. The breeding range extends from lat 50°N to lat 69°N and the wintering areas are located in the Near East, North-eastern and Northern Africa and South-western Europe (Cramp & Simmons 1980, del Hoyo *et al.* 1996, Meine & Archibald 1996, Prange 1999). The breeding range began to narrow significantly during the Middle Ages and this negative trend continued until the middle of the 20th century (Cramp & Simmons 1980). Only during the second half of the 20th century has the population showed signs of increase and begun to re-establish itself in the original area of distribution (Prange 1994, Meine & Archibald 1996, Prange 1999, Wetlands International 2002). Despite these recent positive trends, the Common Crane is still categorized as an SPEC Category 3 species, i.e. a species whose global population is not concentrated in Europe, but which has an unfavourable conservation status in Europe (Tucker & Heath 1994). As a species, the Common Crane is sensitive to human activities. The most important threats to the species are the destruction of and decline in the quality of habitats, disturbance during the breeding season, illegal hunting, unfavourable weather conditions and climate change (Prange 1994, Meine & Archibald 1996).

In Estonia the Common Crane is a common breeding species and passage migrant. The breeding population size has been estimated at 600–700 pairs in Estonia (Prange 1994). Already in 1958 the species was defined as a nationally protected species, and it currently is listed as a category II protected species under the Natural Protected Objects Act. More recently, in March 2003, the Ministry of the Environment approved the Conservation Management Plan for the Common Crane, which forms the basis for the study, monitoring and conservation management of the Common Crane in Estonia during 2003–2007 and onward.

The objective of this study is (1) to analyse the earlier estimates of the distribution and numbers of the breeding Common Crane in Estonia; (2) to provide a recent total population estimate and trend line for the breeding population over the last decades and (3) to analyse the reasons for the changes in the distribution and numbers of breeding cranes in Estonia.

2. Material and methods

This study provides an analysis of all published data on the distribution and numbers of the Common Crane in the wider countryside of Estonia (Kumari 1958, Randla *et* al. 1971, Lilleleht &, Leibak 1993, Renno 1993, Leibak *et al.* 1994; Lõhmus *et al.* 1998; Leito 1999; Nowald *et al.* 1999, Leito 2000, 2002, Leito *et al.* 2003a), and also of unpublished data.

2.1. Census methods

2.1.1. Bird atlas

The occurrence and distribution of the Common Crane throughout Estonia during the breeding season were studied in 1977–1982 (Renno 1993) and in 1997–2001. The territory of Estonia was divided into 567 atlas squares (10 × 10 km UTM-grid squares). To determine the breeding status of the Common Crane, a scale of evidence of nesting was used (Renno 1993). The breeding status was described as follows: possible nesting of the species — species observed in a characteristic nesting biotope in the breeding season; probable nesting — incomplete nest or territorial calls of cranes in a characteristic nesting biotope in the breeding season; confirmed nesting — recently used nest found (also abandoned clutch or destroyed nest) or unfledged young at the nest.

2.1.2. Mapping of territorial calls

Since 1997 the mapping of territorial calls has been one of the main methods used for monitoring the number of breeding Common Cranes in Estonia. For the purpose of carrying out a census of territorial pairs, 10 × 10 km UTM-grid squares are selected and fixed cartographically. A survey square is broken down into four equal 5 × 5 km sub-squares, and these four squares are further broken down into four small squares of 2.5 × 2.5 km. Survey points (listening points) are cartographically fixed in the geometric centre of each small square. The distance between listening points is 2.5 km and there are a total of four listening points on each 5 × 5 km survey square and 16 listening points on each 10 × 10 km square. The cartographically fixed points are then determined in the landscape and these points are used for finding the breeding territories of the Common Crane.

All locations of territorial calls of the Common Crane are fixed at each survey point and marked on the field map according to the defined azimuth and distance. Censuses are conducted in April and May when the breeding (territorial) Common Crane pairs are most vocal. The territorial calls are listened for during the two hours after sunrise and the two hours before sunset. During the breeding season a minimum of three counts are undertaken at each survey point. After the censuses are completed, the observation clusters are analysed according to the classical mapping censuses of breeding land birds (Koskimies & Väisanen 1991).

The main steps in this original census method were developed in Estonia already in the 1980s, although the method was not used until 1997. From 1997 to 2001 censuses of 800 km^2 of different habitats in various parts of Estonia were carried out according to this method.

2.1.3. Single-visit mapping of territorial pairs in mires

The most common census method for counting the Common Crane during the breeding season in Estonia is single-visit mapping of territorial pairs. With this method, censuses are conducted in the early morning for five hours beginning at sunrise from the middle of May to the middle of June. The width of the census transect varies from 200 to 300 metres, depending on the saturation and accessibility of the landscape. The survey plot (a mire) is fully covered with parallel census transects.

This method is very similar to the simplified territory mapping technique used in Sweden for the inventory of birds breeding in mires (Svensson 1978, Boström & Nilsson 1983). The census efficiency of the single-visit mapping method for the Common Crane in Swedish mires is 65% (Bylin 1980, Arvidsson *et al.* 1992). In Estonia the efficiency of this method has been not tested, but it did not seem to differ much from the Swedish estimate.

Censuses according to this method have been regularly carried out in Estonian mires since 1986. During the period from 1986 to 1996 the censuses covered 1024 km^2 (18 mires) and during the period from 1997 to 2001, 1156 km^2 (97 mires).

In 1997–2001, when all three census methods described above were used, censuses were carried out on 107 plots covering 2653 km^2, or 6% of the total area of Estonia. From 1986 to 2001, different censuses of breeding cranes were conducted on 120 plots covering 3089 km^2, or 7% of the total area of Estonia. These censuses included all land cover types and biotopes in Estonia, inhabited and uninhabited by cranes. The size of a survey plot was 0.3–300 km^2 with a mean value of 27.1 ± 43.0 km^2 (± SD, n = 120). The number of territorial pairs was recorded for all survey plots and the population density was estimated.

2.2. Data preparation and analysis

The analysis included the following 16 characteristics: the location of the survey plot, the area of the survey plot, the nesting biotope size, the nesting biotope type, the location of a nest, the biotope type around the nest, the level of human disturbance around the nest, the census year, the census date, the number of counted pairs on the survey plot in the census year, the population density on the survey plot in the census year, the mean population density in Estonia in the census year, the mean population density in Estonia in the census period, the mean brood size on the survey plot in the census year, the mean brood size in Estonia in the census year, and the mean brood size in Estonia in the census period.

The calculation of the population size of the breeding Common Crane in Estonia in 1997–2001 was based on the method of stratified mean (Krebs 1999). To do the calculation, the territory of Estonia was divided up into three strata to provide representative samples and to take into consideration the regional differences in the distribution of the Common Crane. The strata were determined according to the natural joint features of the Estonian landscape based on generalised land cover types identified in the CORINE Land Cover nomenclature (Meiner 1999, Arold 2001). Similar landscape types were combined, with a final determination of three main landscape regions, or strata. The stratification method was considered to be the best approximation for estimating the Common Crane population parameters, taking into account the fact that the survey plots were not of equal size.

The Mann-Kendall test was used to detect trends in time series. One advantage of the Mann-Kendall test is that the standard normal distribution of time series for the estimation of a linear trend is not needed. The Mann-Kendall test is a non-parametric test allowing for analysis of time series that are not characterized by standard normal distribution. The second advantage of the test is its relatively low sensitivity to omissions in data resulting from the non-homogeneous character of the data. The relationship between the population density and biotope area was fitted by the inverse first order model using non-linear regression with the Marquardt-Levenberg algorithm. The best-fit parameter values of the model were compared using a one-way analysis of variance (ANOVA), followed by Tukey's and Scheffe's tests for group mean comparisons.

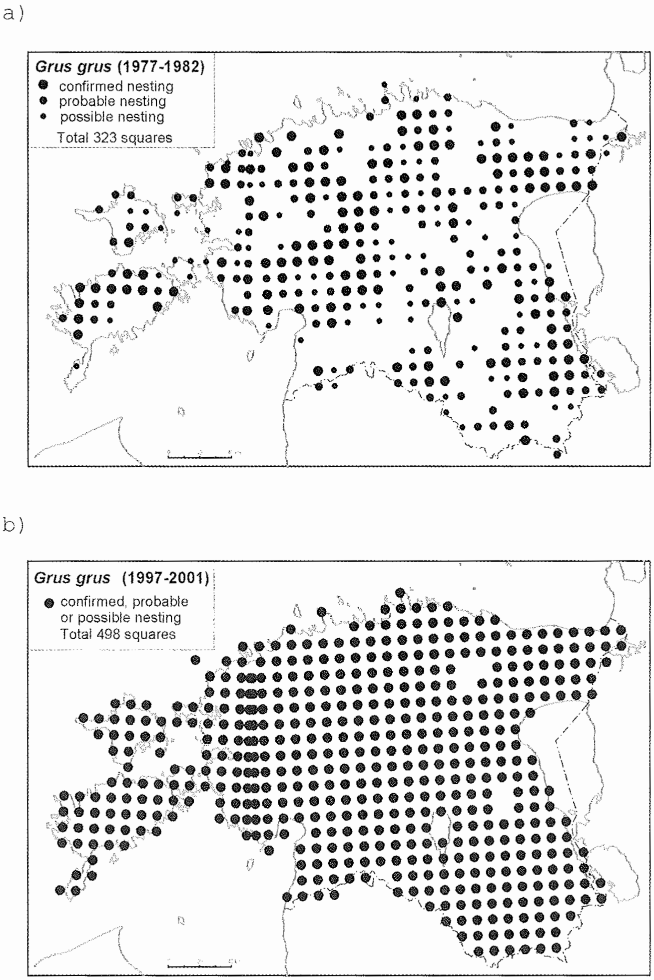

Fig. 1. Distribution of the Common Crane during the breeding season in Estonia in 1977–1982, according to the Estonian Bird Atlas (Renno 1993): (a) in 1997–2001 and (b) on the UTM-grid map of 10 × 10 km squares.

3. Results

3.1. Changes in distribution

According to the Estonian Bird Atlas 1977–1982, the Common Crane was breeding in 323 atlas squares (total number of squares observed was 567), with confirmed breeding in 121, probable breeding in 120 squares and possible breeding in 82 squares (Fig. 1a). According to our data in the period 1997–2001, breeding cranes were detected in 498 squares (total number of squares observed was 567 (Fig. 1b)). Confirmed breeding was observed in 204 squares, probable breeding in 242 squares and possible breeding in 52 squares. Thus, the total number of squares where cranes were detected increased from 323 (57% of atlas squares) in 1977–1982 to 498 (88% of atlas squares) in 1997–2001.

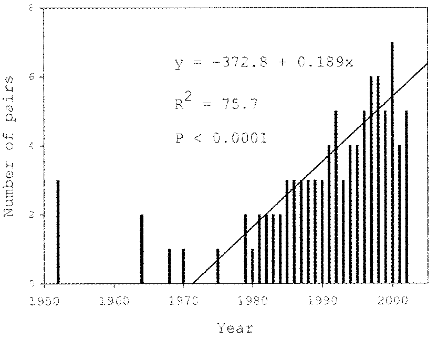

Fig. 2. Number of territorial pairs of the Common Crane at the Nigula bog (area 20 km²) in 1952–2002. The trend line is fitted for the period of 1971–2002; the increase in numbers is statistically significant (Mann-Kendall non-parametric test, P < 0.0001).

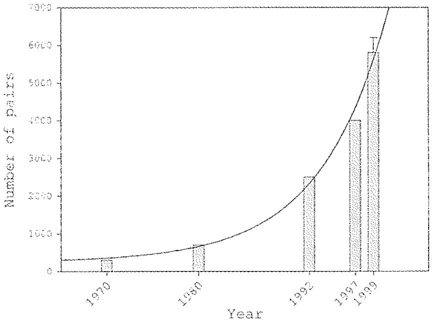

Fig. 3. Estimated population size of the breeding Common Crane in Estonia in 1970–1999. Earlier estimates have been reviewed. The exponential growth curve was fitted to the data (R^2 = 98.2, P < 0.01). A 95% confidence interval for the estimated population mean is shown for 1999.

3.2. Changes in numbers

At the local level of the Nigula bog, the number of breeding pairs varied between 1 and 7 pairs in 1952–2002. The number decreased from 1952 to 1970, then increased significantly from 1971 to 2000. Because of the lack of observation data in the early period, the trend line was fitted only for the period of 1971–2002 (Fig. 2; $R^2 = 75.7$, $P < 0.0001$).

Based on the surveys made in 1970, 1980, 1992, 1997 and 1999, the Common Crane population in Estonia has increased significantly from 300 breeding pairs in 1970 up to 5800 pairs in 1999 (Fig. 3; $R^2 = 98.2$, $P < 0.01$).

3.3. Number and density of cranes in different habitats

In terms of different nesting biotopes, the use of the stratified random sampling approach provided statistically reliable information only for the number of pairs breeding in fens and raised bogs. The Common Crane population size in 1997–2001 was between 2500 and 5900 territorial pairs in fens, with a mean value of 4200 pairs, and between 500 and 900 pairs in raised bogs, with a mean value of 700 pairs, at the 95% confidence limit. In transitional mires there were about 400 breeding pairs and in all other habitats about 500 breeding pairs (Fig. 4).

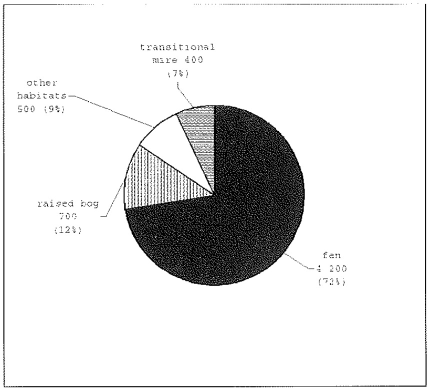

Fig. 4. Mean distribution of the Common Crane breeding pairs in Estonia by main habitat type in 1997–2001 (n = 5800).

The Common Crane population density in fens varied from 0 to 250, with a mean value of 41.3 pairs/100 km² (n = 22, area 150 km²). The highest density in Western Estonia was seen in small quagmires with a mosaic of sedge-reed-bed communities. The smallest fens occupied by the Common Crane were only 0.5–1.0 ha (n = 4). The relationship between the population density of the Common Crane and the fen size was statistically significant (non-linear regression with the

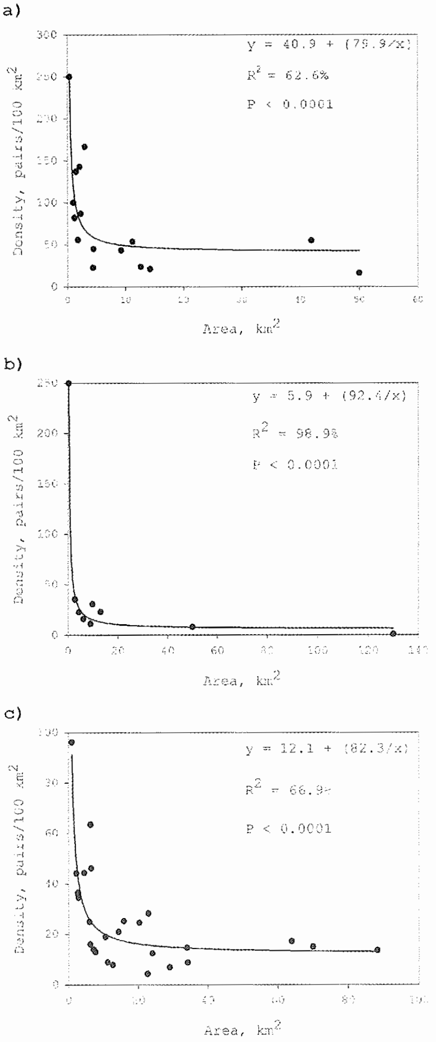

Fig. 5. The relationship between the Common Crane population density and the size of the breeding biotope in (a) fens, (b) transitional mires and (c) raised bogs. The difference between the population densities in different biotopes is statistically significant (Kruskal-Wallis non-parametric dispersalanalysis, $P < 0.001$, $n = 53$).

Marquardt-Levenberg algorithm, $P < 0.001$, $n = 16$) (Fig. 5a).

In transitional mires the population density varied from 0 to 285, with a mean value of 38.3 pairs/100 km^2 ($n = 9$, area 60 km^2). The highest population density was recorded in transitional mires located around raised bogs. The relationship between the population density and the size of the transitional mire was statistically significant (non-linear regression with the Marquardt-Levenberg algorithm, $P < 0.001$, $n = 9$) (Fig. 5b).

The population density in raised bogs varied from 0 to 96, with a mean value of 15.9 pairs/100 km^2 ($n = 48$, area 734 km^2). The relationship between the population density and the size of the raised bog was statistically significant (non-linear regression with the Marquardt-Levenberg algorithm, $P < 0.001$, $n = 28$) (Fig. 5c). Hollow-pool bogs were the most common breeding site in large treeless raised bogs, while treed hollow-pools with ridges were the most common in small raised bogs. The Common Crane did not occupy small treed raised bogs.

To test the differences between the population densities in different habitats, the best-fit values of regression curves were compared using a one-way analysis of variance (ANOVA). The asymptote (y_0) of the model could be interpreted as a typical population density for cranes in large areas (> 10 km^2) for certain biotope types. The comparison of these values between biotopes showed significant differences ($P < 0.0001$) in population density. According to the calculated asymptote values, the population density was highest in fens ($y_0 = 40.9 \pm 12.0$) and lowest in transitional mires ($y_0 = 5.9 \pm 2.7$). In raised bogs this value ($y_0 = 12.2 \pm 2.8$) was two-fold higher compared to transitional bogs. At the probability level $P = 0.05$, all three asymptote values differed from each other (Tukey's and Scheffe's least significant difference values were 4.76 and 5.97, respectively).

The second component of the regression model also varied significantly between biotopes ($P < 0.05$, ANOVA). However, in the case of transitional mires the number of observations is low, and, in fact, for population densities above 50 pairs/100 km^2 there is only one sample, making the calculated best-fit value ($a = 92.4$) unreliable. Fens and raised mires did not differ by best-fit values of 'a'. The second component of the applied regression model may reflect a difference in population density values between studied habitats in small biotope areas (< 10 km^2). In order to verify this assumption additional data on transitional mires are needed.

In terms of landscape regions, the mean population density of the Common Crane on coastal lowlands and islands was equal to 18.5 pairs/100 km^2 ($s^2 = 0.235$, $n = 308$), on inland swampy lowlands and depressions, 18.0 pairs/100 km^2 ($s^2 = 0.152$, $n = 136$) and on uplands and plateaus, 7.3 pairs/100 km^2 ($s^2 = 0.523$, $n = 17$). There were no statistically significant differences between population density mean values of the landscape regions (ANOVA, $P > 0.05$). The mean population density of the Common Crane in Estonia was 17.4 pairs/100 km^2 (calculated as the arithmetic mean of the total number of surveyed territorial pairs ($n = 461$) and the total area of survey plots (2653 km^2)).

4. Discussion

4.1. Changes in distribution area

A comparison of the distribution map of the Common Crane in 1977–1982 (Renno 1993) with the distribution map of CORINE Land Cover types (Meiner 1999) shows strong overlap of the distribution of cranes and the distribution of natural habitat types in Estonia. On the other hand, the Crane rarely occupied coastal areas and was absent in some regions of central and southern Estonia. The cranes were totally absent from artificial and agricultural landscapes.

In 1997–2001 the Common Crane was found throughout all regions of Estonia, occupying also in some artificial landscapes.

As in Estonia, the Common Crane has expanded its range throughout Europe during the last three decades (Prange 1994, 1999, Tofft 1999, Hagemeijer & Blair 1999, Salvi & Moreau 2000, Miikkulainen 2001). In this connection, the Crane's expansion of its range in Estonia reflects the much larger process of the expansion of the species throughout its breeding range during 1970–2000.

4.2. Changes in numbers

According to E. Kumari (1958), there were more Common Cranes in the 18th and 19th centuries in the Estonian mires and grasslands than in the middle of the 20th century. The estimate was based on an analysis of the first recordings of the Eastern Baltic avifauna and on changes in climate and landscape in these time periods in general. Unfortunately, the total population estimate for the Common Crane in the wider countryside was not provided and the earlier numbers of the Common Crane in Estonia are unknown.

The first numerical total population estimate for the breeding Common Crane in Estonia was made in 1970 (Randla *et al.* 1971), based on the answers to a questionnaire covering different forest management units. Data were obtained on 110 Common Crane pairs, and the total number of the breeding population was estimated at 200 pairs. Considering the low level of coverage (recovery rate 59%, $n = 22$) of the survey, especially in inaccessible mires where the population density is the highest and where about 90% of cranes are breeding, we suggest that the population size was underestimated. Based on our calculations, and taking into the account the coverage of the survey and the relative importance of mires not surveyed, the actual population size was about 300 pairs in 1970.

According to the Estonian Bird Atlas (Renno 1993), the Common Crane breeding population in Estonia in 1977–1982 was estimated at 350 pairs. However, in a number of cases more than one pair of cranes was detected per Atlas Square and pairs exhibiting possible breeding behaviour were found in 80 squares. In addition, as in 1970, the large mires were poorly surveyed. Taking a mean population density of 10 pairs/100 km^2 as a basis, as calculated for the Nigula bog, the estimated population size of the Common Crane in mires (total area about 9000 km^2; Valk 1988, Paal *et al.* 1998) could have been close to 900 pairs in 1977–1982. Assuming that the population density in the Nigula bog was probably higher than the average, the actual number of Common Cranes breeding in mires was about 600 pairs and the total population was about 700 pairs. This number demonstrates that the population size of the Common Crane was considerably higher than estimated at that time and that the number of cranes in Estonia had increased already in the 1970s.

In 1992 the Common Crane population in Estonia was estimated at 600–700 pairs (Lilleleht

& Leibak 1993, Leibak *et al.* 1994). The population estimate was obtained by means of direct extrapolation of the mean population density, calculated on the basis of the survey plots, to the wider countryside of Estonia. In terms of trend, it was stated that the population size of the species increased during the period of 1941–1970, as well as in 1971–1990.

We suggest that the method used for calculating the total population of the Common Crane in Estonia in 1992, and in 1997 and 2000, before this study, was not correct and did not allow for direct extrapolation of numbers in the wider countryside, because the size and distribution of the study plots were unequal and the mean population density used was not representative of all Estonia. We used the stratified mean method (Krebs 1999) and the fitted trend line and, based on this method, have re-estimated the total population to be 2500 pairs in 1992. We also found that the population increase in 1970–1990 was much more rapid than previously considered.

In 1997 the Common Crane population in Estonia was estimated at about 1500 pairs (Leito 2002). In terms of trend, it was stated that the periods of 1971–1990 and 1991–1997 reflected a moderate increasing trend (ranked as 10%–50%) (Lõhmus *et al.* 1998, Leito 2000, 2002). By our estimate, the total number of breeding cranes was about 4000 pairs in 1997. In 2000 the population size was estimated at about 2000 pairs (Leito 2002). According to our calculations, the total population was between 5400 and 6200 pairs, with a mean value of 5800 pairs in 1999, at the 95% confidence limit.

Thus, by our estimation, the total population of the Common Crane in Estonia has increased roughly twenty-fold during the last three decades (1970–2000) from about 300 pairs in 1970 to 5800 pairs in 1999. The rate of increase has been the highest during the last two decades, 1980–2000, approaching exponential growth. In recent years, however, based on long-term censuses in the Nigula bog and in some other monitoring areas, we suggest that at the beginning of the 2000s the population increase was probably levelling out and the number of breeding Common Cranes in Estonia has probably stabilized at around 6000 pairs.

The high population density in mires, especially in fens, indicates that the Common Crane prefers these habitats because they offer the best features for nesting sites, e.g. low relief, a suitable plant community, preferred water conditions, openness and a low-level of disturbance (Leito *et al.* 2003b). The availability of food resources around the nest site is probably not so important (not limiting) because, to a large extent, the breeding pairs and pairs with young feed outside of the mires, up to several kilometres away from the nest (Nowald 1999, Peske *et al.* 2003, Leito *et al.* (in prep.)).

The increase in the Common Crane population in Estonia coincides well with the increase in numbers of cranes throughout Europe (Prange 1994, 1999, 2003). Compared to Estonia, the trends in the total population of the Common Crane in Finland (Merikallio 1958, Väisänen *et al.* 1998, Miikkulainen 2001) have probably been less marked, although the trend line is very similar — a decline from the 1950s to the 1970s and an increase from 1980 to 2000, especially in the 1990s. Although the precision and validity of the census methods used in Finland, as in most other cases, are not known and the results may be biased, a general increasing trend in the population size is evident. The increase in the European breeding population has also been confirmed by higher counts of staging cranes at migration stopover sites in France, Germany, Finland and Hungary (Rinne 1995, Salvi 1996, Prange 1999, Le Roy 2002, Végváry & Tar 2002).

4.3. Reasons for changes

4.3.1. Nesting habitats

In Estonia the emergence of new nesting sites connected to human activity has been one reason cited for the increase in the Common Crane breeding population. As a result of reforestation and a large part of the arable land being left uncultivated, forest land has increased in Estonia over the past century more than two-fold (Mander *et al.* 1996, Yearbook Forest 2000, Kohava 2001). Additionally, over the past three decades the number of immature stands has increased and some forests have been thinned, which has resulted in new nesting sites for the Common Crane in the cut areas and thinned forests (Leito *et al.* 2003a, b). The cranes do not breed in dense forest but they will occupy thinned and cut areas of large forests. The increase in the number and distribution of breeding cranes coincided well with the above-described changes in Estonian forests.

New nesting sites for Common Cranes have also emerged as a result of the transformation of former quarries into wetlands. From the 1960s to the 1980s a number of gravel and sand quarries were being exploited. Today, these quarries are either depleted or mining has been suspended or terminated for conservation purposes. Consequently, a number of such abandoned quarries have filled with water, become overgrown with vegetation and been transformed into wetlands. Additionally, many former peat mines have been abandoned and are now occupied by the Common Crane.

4.3.2. Warming of the climate and a shorter migration route

The Common Crane's earlier spring arrival in Estonia and the earlier start of egg-laying and hatching of eggs clearly corresponds to a local warming of the climate. The annual temperature cycle in Estonia shows definite signs of change in recent years, with the winter (January, February) and spring (March, April, May) temperatures becoming warmer. The mean spring temperature in Estonia has increased by 1.4 °C from 1876 to 2000, and, most particularly, the mean temperature in March, which is when the Common Crane arrives in Estonia, has increased by 5 °C (Keskpaik *et al.* 1997, Jaagus & Ahas 2000, Jaagus *et al.* 2002).

Because of the earlier spring, the cranes can arrive and nest earlier in Estonia (Keskpaik *et al.* 1997, 2000), which results in a higher survival rate of the young cranes. The reason is that the earlier the hatching date, the stronger the young cranes are by the departure date (which has not changed) of their first migration, as compared to young hatched at a later date. Without a doubt, the higher survival rate of the young contributes to the population increase.

The breeding Common Crane in Estonia uses all three of the most important European migration routes (Leito *et al.* 2000, Leito & Ojaste 2001, Leito *et al.* 2003a, c); however, major changes have taken place with respect to the western route, which is the most important migratory route for cranes breeding in Estonia (Leito *et al.* 2003a, c). Formerly, the cranes using this route migrated to southern Spain and Morocco for wintering (Cramp & Simmons 1980). Recently, more cranes are wintering in France and even Germany, while Morocco is losing its importance as a wintering area, particularly for young birds (Salvi 1996, Prange 1999, 2001, Alonso *et al.* 2000, Le Roy 2001, 2002). A shorter migration route decreases the energy-expenditure and the risks during migration, which also contribute to a higher survival rate and an increase in the population size.

4.3.3. Conservation activities

Though we cannot prove it directly, we believe that conservation activities have also played a role in the recent increases in the Common Crane population in Estonia, as well as in Europe and the whole world. First, it is evident that hunting bans must have had a positive effect on the Common Crane population through a lower mortality rate, as has been seen with different goose species (Ebbinge 1991, Kalchreuter 1991). In Estonia, the hunting of the Common Crane was prohibited in 1958; and it seems that illegal hunting and accidental shooting of cranes is of very small importance in Estonia at the moment. Unfortunately, the actual bag and hunting mortality rate of the Common Crane in Estonia in the earlier open hunting periods is unknown.

Currently, the hunting of cranes is prohibited in all European countries and even though in some areas illegal hunting and accidental shooting are still a problem, the bag rate is essentially less than in earlier times (Prange 1994, 1995, del Hoyo *et al.* 1996, Meine & Archibald 1996, Prange *et al.* 1999). Thus, the ban on hunting activities at many Common Crane breeding, feeding and roosting sites throughout Europe has probably also contributed to the recent increase in the Crane population (Alonso *et al.* 1991, Bautista *et al.* 1992, Meine & Archibald 1996, Prange 2001).

Secondly, the establishment of many new protected areas, where the Common Crane has been breeding, has probably influenced the population increase in Estonia. The proportion of protected areas in Estonia has risen from 4% in 1970 to 12% in 1999 of the total area of the country, according to national law, and from about 1% to 3.5%, according to the IUCN categories, IA and IB (Fammler *et al.* 2000). Besides the areas of relatively small importance to cranes, there are ten protected areas where recently (based on 2001 estimates) 15–50 pairs, and altogether 250–300 pairs of cranes were observed breeding (Lõhmus *et al.* 2001, updated). As in Estonia, the number of protected areas has increased in most of the countries in the distribution range of the Common Crane during the period 1970–2000 (Tucker & Heath 1994, Prange *et al.* 1995, Meine & Archibald 1996, Tucker & Evans 1997, Prange *et al.* 1999, Fammler *et al.* 2000, Heath & Evans 2000).

In addition to the reasons described above, a greater availability of food resources may have played a role in the increase in the breeding population of the Common Crane during the last three decades in Estonia and in other areas. However, we lack specific data to be able to analyse the influence of this potentially important factor on a larger scale.

5. Conclusions

We have shown that the distribution range and the breeding population of the Common Crane in Estonia increased considerably during the last three decades, i.e. from 1970 to 2000. We found several factors that contributed to the Crane's population increase in Estonia, but we do not know the relative importance of the different factors. We need more specific data to show how habitat and other external characteristics along with genetic and behavioural processes determine reproduction, survival and mortality of species (Prange 1989, Alonso *et al.* 1991, Meine & Archibald 1996, Mewes 1999, Nowald 1999, Jones 2001, Leito *et al.* 2003a).

Another problem is that because the Common Crane is a timid and strictly protected bird species nesting in solitary pairs of low density, collecting data on the breeding of this species is difficult. Nevertheless, we need a great quantity of long-term observations of many individuals and pairs of cranes to ascertain the spatial-social and age structure of the population, the reproduction, survival and mortality rates in different age classes and the habitat use during the breeding and non-breeding periods. For the identification of individuals, colour-ringing and radio- and satellite-tracking of cranes have been used (Alonso & Alonso 1999, Leito *et al.* 2003 a, c). Nevertheless, the number of birds that can be captured and marked in this way is limited. Additionally, the colour-rings are not easy to read from a distance, which can cause mistakes in the identification of individuals, and the transmitter batteries last only up to five years at a maximum, thus, limiting the study period of individuals.

To get around these problems a new method and technology were developed for the identification and recognition of cranes from a distance, i.e. the use of digital recording and three-dimensional analysis of crane calls (sonograms) (Wessling 2000). This method was first applied in Germany in 1998. In 2003 we imported the technology from Germany to Estonia and, during the next years, we hope to generate sufficient new data on the Common Crane breeding ecology.

Despite the lack of sufficient information, we suggest that, in general, the present status of the Common Crane breeding population in Estonia is favourable and there is no need for specific conservation actions at the moment. Estonia has a management plan for the Common Crane in force for the period 2003–2007 and onward; this plan includes all the most important activities for conservation.

The main goal of conservation management is to maintain a viable Common Crane population in Estonia and support the European and global populations. The minimum limit for the population size in Estonia has been estimated at about 300 pairs. To reach this goal there are plans to create 36 specially protected areas (SPA) for the Common Crane with a total area of 3892 km^2. Currently, about 500–600 pairs of cranes are breeding in these areas. Most of the SPAs are already existing protected areas and some SPAs will be new protected areas established under the Natura 2000 network of the European Union. The SPAs will include proportionally all the Common Crane nesting habitats in Estonia.

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Selostus: **Kurkien levinneisyysalueen ja pesimäpopulaation muutokset Virossa**

Kurkien määrä on Virossa viimeisen 30 vuoden aikana (1970–1999) lähes kaksikymmenkertaistunut (300 parista 5800 pariin). Parimäärän kasvamisen myötä myös kurkien levinneisyysalue on laajentunut. Vuosina 1977–1982 kurkia tavattiin 323:lla (57%) ja vuosina 1997–2001 498:lla (88%) 10 × 10 km tutkimsuruudulla. Valtaosa Viron kurjista pesi ajanjaksona 1997–2001 erityyppisillä soilla (5300 paria eli 91%), pääasiassa minerotrofisilla soilla (4200 paria eli 72%). Keskimääräinen paritiheys oli 17.4 paria/100 km^2.Keskimääräinen paritiheys oli minerotrofisilla soilla 41.3, vaihettumissoilla 38.3 ja korvissa 15.9 paria/100 km^2. Pienilla soilla (pinta-ala < 10 km^2) kurjen esiintymistiheys korreloi negatiivisesti pesintäsuon pinta-alan kanssa kaikissa suotyypeissä. Paikalliset tekijät ovat vaikuttaneet kurkien parimäärän kasvuu ja levinneisyysalueen laajenemiseeen. Tärkeimpiä globaaleja tekijöitä ovat ilmaston lämpeneminen ja kurjen elinympäristöjen aktiivinen suojelu. Virossa kurkien parimäärään kasvuun ja levinneisyysalueen laajenemiseen ovat oletettavasti vaikuttaneet myös metsien ikärakenteen nuorentuminen ja harveneminen sekä entisten maa-aineisten ottopaikkojen muuttuminen kosteikoiksi.

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II

Leito, A., **Ojaste, I.**, Truu, J., Palo, A. 2005. Nest site selection of the Eurasian Crane *Grus grus* in Estonia: an analysis of nest record cards. *Ornis Fennica* 82: 44–54.

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Nest site selection of the Eurasian Crane *Grus grus* in Estonia: an analysis of nest record cards

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We describe in detail the nesting habitats of the Eurasian Crane in Estonia and explore relationships between different habitat characteristics and nesting success. We analysed all 161 reported Eurasian Crane nest finds in Estonia. We found that the cranes favorite nesting habitats are different types of mire (71% of all nests), especially fens (44%). We conclude that, despite the fact that the Eurasian Crane breeds in different habitats, nesting sites include the same or similar structural elements (vegetation types, plant species and communities and elements of micro-relief). We found that the date of the beginning of egg laying is significantly related to the size of the nesting habitat and that the annual mean date of the beginning of egg laying in Estonia has advanced considerably during the period 1901 to 2001. We also discovered a significant relation between the distance of neighbouring nests (population density) and the brood size and a negative effect of human activity on nesting success.

1. Introduction

Several studies on the breeding of the Eurasian Crane, including descriptions of nesting habitats, have been conducted (see Blotzheim *et al*. 1973, Cramp & Simmons 1980, Ilyichev & Flint 1987, Prange 1989, Meine & Archibald 1996). However, these studies typically lack a serious analysis of the relations of different characteristics within and between different habitat types, and between habitat characteristics and reproduction. There are several reasons for this lack of analysis. First, in a local study area, it is difficult to locate a sufficient number of nests, especially since the Eurasian Crane is strictly protected in almost all countries, which means that special permission is required in order to actively seek out nests and disturb birds (Prange 1994, Meine & Archibald 1996, Leito *et al*. 2003). Secondly, an integrated analysis of various habitat associations, nesting site characteristics and nesting parameters of a bird species, including the Eurasian Crane, is complicated

Table 1. Nesting habitats of the Eurasian Crane in Estonia and distribution according to habitat of the nests found. Total land area of Estonia without Lake Peipsi and Lake Võrtsjärv is 43,428 km^2 (Mansoo 2001).

Biotope category	Total area (km^2)	Share of habitats of the total area of Estonia (%)	Share of nests of nesting habitats (%)	Number of nests in a habitat type	Distribution of nests in relation to habitats (%)
Raised bog	2,780	6.4	23.6	43	27.0
Transitional mire	1,140	2.6	9.7	9	5.7
Fen	5,150	11.4	43.8	63	39.6
Riverplain	276	0.6	2.3	6	3.8
Coastal lagoon	15	0.03	0.1	7	4.4
Inland lake	243	0.6	2.1	15	9.4
Forest[1]	2,152	5.0	18.3	16	10.1
Total	11,756	27.1	99.9	159	100.0

1. Seven forest site types: *Filipendula ulmaria*, drained swamp, grass swamp, *Equisetum*, *Molina caerulea*, *Molina caerulea-Filipendula ulmaria*, *Carex* and *Carex-Filipendula ulmaria*.

(Prange 1989, Jokimäki & Huhta 1996, Mewes 1996, Lutze *et al*. 1998, Nowald 1999). The process of gathering more-or-less representative data on different characteristics of Crane nests and nest sites and breeding success has a long history in Estonia, and only now are we in a position to make the first analysis.

In our previous study (Leito *et al*. 2003), besides territorial distribution and numbers, we also analysed the distribution of Eurasian Crane breeding pairs in Estonia according to main habitat types, based on censuses of territorial pairs. We found that most cranes (91%) were breeding in different type of mire but there were no significant differences in mean population density values between the landscape regions. We also found a significant relationship between population density and mire size, and that, in the case of small mires (less than 10 km^2), population density correlates negatively with size of nesting habitat. However, our previous analyses include only a (rough) location of breeding territories of Crane pairs.

The most important threats to the Eurasian Crane are the destruction of and decline in the quality of habitats, disturbance during the breeding season, illegal hunting, unfavourable weather conditions and climate change (Cramp & Simmons 1980, Prange 1994, Meine & Archibald 1996). All these factors are also important for the conservation and management of species in Estonia. In this study, we discuss different types and qualities of habitats occupied by cranes and the influence of different habitat characteristics on nesting success by using nest record cards.

The objectives of our study were to (1) describe in detail the distribution of nesting sites of the Eurasian Crane in Estonia according to habitats; (2) find the relationships between habitat characteristics and nest site location, and (3) analyse the effect of different habitat characteristics on nesting success on the basis of nest record card data.

2. Material and methods

2.1. Nest cards

All Eurasian Crane nest finds reported in Estonia before 2001 (n = 161) have been analysed in this study. The nest finds cover almost the whole of Estonia; the largest numbers of nests have been found in the West – in Saare (n = 43), Pärnu (n = 34) and Lääne (n = 18) counties. The oldest reported Eurasian Crane nest finds in Estonia date back to the 1880s, but most of the data originate from the middle and end of the 20th century (61%) and from the years 2000 and 2001 (27%).

In 1999, the authors elaborated a Eurasian Crane nest record card on the basis of the standard nest record card of birds being used in the Estonian Ornithological Society. This nest record card is species-specific and characterized by additional features and available on website of the Estonian

Ornithological Society (www. eoy.ee). All new nest finds were registered and previous finds transferred to this record card in the course of the study.

2.2. Nesting habitat

Seven different nesting habitats were provided (raised bog, transitional mire, fen, river plain, brackish-water or fresh-water coastal lagoon, inland lake, and forest) (Table 1). The raised bog is defined as a classic "peat bog" of temperate northwestern Europe, western and north-central Russia and elswhere. The term refers to the convex cupola of ombrotrophic peat raised a few meters above the level of surrounding land. Nutrition – oligotrophic, source of water – precipitation (Gore 1983).

The fen is defined as a minerotrophic or eutrophic mire where the source of water is rock or soil (Gore 1983). The concept "fen" in this paper compasses all eutophic mires i.e. fen and swamp in British usage (Valk 1988). The transitional mire is defined as a medium type of mires between raised bog and fen. The source of water in transitional mire are both the precipitation and ground (Valk 1988). The transitional mire zone lies between raised bog and a mineral habitat, usually forest.

Each habitat is characterized by a potential vegetation type and micro-relief (different type of hummocks). The habitats are distinguished by a six to seven digit code that describes different structural elements of the habitat and the variation in its ecological conditions. Original description of the structure of habitat, demonstrating the ecological variability of habitats, has been provided on the basis of the classification of Estonian vegetation types (Paal 1997) and land cover types (Meiner 1999).

The area of the "nesting site" is defined as a 5 metre radius circle around the nest. "Nesting site characteristic" indicates the location of a nest within the nesting site in terms of its proximity to trees (under a tree or away from trees, in an open area or in a gap), the composition of plant species estimated by geo-botanical analyse, the vegetation type based on geo-botanical analyse, the openness of the nesting site (treeless, dwarf shrubs, shrubs, shrubs/trees, and forest), and its micro-relief (on a hummock or between hummocks; in cases where a nest is located on a hummock, the type of hummock is defined).

"Water regime in the nesting site" indicates the general level of wetness (permanently dry area, permanently wet area but without open water, permanently flooded area, periodically flooded area, permanent water body).

"Landscape around the nest" indicates the distance of nearest neighbouring habitat in terms of the four quarters of the horizon measured cartographically.

"Disturbing factors" indicates the distance of a building or settlement, and main road and foot path from the nest measured cartographically.

"Nesting success" indicates the number of young hatched and number fledged find out by repeated visits of the nesting site. In the case of unsuccessful nesting, the known or probable reason is indicated.

2.3. Data analysis

The main database includes all nest record cards (n = 161). In addition, a sub-database on nest dimensions was compiled and analysed. This database consists of data on the dimensions of 66 nests.

Analysis of databases was carried out using different statistical methods depending on the distribution pattern of characteristics and other specific features. The main statistical methods used were the Spearman rank correlation coefficient (r_s), Mann-Whitney non-parametric U-test, Student t-test, Kruskall-Wallis non-parametric test, and the correlation as well as dispersion analysis of variance. Trends in time series were detected using Mann-Kendall non-parametric test. MS Excel 7.0, Statistics programmes Statistica and Statgraphics were used in computer analyses of data.

3. Results

3.1. Distribution of observed nests according to habitat type

The largest number of Eurasian Crane nests in Estonia has been found in fens, followed by raised bogs, forests and inland lakes (Table 1). A total of 115 nests have been found in mires (fens, transi-

Fig. 1. The hollow-pool-ridge bog is a typical nesting habitat of the Eurasian Crane in raised bogs.

tional mires, and raised bogs) constituting 71.4% of all the nests found. Different types of mires make up about 20% of the territory of Estonia (Valk 1988, Paal *et al*. 1998). Thus, the share of mires as a nesting biotope for the Eurasian Crane is about 77% and the proportion of nests found in mires is about 72%.

Raised bog: The most frequent nesting habitat of the Eurasian Crane in Estonia is the wooded hollow-pool-ridge bog site type (21 nests = 64% of all nests found in bogs) (n = 33) (Fig. 1). The open hollow-pool bog site type is given slight preference compared to the wooded hollow-pool bog type (20 nests to 13 nests, respectively). From various bog vegetation types, Cranes prefer different herb and dwarf shrub complexes. The rest of the nests were located on quaking mires dominated by sphagnum or other vegetation.

Transitional mire: Nests found in the transitional mire (n = 9) were all located in the mire plain, in sites that were either treeless (3 nests) or covered with tree and shrub communities (4 nests). The preferred vegetation type in the transitional mire was the quaking mire community, especially with *Typha* spp. and *Carex* spp.

Fen: The fen was the most frequent nesting biotope of cranes in Estonia, especially in treeless quagmire or paludified grassland. In total, 45 nests have been found in treeless fens, 10 in fens with a shrub-tree community and one nest in a treed fen (total n = 56). Most of the nests were located in the quagmire (48 nests) and 12 nests in paludified grasslands (n = 60).

If fens with different water regime were compared, the greatest number of nests have been found in fens with high ground water level (34 nests), followed by floodplain fens (20 nests) and spring fens (6 nests). In terms of different fen vegetation types, the greatest number of Crane nests have been found in the sedge-reedbed mosaic community.

River plains: Only six Eurasian Crane nest finds on river plains have been described in Estonia (Table 1). Three nests were located in sparse reedbeds of the alluvial fen and two in alluvial meadows. Four nests were located in an open area and one in a sparse shrub community. There are no reports of Eurasian Crane nests located in the typical saline coastal meadow in Estonia.

Coastal lagoons: Seven nests have been recorded in coastal lagoons. All the nests were situated in treeless areas and none of them on lagoon

Fig. 2. The rich paludified forest with a majority of alder is a common nesting habitat of the Eurasian Crane in Estonian forests.

mineral islands. In terms of water regime, 6 nests were located on the floodplain and one in an area with a stable water regime (n = 7). Most of nests were located in the reedbed and only one in the Greater Tussock-sedge community. As for the different types of reedbed, 3 nests were located in reedbeds of watercourses and 3 nests in reedbeds of temporary floodplains; nests have not been found in terrestrial reedbeds (n = 6).

Inland lakes: A total of 15 crane nests have been found on inland lakes. 12 of the described nests were located in treeless areas and 2 in shrubs along the shore (total n = 14). Nests have not been found on mineral islets in lakes. In terms of water regime, most of the nests were located in areas of permanent innundation (10 nests), however, four nests were found in areas of periodical flooding. Treeless shore quagmire with herb or moss community in the inland lake`s vegetation type was most frequently used by cranes for nesting. The second most frequently occupied vegetation type is the reedbed, followed by the Greater Tussock-sedge community.

Forest: A total of 16 crane nests have been found in forests. In terms of the age of stands, more nests have been found in premature stands (6 nests) than in mature stands (3 nests) (n = 9). Nests have not been found in young growth and young stands. According to dominant tree species, decidious forest with a majority of birch or alder (both, black and gray alder) is the most frequent nesting site for cranes (Fig. 2). In terms of water regime, the majority of nests (75%, 12/16) were located in rich paludified forests or wooded meadows. Three nests were found in floodplain forests and one in a poor paludified forest. Nests have not been found in dry forests on mineral soil.

3.2. Size of the nesting habitat

The area of the nesting habitat of the Eurasian Crane in Estonia varies from 0.5 to about 10,000 ha. For the recorded nests, a habitat size of 1–10 ha was most frequent (40%), followed by a size of 101–1,000 ha (25%), more than 1,000 ha (18%), 11–100 ha (14%) and less than 1 ha (9%) (n = 159). The smallest nesting habitats used by cranes are small fens and lakes in the forest and the largest habitats are large mire expanses. The habitat size differ significantly between the different habitat types (Kruskal-Wallis non-parametric test, $P < 0.0001$, n = 159). On the average, the largest nesting habitat is the raised bog, compared to fen, coastal lagoon, inland lake and forest.

There is also a significant correlation between the size of the nesting habitat and the beginning of egg laying (Kruskal-Wallis non-parametric test, $P < 0.01$, n = 91). The earliest date of egg laying was observed in the habitat size category of 1–10 ha (mean date 21 April), followed by size under 1 ha (25 April), 11–100 ha (26 April), 101–1,000 ha

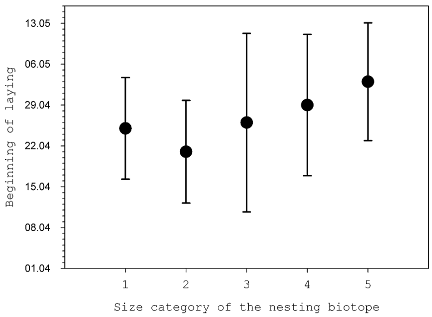

Fig. 3. Relationship between the beginning of egg laying (mean annual date ± SD) and the size of the nesting habitat of the Eurasian Crane in Estonia. Habitat size categories: 1 = less than 1 ha; 2 = 1–10 ha, 3 = 11–100 ha, 4 = 101–1,000 ha, 5 = more than 1,000 ha.

(29 April) and more than 1,000 ha (3 May). Variation in the beginning of egg laying is greatest in the habitat size category of 11–100 ha (Fig. 3).

3.3. Openness and wetness of the nesting site

In terms of openness around the nesting site the greatest number of nests have been found in an open area (89 nests = 61%), 24 nests (16%) have been both in sites surrounded by shrubs as well as in those surrounded by shrubs and single trees, 12 nest sites (8%) in shrubs, and 5 nest sites (3%) in sparse forest (n = 154).

No statistically significant correlation between openness and other single characteristics, other than the combined nesting site characteristic (both openness and hummock type (r = –0.27, P < 0.01, n = 154) was found. The majority of nests have been found in an open space (137 nests), followed by those in a gap (5 nests) and those under a tree (4 nests) (n = 146).

In terms of micro-relief and hummock type, most of the nests were located on a grass hummock (88 nests), followed by nests on level ground (46 nests), on a moss hummock (4 nests), between hummocks (3 nests), on a waste hummock, and stump tussock (2 on each) and on a stone hummock (one nest) (n = 146).

Most of crane nests were situated in permanently wet (watery) areas without open water in the nesting site and only one nest was found in an almost dry area (Fig. 4). Most of the nests (97 nests = 64%) were located in sites where the depth of water at the nest was only 0–15 cm (usually a permanently wet area but without open water), followed by those a water depth of 16–30 cm (29 nests), over 50 cm (19 nests), and 31–50 cm (6 nests) (n = 151).

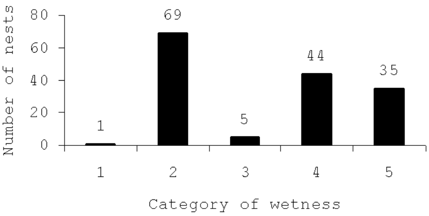

Fig. 4. Distribution of Eurasian Crane nests found in Estonia, according to wetness of the nesting site (n = 154). Categories of wetness: 1 = permanently dry area, 2 = permanently wet area but without open water, 3 = permanently flooded area, 4 = periodically flooded area, 5 = permanent waterbody.

3.4. Distance between nests

Most of the neighbouring crane nests were located at a distance of more than 1.0 kilometre (65 nests), followed by a distance of 0.5–1.0 km (41 nests), a distance of 0.3–0.5 km (14 nests), a distance of 0.2–0.3 km (4 nest), and a distance of less than 0.2 km (4 nests) (n = 120). 120 metres is the smallest distance measured between two occupied neighbouring crane nests in Estonia.

Mean brood size (1.65 nestlings, n = 20) in cases where the distance between neighbouring nests was 0.5–1.0 km was significantly larger than in cases where the distance was more than 1 km (1.16 nestlings, n = 32) (Student t-test, P < 0.05, and the Mann-Whitney U-test, P < 0.05, n = 52).

3.5. Nest size and material

The height of the found nests varied between 1 and 45 cm, with a mean value of 14 ± 9 cm (± SD, n = 60). The 1–10 cm height category contained the greatest number of nests (33 nests), followed by

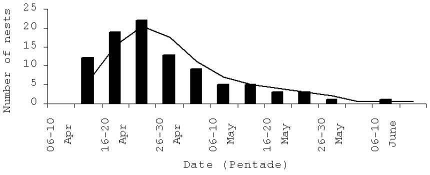

Fig. 5. Timing of the beginning of egg laying of the Eurasian Crane in Estonia, according to nest record cards (n = 93).

categories 11–20 cm (19 nests) and 21–30 cm (5 nests) (n = 60). The outside diameter of nests varied between 40 and 130 cm, with a mean value of 78 ± 19 cm (± SD, n = 64); however, the majority of nests had a diameter of 51–100 cm (57 nests = 89%). No significant correlation between the height and diameter of a nest was found.

Crane nests made of withered grass (hay) were most frequent (83 nests), followed by nests made of reed (30 nest), moss (16 nests), and mixed material (12 nests) (n = 141). The type of nest material depends on the habitat because cranes build their nests from vegetative material growing in the vicinity of the nest. Nevertheless, an analysis of variance indicated that the number of fledglings is significantly higher in nests made of hay than in nests made of reed (Mann-Whitney U-test, P < 0.01, n = 113).

3.6. Human activity and disturbance

Most of Crane nests were located in the zone of weak human disturbance (a distance of more than 0.5 km to the nearest building or settlement, main road or path from the nest more than 0.5 km) (104 nests), followed by nests in areas with medium human disturbance (distance 0.1–0.5 km) (45 nests) and in the zone with strong disturbance (distance less than 0.1 km) (6 nests) (n = 155).

Because of the few number of nests found in the zone of strong human disturbance, it was possible to find a statistically reliable relation only by comparing nesting success (brood size) for nests exposed to strong or medium human disturbance (0.81 ± 0.81 (SD) juveniles) (n = 21) and weak human disturbance (1.41 ± 0.80 (SD) juveniles) (n = 46). The mean number of juveniles in the nests subject to weak human disturbance was significantly larger than in the nests located in the zone of medium human disturbance. (Student's t-test, P < 0.01 and Mann-Whitney U-test, P < 0.01, n = 67). The number of nestlings correlated significantly with the number of fledglings in the brood (Spearman rank correlation coefficient, $r_s = 0.91$, P < 0.01, n = 36).

3.7. Nesting phenology

According to the nest record cards, the date of the beginning of egg laying of the Eurasian Crane in Estonia varies between 11 April and 6 June, with a mean value of 22 April ± 10 (SD) days (n = 93). The majority of cranes lay their eggs in the period from mid April until the end of May (Fig. 5).

We found that on Saaremaa Island, in the West Estonian Archipelago, cranes start laying eggs at a significantly earlier date than on the mainland (Student t-test, P < 0.05, n = 93). The average date of the beginning of egg laying on Saaremaa is 18 April ± 9 (SD) days (n = 23), and 30 April ± 11 (SD) days (n = 70) on the mainland. The difference is 12 days, i.e. almost two weeks.

An analysis of the variation of the beginning of egg laying by cranes over time indicates a significant trend of advancement in Estonia over the whole 1901–2001 period (Fig. 6). The average change for a ten-year period is almost two days.

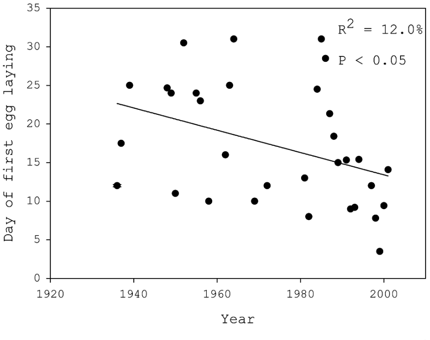

Fig. 6. Relationship between the annual mean date of the laying of the first egg (± SD) and the year, for the Eurasian Crane in Estonia, 1901–2001. Annual mean dates of the laying the of first egg are displayed in days. Cranes started to lay earlier in more recent years (r = –0.43, P < 0.01, n = 93).

4. Discussion

4.1. Nesting habitat

We analysed characteristics of nesting habitat for the Eurasian Crane on the basis of nest cards. Potentially, the territorial distribution of nest finds can be affected by the actual numbers and distribution of the breeding crane population and by the distribution of birdwatchers. Nevertheless, the spatial distribution of nest finds coincides well with the distribution map of Eurasian Crane occurence depicted in the Estonian Bird Atlas, 1977–1982 (Renno 1993), and with the proportions of breeding habitats determined on basis of censuses of territorial pairs carried out in 1997–2001 (Leito *et al.* 2003). According to the latest population estimate for the period 1997–2001, 91% of cranes nest in mires, primarily in fens (72%) (n = 5,800 pairs) (Leito *et al*. 2003).

Most common Eurasian Crane raised-bog nesting site is a treeless or treed herb and dwarf shrub-rich bog of hollow-pool complex type. In the transitional mire the preferred nesting site is a quaking mire field that is either treeless, or covered with tree and shrub or tree communities. In the fen, cranes prefer a treeless quagmire or paludified grassland with a mosaic sedge-reedbed community and a high ground-water level. In the coastal lagoon, cranes choose the open, sparse *Schoenoplectus tabernaemontanii* dominated reedbeds of watercourses. On the inland, treeless lake shore quagmires with herb communities and reedbeds in watercourses are the preferred nesting sites for cranes, and, in the forest, wet sparse premature rich paludified decidious forests or wooded meadows. Cranes avoid saline habitats like coastal meadows, and reedbeds growing in salty water.

In general it can be stated that, despite the fact that the Eurasian Crane nests in different biotopes in Estonia, all nesting sites include similar structural elements (vegetation types, plant species and communities and elements of microrelief).Our study showed that in terms of plant communitis, identical or similar reedbed and sedge communities occur in fens, river plains, as well as coastal lagoons and inland lakes. Different nesting sites are characterized by similar water regime – flooding or long-term floods in the fen, river plain, coastal and inland lake, and also in swamp and floodplain forests. Occurrence of hummocks is characteristic to all nesting habitats; some difference could be found only in the types of hummock.

In neighbouring Latvia, the most frequent nesting habitats of the Eurasian Crane are similar to those in Estonia – the raised bog, open swampy meadow (fen), reedbeds of inland lakes, alder-birch swamp, marshy clearings in the forest (ranked according to the frequency of occurrence) (Nowald *et al*. 1999). In South-Western Lithuania, the largest number of crane nests have been found in black alder and birch stands (Aleknonis 1983). The nests were located in rich paludified forests, under the trees surrounded by water or on temporarily flooded patches of fens not very deep in the forest.

In Finland, the cranes traditionally mostly breeds in large peatlands of different type (55% of found nests), less frequently by lakes (37%) and on the coast (8%, n = 230) (Karlin 1985, 1995). Extensive drainage in the last decades has caused certain changes in the distribution and biotope use of cranes. An increasing number of cranes breed on lakes and the coast (Karlin 1995).

In Germany, which is situated further south than Estonia, the cranes mostly breeds in relatively small wetlands of different types (ponds overgrown with plants, patches of mire and swamp pools), in the forest, or in mosaic agricultural landscape (Prange 1989, Mewes 1996). In Denmark, on the western border of the cranes` breeding range, a small number of pairs breeds in small peat bogs and swampy fresh-water lakes in inland` but also on coastal tundra-like wetlands between dunes with salty and brackish water (Tofft 1999).

To generalize, it could be stated that cranes are well adapted to breed in different types of wetlands available in an area, but prefers mires and other swampy habitats and avoids, whenever possible, saline habitats on the sea coast.

4.2. Breeding biology

We found that the date of the beginning of egg laying of the Eurasian Crane is significantly related to the size of the nesting habitat. The relationship is non-linear and the reasons for this interdependence are not yet known. It may be that the microclimatic conditions (air temperature, water level, ice and snow cover) are significantly different in different sized nesting sites within the same habitat type and in different habitat types, affecting the timing of the egg laying of cranes. Unfortunately, data on micro-climatic conditions of nesting sites were not gathered on the nest record cards, and we cannot therefore test this hypothesis.

It was surprising that, except for the biotope class and the depth of water, no significant relation between the wetness of the nesting site and any other characteristic was detected. One reason for this could be that the predators of the clutch and small nestlings of the Eurasian Crane are mostly the Raven *Corvus corax* and the Hooded Crow *Corvus corone*, for whom water is not a barrier. The most dangerous predators of bigger nestlings and fledglings are the Red Fox *Vulpes vulpes* and the Golden Eagle *Aqulila chrysaetos;* the nesting site has usually become drier by that time, and young cranes are often killed at a distance from the nest as well. Consequently, water cannot provide significant protection against predators.

We found that the mean brood size in neighbouring nests a smaller distance (0.5–1.0 km) apart was significantly greater than for those that were a longer distance (more than 1 km) apart. In our opinion, the habitat quality is one of the reasons for the difference in nesting success and population density of cranes. On the basis of different breeding success by different distances between neighbouring nests we believe that the habitat quality is lower when the distances between nests are longer (or the population density is lower). However, it is also evident that nesting success decreases when the distance between nests becomes too short, because then competition between pairs and families with young increases substantially despite the original quality of a nesting site in terms of other important characteristics (food resources, predators, disturbance and hiding places) remaining unchanged (this concerns the same or very similar nesting habitats).

We have several direct observations of heated boundary quarrels between cranes nesting close to each other. This means, that, if the population density exceeds a critical level, nesting success will decrease just as it does with increasing distances between nests in increasingly low quality nesting habitats. This relationship is similar but not the same as the classical density-dependence relationship between population density and population growth or reproduction described and modelled by many authors (see Schwerdtfeger 1979, Hanski 1990, Holyoak 1994, Cappuccino & Price 1995, Krebs 1998).

Differences and significant dependence of breeding success on distances between neighbouring nests (population density) find out on the basis of detailed analyse of nest record cards in this study coincide well with our previous findings in differences of population densities in different habitats based on a large-scale analyse of habitats occupied by cranes (Leito *et al.* 2003), confirming once more that the quality of different habitats are different for breeding cranes. As the population density was highest in fens (Leito *et al.* 2003), we believe that the cranes prefer the fens because of highest quality of this habitat for breeding.

Surprisingly, nest material had a certain effect on nesting success. The number of fledglings in cases where nests were made of hay was significantly higher than in the cases where they were made of reed. The reason for this is not known, possibly hay has a better mechanical and/or thermoregulatory characteristics for hatching eggs and for nestlings compared than reed.

We found that human activity had a significantly negative effect on the breeding success of cranes in Estonia. The mean brood size in nests close to roads or buildings was significantly smaller than in nests that were further away from human disturbance. This result is not surprising, but it was important to prove that human activity really has a negative influence on the breeding success of cranes, confirming the earlier but often too generalised declarations to that effect (Cramp & Simmons 1980, Prange 1994, Meine & Archibald 1996).

An interesting finding is that the average timing of egg laying by cranes in Estonia has advanced significantly (by 12 days in total) during the period 1901–2001. We suppose that the main reason for this is the warming of the climate, especially the mean spring temperature, in Estonia, as well as in the whole of northern Europe (Jaagus & Ahas 2000, Jaagus *et al.* 2002). Because of the earlier spring, cranes arrive and nest earlier, at least in Estonia (Keskpaik *et al.* 1997, 2000). Earlier nesting has probably contributed to the population increase described in almost all areas of Europe during the last decades (Leito *et al*. 2003, Prange 2003).

5. Conclusions

We conclude that the Eurasian Crane breeds in several types of wetland with similar ecological elements (vegetation types, plant species and communities, and elements of micro-relief, openness and wetness of the nesting site and surroundings). In Estonia, the favourite nesting habitat for cranes is mire, especially fen. They avoid saline wetlands for nesting. In general, the Eurasian Crane is well adapted to occupay different habitats (wetlands) occurring in an area. We have found that the most important habitat-dependent factors affecting nest site selection and reproductivity of the Eurasian Crane in Estonia are the size of the nesting habitat, vegetation type, micro-relief and ground type, openness and wetness, and, more indirectly, nest material, population density, and human activity.

The results of our study are useful for the management and conservation of breeding populations of Eurasian Cranes, because the characteristics we have analysed are also important population limiting factors (Prange 1989, 1994, Meine & Archibald 1996, Leito *et al*. 2003). In Estonia, the breeding habitats seems currently to be in a good condition, but human activity has already had a remarkable negative effect, as we demonstrated in this study. One problem lies in the fact that we do not actually know the relative importance of different factors affecting the reproduction and mortality of Crane populations (Alonso *et al.* 1991, Prange 1989, Meine & Arcibald, Mewes 1999, Leito *et al*. 2003). For this purpose, we have already started more massive and integrated study on habitat-dependency relationships in breeding Eurasian Cranes using GIS-based methods.

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Virolaisten kurkien pesäpaikat

Pesälöytöjen perusteella kurki asuttaa Virossa monenlaisia kosteikkoja. Eniten pesiä (yhteensä 161) on löydetty minerotrofiselta suolta (n = 63), sitä seuravaat korpi (n = 43), metsä (n = 16), järvi (n= 15), vaihettumissuo (n = 9), kluuvijärvi (n = 7) ja joen luhtaniitty (n = 6). Erilaisista pesimäbiotoopeista huolimatta pesäpaikoille ovat ominaisia monet yhteiset tai samankaltaiset rakenneosat (kasvilajit ja -yhdyskunnat, kasvillisuustyyppi, pinnanmuoto ja mättäisyys) tai muut ominaisuudet (avoimuus ja vetisyys).

Yleistettynä kurjen tyypillinen pesäpaikka on avoin tai puustoinen, allikkoinen keidasräme, vaihettumissuolla avoin, pensaikkoinen hetteikkö sekä minerotrofisella suolla avoin, ruovikkoinen ja sarainen hetteikkö tai niitty. Kluuvijärvillä tyypillinen pesäpaikka on avoin, vedessä kasvava harva ruovikko, sisämaan järvillä avoin tai puoliavoin sarahetteikkö tai vedessä kasvava ruovikko sekä metsässä keski-ikäinen harva soistuva lehtimetsä tai lehtoniitty.

Kurjen pesimämenestys riippuu olennaisesti naapuripesien etäisyydestä (populaation tiheydestä), pesämateriaalista (kuivalla ruoholla sisustetut pesät tuottavat ruokopesiä paremmin) sekä ihmistoiminnasta (mitä lähempänä pesää on tie, talo tai taajama, sitä alhaisempi on tuotos). Munimisen alku on yhteydessä pesimäbiotoopin pinta-alaan. Virolaisten kurkien munimisen alun vuotuinen keskipäivämäärä on ajanjaksona 1901–2001 muuttunut huomattavasti varhaisemmaksi.

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III

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The impact of agriculture on autumn staging Eurasian Cranes (*Grus grus*) in Estonia

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This paper explores the relation between the local numbers and distribution of autumn staging Eurasian Cranes (*Grus grus* Linn.) and agricultural land use during recent decades in Estonia. The analysis is based on the long-term monitoring data of staging cranes and the statistical data of land use in Estonia. We found that great changes in cropping area, as well as in crane numbers have taken place in Estonia since the 1960s. We also found a significant positive correlation between crane numbers and the cropping area of summer wheat, winter wheat, winter rye and all cereals together, and a negative correlation with the area of potatoes. Generally, arable land, particularly that used for growing cereals, has a great influence on the local numbers and distribution of staging cranes. Based on our findings, we predict that changes in the local numbers and distribution of Eurasian Cranes staging during their migration in Estonia and elsewhere will depend on changes in agricultural land use in staging areas, rather than on the size of the breeding population. As about 10 percent of the European Eurasian Crane population stop over in Estonia during the autumn migration, the country has an important role to play in the protection of the species.

Key-words: Eurasian Crane, staging cranes, crane protection, land use change, agricultural policy, Estonia

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Introduction

The Eurasian Crane is distributed in Eurasia from latitude 69°N to latitude 40°N and from longitude 6°E to longitude 165°E (Cramp and Simmons 1980, Prange 1989, Meine and Archibald 1996). Its recent European breeding population is about 110,000 pairs (Prange 2003, BirdLife International 2004). Breeding populations have increased across most of Europe. In Estonia the breeding population of the Eurasian Crane has increased from about 300 pairs in 1970 up to 6800 pairs in 2006 (Leito et al. 2003, 2006, Leito pers. comm.). Eurasian Cranes are omnivores, mostly feeding carnivorously during breeding and herbivorously during the migration and wintering periods (Cramp and Simmons 1980, Prange 1989, Díaz et al. 1996, Avilés et al. 2002). The composition of their diet depends on the season and local foraging opportunities. In Estonia, the main feeding habitats for cranes in the autumn are fields of different cereals and mowed grasslands (Leito et al. 2006).

During the period from the 1960s to the 2000s, the numbers of cranes that stopped over during the autumn migration has increased to a greater or lesser extent in all of the most important staging areas in Europe. The growth and relative importance of staging sites have, however, varied greatly from one year to another (Lundin 2005). In Estonia, the total number of staging cranes rose continuously during the 1960s and 1970s and has stabilised in the period from the 1980s to 2000s. At the beginning of the 1960s, up to 5000 cranes, and in the 1980s and 1990s, between 20,000 and 30,000 cranes were counted (Leito et al. 2006). All together, the Eurasian Crane population migrating on the West-European migratory route has increased from about 40,000 to 150,000 birds, and the number of cranes migrating on the Baltic-Hungarian route has increased from about 30,000 to 90,000 during the past 30 years (Prange 1999, 2003, Lundin 2005). Cranes breeding in Estonia use all the Eurasian Crane migratory routes in Europe, but are most numerous on the West-European and Baltic-Hungarian migratory routes (Leito et al. 2006).

Although Eurasian Crane numbers have increased substantially throughout Europe during recent decades, its breeding range has not yet reached the former distribution range, and its population has not yet recovered to the level that preceded its decline. In the list of Species of European Conservation Concern (SPECs) the Eurasian Crane is listed in SPEC category 2 (a species whose global populations are concentrated in Europe and which has an Unfavourable Conservation Status in Europe) (BirdLife International 2004).

Another aspect of the concentration of cranes on arable land during migration and wintering is that, if present in large numbers, cranes may cause serious damage to crops. There are two possible ways to solve this problem – to compensate the damages and/or create artificial feeding fields for cranes, and both schemes are in use (Koskinen et al. 2003, Lundin 2005, Nowald 2005, Petit and Couzi 2005). In Estonia, on the basis of the Fauna Protection and Use Act, the Regulation on Procedure and Methodology for Assessment of Damage Caused by Protected Animals or Birds on Migration was implemented in 1994. The guiding principle of the Regulation is to compensate the actual crop damage caused by animals and birds on migration, including that of staging cranes.

Many different policy measures, including agri-environment schemes, have been implemented across Europe, mostly addressing water, biodiversity, and landscape protection. In the late 1990s about 20% of farmland in the European Union (EU) was covered by national agri-environmental programmes (OECD 2003, Bayliss et al. 2005, Carey et al. 2005, Herzog 2005). Evaluation of their effects on biodiversity is, however, difficult from a methodological standpoint, and the existing studies are often controversial. More research on agri-environment schemes, other policy measures, and farming is needed in order to assess and improve their actual influence on different species, including cranes (Alonso et al. 1987, 1994, Prange 1999, Alonso et al. 2003, Bayliss et al. 2005, Lundin 2005).

We conducted a thorough survey of the numbers and distribution of Eurasian Cranes staging during the autumn migration in Estonia in relation to changes in agricultural policy and land use, particularly changes in cropping areas. The main goal of this study was to analyse the long-term dynamics of agricultural land use and numbers of autumn staging cranes in Estonia in order to assess whether and how agricultural practice affects the local numbers and distribution of staging cranes and to ascertain the importance of agricultural policy and land use for migrating birds.

Material and methods

Crane censuses

The autumn staging of the Eurasian Crane has been monitored in the Matsalu area since 1961, on Hiiumaa Island since 1982 and throughout Estonia since 1983. In Matsalu and Hiiumaa, censuses have been carried out almost every year. Total crane counts were conducted in the years 1983, 1994, 1999, 2000 and 2003. In these years the total counts were carried out in all the sites in Estonia where cranes stay during the autumn. Censuses were performed using the standard method developed in Estonia (Keskpaik et al. 1986). The census period lasts two weeks, from the middle to the end of September, with a central counting day on the weekend in the second half of September. According to this method, cranes are counted at the roosting sites during the flight from feeding site to roosting site in the evening. If the evening census is not successful due to bad weather (fog or heavy rain), the census is repeated the next morning.

Agricultural land use

The data on area and yields of winter rye, winter wheat, summer wheat, barley, oats, potato and hay, and for the total area of cereals and for all crops together in Hiiumaa and Läänemaa Counties and for the whole of Estonia from 1965–2005 were collected from the archive of the Estonian Farmers' Union and from the Statistical Office of Estonia (2006). Data on crop yields were not used for further analyses because the data was not complete for every year. The area characteristics of cultivated crops that we used should be even better than crop yield data, because cranes feeding on fields, apart from eating germinated grains or the leaves of sprouted cereals, also eat invertebrates, amphibians and small mammals living in the fields. In this way, the food source for cranes on arable land contains both the crops cultivated there and the accompanying edible small animals, and our results reflect the effect of the available food complex on crane distribution and numbers.

In Hiiumaa County (area 1019 km^2), the cultivated areas of crops coincide with the feeding area of cranes, since the birds feed on all fields throughout the island. The crane staging population of the Matsalu region is spread over about 2000 km^2, which makes up about 84% of the territory of Läänemaa County (area 2394 km^2). Consequently the agricultural indicators for the whole of Läänemaa County are representative for the Matsalu crane population. The total land area of Estonia without Lake Peipsi and Lake Võrtsjärv is 43,428 km^2 (Maansoo 2001), and agricultural land currently makes up about 20.5% (8890 km^2) of this (Statistical Office of Estonia 2002).

Data analysis

The coefficient of variation (*CV*) was calculated in order to demonstrate the temporal variation of crane numbers and cropping area. Ordination of cropping areas of different crops according to year in Hiiumaa, Matsalu and in Estonia as a whole were analysed using principal component analysis (PCA). The Spearman rank order correlation coefficient (r_s) was used to examine the relationship between crane numbers and cropping area in the same year in the Hiiumaa and Matsalu areas over the period 1965–2004. The Mann-Kendall test (*MK*) was used to find the presence of monotonic trends in time series. Locally weighted regression (LOWESS) was used to illustrate trends in the time series data of crane numbers. Correlations and LOWESS were calculated using the computer programme Statistica.

Results

Crane numbers and distribution

During the period 1982–2005, the number of autumn staging cranes on Hiiumaa has varied between 960 in 1998 and 4230 in 1993 ($CV = 1.69$, $n = 21$ years) (Fig. 1). Four different periods in crane numbers can be distinguished on the basis of figure 1: (1) relatively stable numbers at a low level in the 1980s; (2) population growth with a peak in numbers at the beginning of the 1990s; (3) a rapid decrease in numbers until 1998, and (4) relatively stable numbers from 1999–2005, remaining at the same level as in the 1980s.

During the period 1961–2005 the number of staging cranes in Matsalu has varied between 700 in 1996 and 21,500 in 1994 ($CV = 2.41$, $n = 30$ years) (Fig. 2). Three main periods can be distinguished for Matsalu on the basis of figure 2: (1) a substantial population growth from 1965–1983, (2) a period with fluctuating numbers at a level of about 10,000 cranes, and (3) a new growth period during the last decade since 1995. There is a significant positive trend in staging crane abundance over the whole study period 1961–2005 ($MK = 2.66$, $p < 0.01$, $n = 30$ years).

Based on total counts during the period 1983–2003, the number of autumn staging Eurasian Cranes in Estonia has varied between 18,000 in 1997 and 30,000 in 1994 ($CV = 0.51$, $n = 5$ years). The total number of cranes has fluctuated without any visible trend (Fig. 3). A total of 51 crane staging sites in 8 concentration areas were established in the 1980s, and 61 staging sites in 10 concentration areas in the 1990s. The main concentration areas of staging cranes are located in the western, south-eastern and northern part of Estonia (Fig. 4). All of the most important staging sites are situated in areas of large fields close to wetland. The most important gathering area has been Western Estonia, including the islands of Hiiumaa and Saaremaa, where, in different years between 1983 and 2003, 72% and 87% ($n = 5$) of all cranes were counted. The relative share of all staging cranes in Matsalu has been 48–71% ($n = 5$) during the period 1983–2003. This

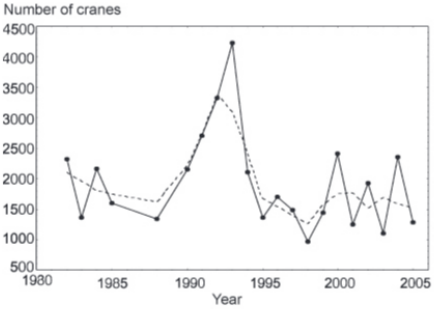

Fig. 1. Temporal dynamics of crane numbers on the island of Hiiumaa. The solid line represents the actual counted crane number and the dashed line reflects robust locally weighted regressions (LOWESS) over time.

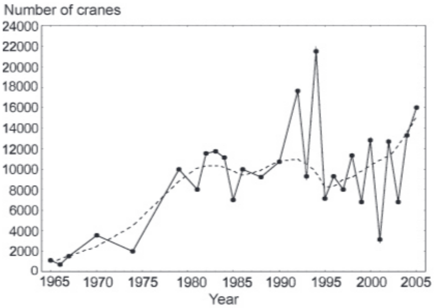

Fig. 2. Temporal dynamics of crane numbers in Matsalu. The solid line represents the actual counted crane number and the dashed line reflects robust locally weighted regressions (LOWESS) over time.

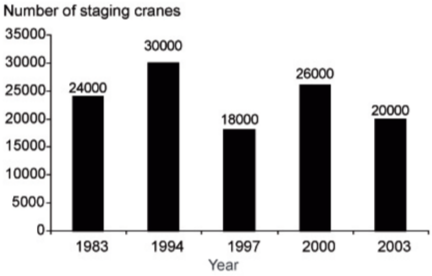

Fig. 3. Total numbers of autumn staging Eurasian Cranes counted in Estonia, 1983–2003 (After Leito et al. 2006).

area is characterized by a large shallow-water sea bay and large fields in the surroundings. There is a significant positive correlation between the number of cranes staging in Hiiumaa and in Matsalu (r_s = 0.47, $p < 0.05$, $n = 21$) and between Matsalu and Estonia as a whole ($r_s = 0.90$, $p < 0.05$, $n = 5$).

Relationships between crane numbers and cropping area

During the period 1965–2004, the total area of cropland in Estonia has varied from 259,248 ha in 2002 to 444,223 ha in 1980 ($CV = 0.55$, $n = 40$) (Fig. 5a). The dynamics of the total area of cropland in Läänemaa County, Hiiumaa County and in the whole of Estonia has been similar (Fig. 5a, b). Five main periods in the total area of field crops can be distinguished for Estonia on the basis of figure 5: (1) the growth in total area in the period 1965–1976, (2) a relatively stable total area in the period 1977–1992, (3) a rapid decrease in the period 1993–1996, (4) a new increase and stabilisation on a lower level at the end of the 1990s, and (5) stabilisation in total area of field crops at a new level close to that of the 1960s. There is no significant linear trend in total area of field crops in Hiiumaa County ($MK = 0.32$, $p > 0.05$, $n = 49$), Läänemaa County ($MK = 1.14$, $p > 0.05$, $n = 40$) and in Estonia as a whole ($MK =$

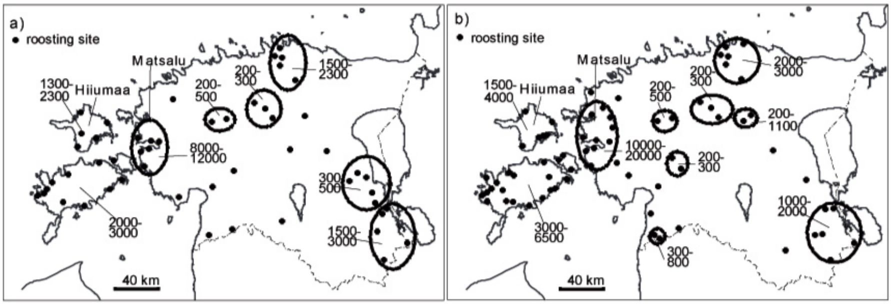

Fig. 4. Distribution of autumn staging Eurasian Cranes in Estonia in the 1980s (a) and 1990s (b).

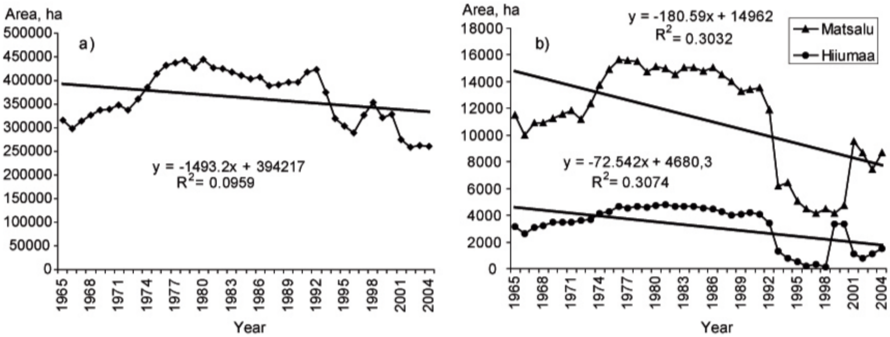

Fig. 5. Total cropping area in the whole of Estonia (a), and in Hiiu and in Lääne Counties separately (b) from 1965–2004. The trends are not significant (*MK* test, $p > 0.05$, $n = 40$).

0.47, $p > 0.05$, $n = 40$) over the whole study period 1965–2004.

The PCA analysis of the total area of cropland in Estonia indicated great changes in the relative share of different field crops in the period 1965–1990: the share of oats and potato had decreased and the share of cultivated grassland had increased (Fig. 6a). The total cropping area of all cereals together, except for summer wheat has decreased since the 1990s. In the Matsalu area (Läänemaa county) and on Hiiumaa (Hiiumaa county) the changes have been different compared to Estonia as a whole. In Matsalu the relative share of different field crops has been stable during the period 1965–1990, and has changed substantially in the period 1991–1995, when the cropping area of all cereals together decreased. Since 1996 the area of cultivated grassland and summer wheat has decreased (Fig. 6b). On Hiiuma

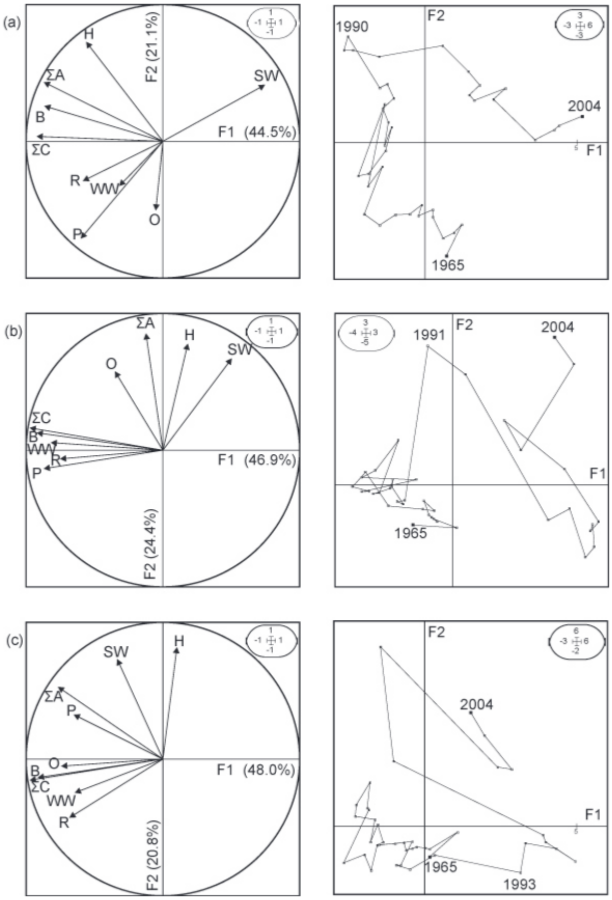

Fig. 6. Results of Principal Component Analysis (PCA) based on the correlation matrix of agricultural land use data. The plots on the left side illustrate the correlation of the agricultural variables (arrows) with the first two axes of (F1×F2) of the PCA. The plots on the right side illustrate the temporal dynamics of consecutive years with respect to the first two principal components: (a) Whole of Estonia, (b) Lääne County (c) Hiiu County. Abbreviations: R – winter rye, WW – winter wheat, SW – summer wheat, B – barley, O – oats, ΣC – total cropping area of cereals, P – potato, H – cultivated grassland, ΣA – total area of arable land.

the changes have been similar to Matsalu during the period 1965–1990, but in the period 2001–2004 the structure of cropland on Hiiumaa has been more stable (Fig. 6c).

We found a significant positive correlation between the number of staging cranes and the cropping area of winter rye, winter wheat, summer wheat and all cereals combined, and a negative correlation between crane numbers and the cropping area of potato (Table 1). The correlation was strongest with the cropping area of winter rye (r_s = 0.58, $p < 0.05$, $n = 21$) and winter wheat ($r_s = 0.58$, $p < 0.05$, $n = 21$) on Hiiumaa, and with the cropping area of all cereals combined in Matsalu (r_s = 0.56, $p < 0.05$, $n = 28$). No statistically significant correlation between crane numbers and the area of cultivated grasslands was found in either Matsalu or Hiiumaa.

Table 1. Significant Spearman correlation coefficients (r_s) between the cropping area and the number of staging cranes in the Hiiumaa (n = 21 years) and Matsalu (n = 28 years) areas.

Locality	Crop	r_s	p-value
Hiiumaa	Winter rye	0.58	< 0.05
Hiiumaa	Winter wheat	0.58	< 0.05
Matsalu	Summer wheat	0.47	< 0.05
Matsalu	Potato	-0.41	< 0.05
Matsalu	All cereals together	0.56	< 0.05

Discussion

We found that the total numbers of Eurasian Cranes staging in Estonia during the autumn migration rose rapidly in the 1960s and 1970s, and stabilized in the 1980s. It is evident, that one reason for the increase in total numbers of autumn staging cranes in Estonia since the 1960s should be the overall growth in crane numbers breeding and passing through (Leito et al. 2006). Unfortunately, we cannot correlate directly the size of the local breeding population and the autumn population because we do not know the proportion of local birds in the autumn counts. On the basis of colour banding and radio tracking we know only that cranes from the local population and from Finland are mixed in Estonia during the autumn migration (Lundin 2005, Leito et al. 2006).

The Eurasian Crane breeding populations and the numbers of autumn staging cranes increased simultaneously up to the 1980s; after that the rise in staging crane numbers stopped, although the breeding population has continued to grow up to the present day (Leito et al. 2003, 2006). This difference is most likely related to agricultural land use changes. We found that staging crane numbers were positively correlated with cropping area of cereals and negatively with the extent of potato fields. It was predictable that the strongest relationship was between crane numbers and the area of winter rye and wheat. This is because, with these crops cranes can feed on newly sown fields and on green crops during one autumn, and on germinated fields and stubbles during the next. In this way the cranes exploit the same fields over a long period during two autumn seasons. Perhaps this is also one of the reasons why the correlation with barley fields was not as strong and was statistically insignificant compared to winter cereals. Breeding cranes are very fond of feeding in germinated barley fields and of picking the grains (Leito et al. 2006), but by the time most migrating cranes arrive in Estonia, the majority of fields have already been harvested, and the birds can only utilize the stubble fields. For that reason barley fields can be used by staging cranes mostly as stubble fields and only during one season. Only local breeding birds and very few early migrants can use germinated barley fields for feeding.

There is a similar but not exactly identical situation with summer wheat in Estonia. Whereas the barley harvest already begins in early August, summer wheat only ripens from late August. Early-arriving cranes will to a certain extent also feed on the germinated summer wheat fields. Another reason why the correlation between crane abundance and the cropping area of rye and wheat was stronger than with barley may be the greater abundance of other food for cranes, such as insects, amphibians and small mammals on these fields. This aspect of crane food has not been studied in Estonia, but some studies from wintering grounds in Spain demonstrate the importance for cranes of additional food other than the main crop they feed on in their habitat (Reinecke and Krapu, 1986; Díaz et al., 1995; Guzmán et al., 1999; Avilés et al., 2002). Visually, rye and wheat fields seems to be much richer in additional food for cranes, if only because of the higher stand of the germinated crop and stubble compared to barley.

In the summer non-breeding cranes in Estonia locally feed in potato fields (Leito et al. 2006). They pick new potatoes right from the furrow. In the autumn the fields are harvested and only a few potatoes or other food remain for the cranes. The negative correlation between autumn crane abundance and the extent of potato fields can be explained mostly by the conflicting relationship with the area of other crops more important for feeding cranes, i.e. when the area of potato crops in a locality increases, the cropping area of cereals and the potential food source there decrease respectively.

The main driving forces in present day rural landscapes in Estonia are land reforms, political campaigns, land amelioration, concentration and intensification of agricultural production. Most probably, newly cultivated lands, especially large field systems, have been the most important factor for the rise and development of autumn staging crane assemblies in Estonia during the 1950s and 1960s (Leito et al. 2006). During the period from the 1960s to the late 1980s collective farms throughout Estonia were becoming fewer and bigger, and their land use was getting more concentrated to the farm centres and to newly-cultivated fields. By this time large tracts of farm land in the periphery had already been abandoned. These processes were direct results of State policy – to support intensive land use in large collective farms.

After Estonia regained her independence in 1991, the transition from a centralised system to a market economy, land reform, and the privatisation of state farms began (Alanen 1999). This resulted in profound changes in agriculture and related land use. The agricultural reform was carried out during the period from 1992 to1997 – collective farms were dissolved and re-organised mostly into joint-stock enterprises or private farms. The changed trade conditions caused vast changes in land-use – large fields were abandoned and the total area of cereals declined. The cultivation area of agricultural crops decreased and the area of unused arable land increased 20-fold by 1999 (Sepp and Hiiemäe 2003). According to expert estimates, in 1999 there were 330–350 thousand hectares of unused arable land in Estonia. (27–31% of all arable land). In accordance with the data of the Statistical Office of Estonia (2002), in 2001, 32.6% of arable land went unused. Some recent changes in the distribution of cranes on migratory routes and in wintering areas are clearly caused by changes in agricultural land use, depending on EU agricultural policy (Alonso et al. 1987, Alonso et al.1994, 2003). More recently, before and after accession to the EU in 2004, rural development programs have been established that encourage the re-cultivation of abandoned agricultural land.

Besides the food sources discussed above, the comprehensive protection of the species and its habitats, and the warming of the climate are probably related to changes (increase) in the distribution and numbers of cranes staging in Estonia in the autumn. The hunting of Eurasian Cranes is currently prohibited in all European countries and illegal hunting is significantly reduced (Meine and Archibald 1996, BirdLife International 2004). In Estonia, the hunting of the Eurasian Crane was prohibited in 1958 and illegal hunting is insignificant (Leito et al. 2006). Also, the establishment of many new protected areas in places where the Eurasian Crane has been breeding and resting has probably contributed to the population growth in Estonia and elsewhere. The proportion of protected areas in Estonia has risen from 4% in 1970 to 12% in 1999 and 16% in 2006 of the total area of the country (Fammler et al. 2000, Leito et al. 2007). Recently, more cranes are wintering in France and Germany, particularly because of climate warming, and their migratory route is shorter compared to earlier times (Cramp and Simmons 1980, Alonso et al. 2003, Lundin 2005). A shorter migration route decreases energy-expenditure and risks during migration, which contribute to a higher survival rate (Berthold 1993, Leito et al. 2003).

In general, we found that migrating crane patterns in Estonia are related to cropping patterns.

And, as the agricultural land use on a county level has changed greatly, depending on agricultural policy, we conclude that it too has had a great impact on migrating cranes. Agri-environmental measures play an important role in decreasing the area of abandoned land and increasing the area of grasslands and cereals. Also direct subsidies to cereal growers have helped enlarge the area of fields that are suitable for the autumn staging of cranes. The resulting abundance of food for staging cranes has led to an increase in crane numbers.

The changes in the pattern of land-use in Hiiumaa and Matsalu have been similar to the general trends in Estonia, except for the last years, when the structure of arable land use in Hiiumaa and Matsalu has been more stable compared to Estonia as a whole.

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IV

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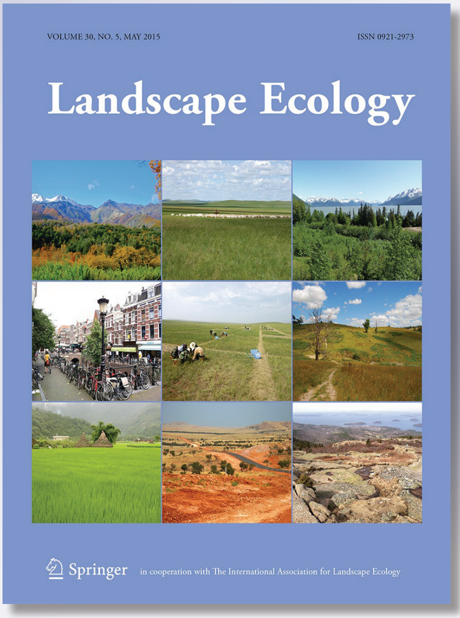

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RESEARCH ARTICLE

The potential impacts of changes in ecological networks, land use and climate on the Eurasian crane population in Estonia

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Abstract

Context The Eurasian crane (*Grus grus*) is an iconic and sensitive species. It is therefore necessary to understand its landscape ecology in order to determine threats.

Objectives (1) To map the distribution of cranes and then model their habitat requirements in Estonia, linked to the current level of protection. (2) To determine the environmental characteristics of, and the habitats present in, sites utilized by the birds, and their sensitivity to change.

Methods (1) The distribution of cranes was recorded by observation and by tracking individuals. A model of potential breeding sites was compared with the occurrence of the bird in Estonia and then linked to protected sites. (2) The seasonal distribution of the bird was overlaid with a European environmental classification and the CORINE land cover map. A model of climate change was also utilized.

Results (1) A new map of European migration routes, wintering and stopover sites is presented. (2) The bird requires a habitat network, with wetlands being essential for nesting and roosting. The composition of habitats used for feeding varies according to geographical location. (3) In Estonia not all potential breeding sites are occupied and many existing sites are not protected. (4) Climate change could threaten populations in the south but could be beneficial in Estonia.

Conclusions (1) The existing ecological network in Estonia is adequate to maintain a viable breeding population of the Eurasian crane. (2) Climate change could support the breeding of cranes but complicate their migration and wintering.

Keywords Eurasian crane · Flyways · Wintering sites · Breeding habitats · Wetlands · Cereal fields · Protection

Introduction

The Eurasian crane (*Grus grus*) has an exceptionally wide distribution, extending from latitude 70°N to 40°N and from longitude 0°E to 130°E (Deinet et al. 2013; Species Assessments 2014). The European breeding population comprises over 120,000 breeding

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pairs and 500,000 individuals, and the numbers are expanding throughout the continent (Deinet et al. 2013; Species Assessments 2014). For example, in the United Kingdom (UK), the population increased from one pair in 1981 to 22 pairs in 2012 (Prowse 2013; The Great Crane Project 2014), and the most recent figures show a further increase. Unlike Estonia, the crane became extinct in the UK in approximately in 1650 due to hunting and drainage projects, although the major wetlands such as the Norfolk Broads, where it now breeds, would have still been present at that time (Great Crane Project 2014). In Estonia, there were 300 pairs in 1970, increasing to 7,500 pairs by 2012. However, the rate of increase has slowed in recent years (Leito et al. 2005; Leito 2012; Elts et al. 2013). The expansion is probably due to the large number of potential crane nesting sites in Estonia connected with the high frequency of natural wetlands and new wetlands that have emerged as a result of the transformation of former gravel, sand and peat cutting quarries into wetlands (Leito et al. 2003, 2005).

The adjacent presence of cereal fields and grasslands, as described by Leito et al. (2006) is also important. Apart from a major increase in forest area during the 1980s (Palang et al. 1998), the balance of land use and associated land cover has remained relatively constant in Estonia over the last 20 years. The present pattern of land use is unlikely to change, unless there is a major increase in cereal prices, which may lead to some abandoned fields on poorer soils being converted back into crops. However, the wetlands are unlikely to be drained because of the high costs involved. The adjacent scrub is also unlikely to be cleared, as it generally present on water saturated soils. Other factors, such as hunting, have also remained stable, and it is therefore difficult to attribute the increase in crane numbers to a specific individual factor.

The Eurasian crane is an iconic species and has considerable support amongst ornithologists and the public, to the extent that sites for observation throughout Europe are available on the internet (Kraniche 2014; The Great Crane Project 2014). Substantial new important information on crane distribution, breeding, and migration has recently been made available in the proceedings of international crane research meetings, e.g. Ilyashenko and Winter (2011), Harris (2012) and Nowald et al. (2013). Other sources of data are in a bird atlas (Saurola et al. 2013), and on the internet (European Crane Working Group 2014; Kraniche 2014, Migration map 2014; Satelliittikurjet 2014).

Approximately 90 % of the Estonian crane population overwinter further south in Europe, and the remainder in Africa (Species Assessments 2014). The Eurasian crane has three main flyways (migration routes) in Europe—the West European Flyway, Baltic-Hungarian or Central European Flyway, and the East European Flyway (Nowald 2010), as discussed in detail below. The West European and Central European Flyways are approximately 3,500 km in length, and the East European Flyway is approximately 6,000 km in length. The most northern regular wintering areas of cranes are situated in northern France on the West European Flyway and in southern Hungary on the Central European Flyway. However, during the winter of 2012, up to 10,000 cranes also wintered in northern Germany (Nowald et al. 2012, 2013). The distance between the southern border of the main breeding area of cranes, shown in Fig. 1, and the nearest regular wintering area, is approximately 500 km on the West European and Central European Flyways and 1,300 km on the East European Flyway, as shown in Fig. 2 (Leito et al. 2011; Deinet et al. 2013; Nowald et al. 2013). Cranes breeding in eastern Finland and eastern Estonia use all three main European Flyways (Leito et al. 2011; Saurola et al. 2013; Suorsa and Hakkarainen 2013; Migration map 2014).

Leito et al. (2008) have discussed the increase in numbers of Eurasian cranes in Estonia up to 2006 and emphasized the importance of cereal fields as opposed to other crops. They concluded that changes in the ecological networks at the stopover areas could be more important than the conditions in the breeding sites. At all sites, the cranes need a combination of habitats such as wetlands and cereal fields. Another factor affecting the distribution and numbers of cranes is likely to be the impact of climate change on temperature regimes and habitat patterns. For example, according to climate change scenarios for the late Twenty-First Century, Huntley et al. (2007) have predicted that the distribution of the Eurasian crane may change in many parts of Europe. However, the future for this species appears less vulnerable than other crane species (Hansbauer et al. 2014). The present paper therefore models the distribution of breeding habitats of cranes in Estonia

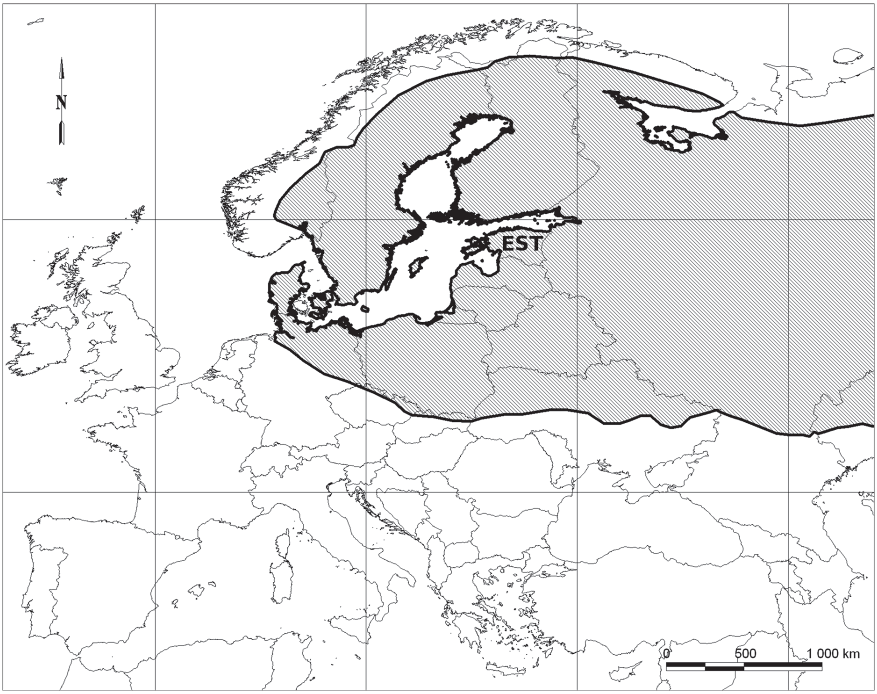

Fig. 1 The *shaded area* represents the main European breeding area of the Eurasian crane

and compares it with the distribution of designated protected areas, in order to establish the degree of protection provided. The current status of relevant habitats is then discussed in relation to the requirements of the bird, and set into the context of land cover and potential habitat change in Estonia. New information is then provided on the distribution of the flyways in relation to overwintering areas and their relationship with the European environment. A climate change scenario is then applied and the potential implications on crane populations discussed. The main objective of this paper is therefore to examine the stability of the habitat network used by cranes in Estonia and then compare this with potential shifts in land use and climate elsewhere in Europe.

Habitat requirements of cranes

Eurasian cranes are omnivores and feed carnivorously during breeding, but mainly on herbaceous material during migration and over-wintering (Cramp and Simmons 1980; Prange 1989). In wintering sites in Spain, the cranes mainly feed on sown cereals and stubble but also on fields of harvested maize, sunflower, sugar beet and potato. However, in the *dehesas* (open evergreen and cork oak woodlands in Spain) the cranes feed on bulbs and acorns (Avilés et al. 2002; Alonso et al. 2004; Lundin 2005; Munillo 2014). In France, the cranes mostly forage on maize stubble and sown cereals (Lundin 2005; Salvi 2013). Maize stubble fields are also the main foraging sites of staging cranes in Germany and Hungary (Lundin

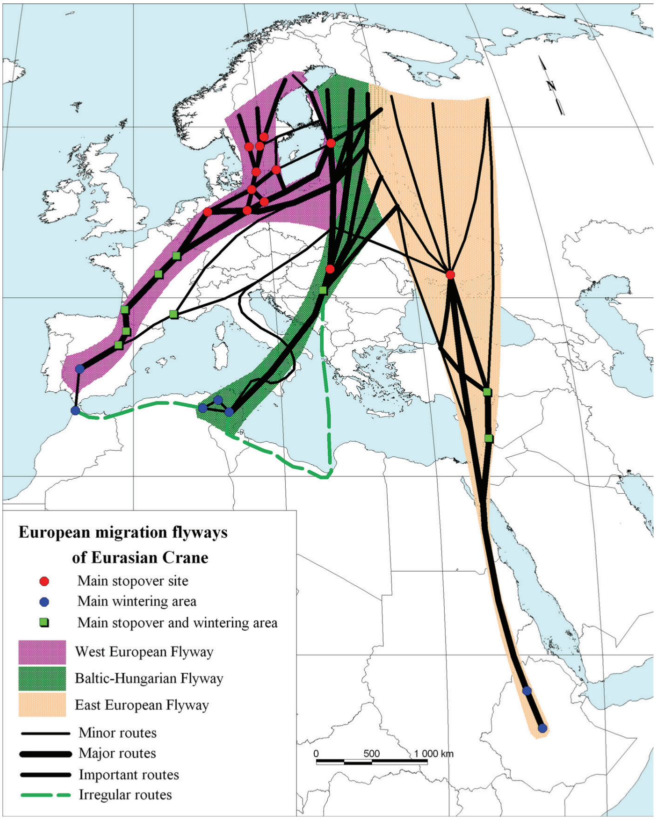

Fig. 2 Generalised map of the European Flyways (migration routes) of the Eurasian crane (*Grus grus*). The main stopover areas, stopover and regular wintering sites, and wintering areas are shown on the key, as well as different types of routes followed

2005; Prange 2012; Végvári et al. 2012; Prange 2014). In Estonia, the birds feed mainly in cereal fields, meadows and mown grasslands, but nest in wetlands such as mires, fens, coastal lagoons, inland lakes and swamp forests (Leito et al. 2005, 2006).

According to Cramp and Simmons (1980), Prange (1989) and Leito et al. (2006), cranes require the following essential habitats in the breeding season:

- water, or at least a wet habitat patch for nesting;
- water for roosting;
- feeding places in fields and meadows.

However, during migration and wintering they only need the latter two types of habitats. The ground or water must not be frozen for periods of more than 1 week because the birds cannot roost or feed safely under such conditions. The regions with resident cranes in Europe, e.g. Southern England, are only frozen for short periods. The above habitat types have remained relatively stable in Estonia over the last 20 years, although there had previously been a major increase in forest cover, as described by Raet et al. (2008). Cereals also increased in area in the 1960s, but have been relatively stable over the last 20 years. Cereal fields are important for feeding, as shown by Leito et al. (2006, 2008). Autumn sown cereals comprise less than 20 % of all grain crops in Estonia (Vasiliev et al. 2008), but may be important locally. Cranes extensively utilize cereal fields in late August and early September, eating both the sown grain and young green shoots. They also forage on harvested wheat, or preferably barley stubble or germinating cereals. Crane families start to feed on ripe barley stands but also continue to utilize barley fields after harvesting (Leito et al. 2006, 2013). From late August until departure in October, cereal stubble is the most important type of feeding habitat in Estonia for local birds, as well as those stopping over from Finland and Russia. Estonian farmers suffer damage from local and passing cranes mainly on ripe barley stands before harvesting, and on autumn sown cereals from mid-August to late-September. However, in general, crop damage caused by cranes is not a serious concern in Estonia (Leito et al. 2013), but is an increasing problem in several important stopover and wintering areas in Hungary (Végvári et al. 2012), Germany (Nowald et al. 2010b; Prange 2012) and France (Salvi 2013). A frequent problem for cranes in most stopover and wintering sites, and in some nesting sites after the young are fledged, is the lack of grain on the ground after harvesting (Leito et al. 2006). Sepp (pers. comm.) has reported that, currently, in Ethiopia cranes still feed on grain that is shed when using traditional harvesting methods, as well as on weed seeds. But this important food may be lost in great extent after mechanisation of harvesting in future. The stubble on fields after harvesting is important for cranes, who feed on both the herbaceous and animal material present. The weed populations of cereal fields, although widespread 40 years ago, have almost disappeared in Northern Europe, because of herbicide use (Dahl 2007), and are now insignificant.

However, there have been some changes in landscape patterns in Estonia, e.g. an increase in field size (Kaasik et al. 2011), which may favour cranes. Additionally, the wet meadows surrounding water bodies, which were formerly mown, are now often abandoned (Kukk et al. 2010). The resultant long grass may provide shelter from predators for the young birds, but may subsequently be colonized by scrub of species such as *Salix*, which reduces its value to the cranes. These changes are relatively minor compared with the large increase in crane numbers. One important reason for the increase in the European population of cranes could be the persistence of natural and artificial wetlands along the migratory routes and in the breeding areas, following the major losses of the 1950s and 1960s. Many of the main wetlands used by cranes outside Estonia e.g. in France and Spain are protected and are not therefore threatened by drainage, but only by climate change. Irrigation channels used for crops may also be important. The role of crane conservation measures is difficult to prove, but is likely to be pivotal, as the major population increase started around the time of the setting up of the RAMSAR Convention which helped to conserve existing wetlands. In some cases, this has even led to reintroductions, for example in the South-West of England (The Great Crane Project 2014). There is also the possibility of population dynamics being integrated with changes in the environment.

In Estonia, not all locations that are suitable for nesting are occupied, and some birds have even moved into new habitats, such as exhausted sand and gravel pits, sea islets and coastal lagoons. Full capacity has not therefore been reached, and the existing habitat network should therefore be sufficient for further crane population increases. In addition, there is currently no evidence that the present wetlands are likely to be drained, because the costs would likely be too high, bearing in mind the current financial situation in the agriculture industry.

Methods

Potential breeding habitats map

The geographic distribution of nesting habitats of the species was analysed using an approach termed species distribution models (SDMs) which are a collection of statistical models that describe how environmental variables are associated with the geographical distribution of a given species (Guisan and Zimmermann 2000).

Machine learning methods are able to address non-linear relationships between response and predictor variables and in the present project, maximum entropy (Phillips et al. 2004, 2006; Phillips and Dudik 2008) has been used as it requires only the presence of species not numbers (Fourcade et al. 2013; Renner and

Warton 2013). Thus, because only the presence of nest sites and habitats was available for use within this study, MAXimum ENTropy (MAXENT) was selected as the most appropriate modelling method.

Various types of data were used to model the potential distribution of crane nesting sites. Initially, original Eurasian crane nest record cards (Leito et al. 2006) were used to provide data on the precise locations of nests. In total, it was possible to obtain usable data on 96 nests from the period 1984 to 2012. However, the spatial coverage and representation of these data does not cover the whole range of suitable nest sites in Estonia, because the data focussed mainly on the reed beds and fens typical of coastal areas and the western part of Estonia (N = 75). The second source of nest sites was recent data from the Estonian Breeding Bird Atlas, which has relatively even spatial coverage over the whole country and also represents all the possible nesting habitats, including mires and wet clear-cuts (N = 96). The third source was the breeding bird survey program of mire birds in the National Environmental Monitoring Programme (Leivits 2013). In contrast to the first two sources, the samples from the last data set, represents only the niche covering the mire breeding population. The latter samples do not always represent the exact nest points, however, because when using the line transect census method, identifying the calling territorial pairs of cranes may not reveal the actual location of the nests (N = 665). The sample sizes reflect the data records that have coordinates and are therefore usable.

The raster layers used for the environmental variables were (1) the classes of the Corine Land Cover (CLC) map (details given below), (2) soil type (Estonian Soil Map from the Estonian Land Board) and (3) Landsat-7 Enhanced Thematic Mapper Plus (ETM+) multispectral bands (data available from the United States Geological Survey). Green (2), red (3) and near-infrared (4, 5) channels were used. Different spectral bands enable the identification of finer scale patterns in the vegetation. For example, near-infrared channels indicate the amount of water between the plant cover whereas green channels indicate the vegetation composition at a specific site. To eliminate different habitats with similar reflectance values, general environmental variables, i.e. maps of land cover and soils, were used in the model. All used bands were first calibrated to absolute radiance values (Barsi et al. 2007). The mosaic of ETM+ images was compiled from five different scenes, dating from July to August 2006. Each described band was used as a separate variable in the MAXENT model.

The MAXENT program version 3.3.3k was utilised in the R environment (Hijmans et al. 2013; R Core Team 2013). Of the total sample, 20 % was used for testing the model. By varying the sets of training samples from the three different data sources described above, several models were fitted. As several data points fell outside the extent of the variable rasters used, the sample size was therefore reduced. From several models, two candidates were selected for further investigation. The first model was based on the first and second sources of samples (nest cards combined with the breeding bird atlas, and giving the precise location of nests). The second model was based on the third source of samples (mire breeding bird survey). The area under the receiver operating characteristic (ROC) Curve of the test samples was used to evaluate the models. The predicted probability maps were reviewed by experts to assess the maps from the species habitat selection aspects. Models that are based on different samples have both advantages and disadvantages, and emphasize the different niches of potential nesting sites. However, the second model strongly overemphasizes raised bogs, but not fens and transitional mires, which are important breeding habitats for cranes. Taking into account the overall better predictive performance of the first model and the more balanced representation of different nesting sites, this was therefore selected for further study. The variables with highest contribution were: land cover (66 %), soil type (22 %), and ETM+ red band (11 %).

The habitat prediction or nest-site suitability map (0/1 discrete raster) was calculated from the predicted probability map (0 to 1 probability raster) using a logistic threshold that represents the pixel values when the test sample sensitivity (true positive rate) and test sample specificity (true negative rate) are maximized. For example this happens when the situation occurs that the sum of correctly predicted presences and absences in the test samples is at its maximum. The respective logistic threshold value for the selected model was 0.32 (32 %). All pixel values of the probability map greater than the obtained threshold value were then classified as suitable nesting areas. The suitability map of the potential nesting sites of cranes in Estonia was then calculated from the

Table 1 Base data for the determination of the stopover and wintering sites of Eurasian cranes (*Grus grus*) from the Estonian population

No.	Country (no. of selected areas)	In certain state		In selected areas		Proportion (%) in selected areas	
		No. of individuals observed	No. of observations	No. of individuals observed	No. of observations	No. of individuals	No. of observations
1.	Algeria (1)	2	35	2	14	100	40
2.	Belarus (5)	13	471	12	418	92	89
3.	Estonia (3)	153	2040	136	1746	89	86
4.	France (3)	119	567	108	494	91	87
5.	Germany (3)	143	820	113	494	79	60
6.	Hungary (2)	35	291	32	210	91	72
7.	Latvia (1)	8	47	2	37	25	79
8.	Serbia (1)	7	66	4	48	57	73
9.	Spain (3)	110	695	101	557	92	80
10.	Tunisia (1)	2	129	2	67	100	52

On average 82 % of individuals and 72 % of observations were related with selected areas

predicted probability map using the 32 % threshold value. The land cover of the suitable nesting sites of cranes (probability over 32 %) was analysed by overlay analysis based on the CLC map. The land use composition of nature protection areas was calculated by overlay analysis separately for the suitable nesting sites of cranes (probability over 32 %) and for the areas where nesting is unsuitable (probability up to 32 %). The overlay analysis was also used to calculate the share of land cover types, conservation and protected "green" areas individually for suitable nesting sites and unsuitable nesting sites. The nature conservation layer was composed of areas of four types of protected sites that have actual conservation measures in place. These include GIS layers according to the Nature Conservation Act as follows: (1) protected areas; (2) limited conservation areas; (3) single protected natural features; and 4) species protection sites (data from Estonian Environmental Registry, EELIS, February 2014). The network of protected areas (termed the Green Mask) was compiled using layers based on the thematic plans of the counties in the Green Network of Estonia (see, e.g. Raet et al. 2010).

Stopover and wintering sites land cover analysis

Each European crane Flyway (migration route) consists of a network of stopover sites which are needed for energy loading during the migration period. Stopover and wintering sites for cranes have two important components, an overnight location on a wetland, e.g. marshes, lagoons and shallow lakes, and a feeding area on adjacent agricultural land. To select the most important stopover and wintering site of cranes from the Estonian population along the flyways, the database of recoveries of colour-ringed cranes and data from satellite telemetry was used. In total there were 5,967 recoveries from 234 individuals from which 5,161 observations (86 %) from 218 individuals (93 %) were used to select 23 stopover or wintering sites in ten countries (Table 1). The distance between the overnight sites and feeding areas varied between stopover locations in different landscape types, and with food availability. The maximum distance between the overnight site and feeding area was 20–34 km on the West-European Flyway in Estonia (Matsalu, Meelva) (Keskpaik et al. 1986; Leito et al. 1987), 20–40 km in Germany (Rügen-Bock, Rhin-Havelluch) (Albrecht et al. 2010; Nowald et al. 2010), and 25–40 km in Spain (Gallocanta, Orellana) (Alonso et al. 1997; Guzmán et al. 1999; Alonso et al. 2004; Bautista and Alonso 2013). The average maximum distance between overnight resting places and feeding areas, both on stopover and wintering sites on flyways, was estimated to be 30 km. This distance around the known overnight sites, and in three cases around the centre point of feeding sites, was therefore used as the buffering measure for overlaying the crane sites on the CLC map.

The locations of the crane stopover sites were overlaid on the Corine land cover (CLC) map (version 16; 2006) in order to determine their land cover composition. CLC was created by visual interpretation of remote sensed images and provides 44 classes aggregated at three different levels (European Commission 1994). Currently, CLC is the only cartographic product that offers a consistent land cover classification across the European migration and wintering sites, although certain classes may not be measured accurately because small patches may be assigned to the wrong category because of the coarse resolution of the map. In this study, not all the crane wintering locations were included because CLC does not include Algeria and Tunisia.

The land cover composition at the migration and wintering sites was calculated as the proportion of each CLC class within every buffer polygon (30 km radius circles), through polygon clipping and area measurement procedures performed in ArcMap v. 10.1. Not all the classes were included in the analysis, because cranes do not use some land cover types, such as coniferous forest. Only the following land cover types used by cranes were included:

2.1.1	Non-irrigated arable land
2.1.2	Permanently irrigated land
2.4	Heterogeneous agricultural areas
3.2.1	Natural grassland
4.1	Inland wetlands
4.2	Coastal wetlands
5.1	Inland waters
5.2	Marine waters (excluding class 5.2.3, sea and ocean)

In addition, in order to provide a comparison between the sites occupied by cranes and wider landscapes, CLC was analysed at control points 60 km south from the initial location because other compass points were either in the sea or impractical. These sites acted as controls to show differences in land cover between the nest sites and independent locations.

In addition to the land cover analysis at each site, comparisons were carried out between the Estonian sites and all other migration and wintering sites in Europe, in order to determine whether the composition around the wetlands at these sites was similar to those in Estonia. The average percentage of each land cover class at the Estonian sites and all other locations was calculated. Similarly, the average values for the Estonian sites were compared with all other sites aggregated by stopover sites only, by wintering and stopover areas, or by wintering areas.

Environmental stratification and climate scenario methodology

The methodology for the construction of the European environmental stratification (EnS) involved screening climate parameters and extracting those that expressed the most variation. Principal components analysis followed by cluster analysis was used to create 84 environmental strata (EnSs), which were then joined hierarchically into 13 environmental zones (EnZs). The methodology is described in detail by Metzger et al. (2005), and the application of climate change models by Metzger et al. (2008). Descriptions of the individual Classes and Zones are provided in Metzger et al. (2012). A post-processing stage was required to re-assign scattered small regions of only a few square kilometres into neighbouring strata.

To assess how the main European environments would shift under different climate change scenarios, climate functions were fitted to the EnS (Metzger et al. 2008). The TYN SC1.0 has a resolution of 10 arcmin longitude-latitude and contains 20,400 monthly grids of observed climate, for the period 2001–2100 (Mitchell et al. 2004). It comprises five climatic variables, namely: cloud cover, diurnal temperature range, precipitation, temperature, and vapour pressure. The original EnS map was resampled to match the 10 arcmin resolution of the climate dataset. Each grid cell was then linked to the values of the climate variables contained in the CRU TS1.2 and TYN SC1.0 datasets. Fisher's Discriminate Functions were calculated for each EnS stratum and used in ArcGIS to determine the future distribution of the 84 strata from the monthly climate variables. Separate maps were created for the three time slices (2020, 2050 and 2080). For simplicity, only the most likely scenario was used in the present study, namely the CGCM2 Circulation Model-A2 emissions scenario.

The analysis of the EnZs shift at the crane migration sites was carried out based on the projected climate

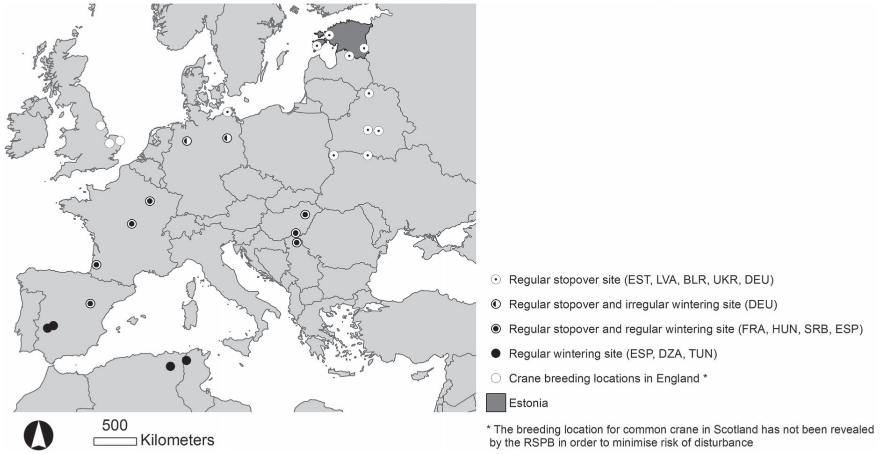

Fig. 3 Distribution of the stopover, stopover and irregular wintering, stopover and regular wintering, and wintering sites of the Estonian population of the Eurasian crane (*Grus grus*). Legend for country codes (according to ISO 3166-1): *BLR* Belarus, *DEU* Germany, *DZA* Algeria, *ESP* Spain, *EST* Estonia, *FRA* France, *HUN* Hungary, *LVA* Latvia, *SRB* Serbia, *TUN* Tunisia, *UKR* Ukraine

change at the time steps 1990, 2050 and 2080, as modelled in Metzger et al. 2008 using the scenario described above. The assessment of the proportion of the EnSs in mainland Europe was derived by overlay, clip and area measurement operations in ArcMap 10.1. The EnSs were then grouped into the EnZs, and the average geographic coverage of each Zone obtained for each migration site type: staging, migration, and wintering. To assess shifts between EnZs, the process was repeated for the three time steps, 1990, 2050 and 2080, under the aforementioned climate change scenario.

Results

Description of the European flyways, wintering sites and the potential impact of climate change

The Eurasian crane nests mainly in Northern Europe, as shown in Fig. 1, and migrates south from there in the autumn. The main exception to this pattern is Southern England where the cranes both breed and overwinter in the same location. The birds returned to the Norfolk Broads in 1979 and the latest figures for cranes in the UK, as reported in The Norfolk Crane Story (2014), are 18 confirmed pairs, two probable, two possible and seven non-breeding. The total number of chicks fledged was 12. Figure 3 includes the distribution of the sites where cranes have bred in Britain. In 2013 a pair also bred in Scotland, but the site is confidential and is not shown on the map. The Great Cranes project has also attempted to reintroduce the birds into Somerset, South-West England, but there is still not a breeding population in this region.

However, the majority of birds follow a general network of flyways and routes across Europe that connect the northern and southern parts of the breeding range to the rest of the continent, as shown in Fig. 2. The Figure depicts the most recent version of the flyways and was derived from the data sources described in the methods section. In addition, individual cranes may change their migration flyways and use different migration routes and wintering areas in different years (Leito et al. 2011; Saurola et al. 2013; Suorsa and Hakkarainen 2013; Satelliittikurjet 2014). Therefore, although the migration routes of the cranes

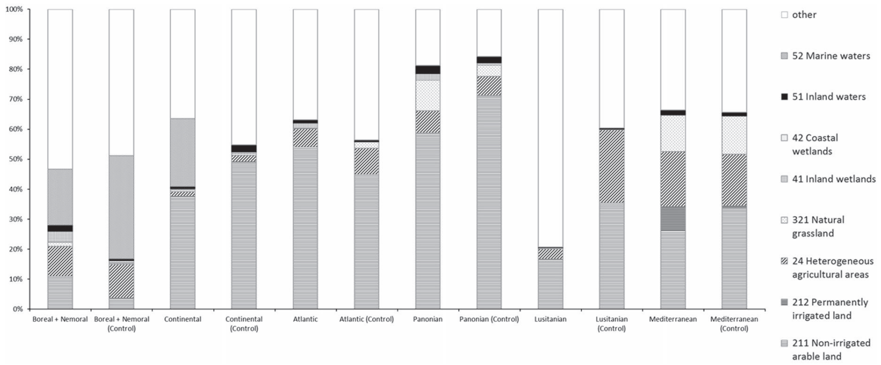

Fig. 4 Percentage cover of eight relevant CLC classes at stopover sites of the Eurasian crane (*Grus grus*) compared with control points 60 km south from the initial sites

are integrated, their migration strategy is variable and flexible, presumably according to local conditions and seasonal variability.

A detailed migration map of Estonian cranes has been produced and is shown in Fig. 3. This indicates the main stopover and wintering areas of the local crane population analysed in this article. This map includes two sites in Germany where the cranes may overwinter if the season is mild. Figure 2 shows the routes followed by the migrating birds. These routes cover thousands of kilometres and the birds have been using them for many centuries. The flexibility mentioned above indicates that, if conditions change in the future, the birds are likely to be able to adapt.

Figure 4 shows the results of overlaying of the crane sites with the CLC map as compared with controls, summarized by EnZs. Almost all stopover sites have more land cover associated with water than the controls, confirming the primary requirement of cranes for roosting sites. The areas of water are small, which may in part be due to the minimal patch size of 25 ha in CLC, but it also suggests that the cranes can manage where wetlands form a relatively small part of the landscape. However, the surrounding network shows contrasting patterns between the northern Zones, where forest dominates and cereals occupy only a small area, and the southern Zones. The latter have a much higher proportion of agricultural land, varying from cereals in the Continental Zone to irrigated arable land and other types in the Mediterranean Zones. Cranes are therefore sufficiently flexible to find feeding places within a range of different landscapes, confirmed by their ability to fly up to 30 km to locate suitable foraging areas.

Table 2 shows the results of the identification of various types of sites with the EnS, and reveals a diagonal distribution pattern from north to south through the series. The stopover sites are in the Nemoral, Continental, Atlantic North, Atlantic Central and Pannonian Zones, as defined by Metzger et al. (2005). According to the mean values of the individual classes, none of the sites will be frozen at the time of winter migration. Table 3 shows the actual mean temperatures in summer and winter in the relevant EnZs and EnSs to provide detail about the requirements of cranes. The Boreal and Nemoral Zones are deeply frozen throughout the winter months but only one continental class is frozen, which shows why the cranes stopover in the continental zone in favourable winters. The mean figures may mask short frozen periods, which could explain the uneven pattern. Even small shifts in temperature regimes could therefore influence the stopover sites in the areas affected, especially given the degree of behavioural flexibility shown by the cranes. Another feature of the results, emphasizing the importance of low temperatures, is that summer temperatures in the northern Zones are higher than those in the winter period in the Mediterranean.

The sites outside North Africa belong to several different classes that are common to Ethiopia and the

Table 2 Average percentage of the stopover, stopover and regular wintering, and wintering sites of the Eurasian cranes (*Grus grus*) from Estonia in the EnZs of Metzger et al. (2005)

	Stopover	Regular stopover and irregular wintering	Stopover and wintering	Wintering
ALN	–	–	–	–
BOR	21.1	–	–	–
NEM	49.3	–	–	–
ATN	–	50.0	–	–
ALS	–	–	–	–
CON	29.6	50.0	–	–
ATC	–	–	28.6	–
PAN	–	–	42.9	–
LUS	–	–	14.3	–
ANA	–	–	–	–
MDM	–	–	12.9	37.1
MDN	–	–	1.3	0.9
MDS	–	–	–	62.0

ALN Alpine North, *BOR* Boreal, *NEM* Nemoral, *ATN* Atlantic North, *ALS* Alpine South, *CON* Continental, *ATC* Atlantic Central, *PAN* Panonian, *LUS* Lusitanian, *MDM* Mediterranean mountains, *MDN* Mediterranean North, *MDS* Mediterranean South

Dead Sea area, as described by Metzger et al. (2013). All the sites are linked to various water bodies, but with very different mixtures and proportions of surrounding land covers. Therefore, these results also highlight the flexibility of cranes in adapting to a range of habitat networks, providing that the primary requirement of wetland for roosting is available.

The results from applying the climate change model described above are given in Table 4. The likely impact of this scenario is, at first glance, minimal for cranes because the core area of wintering sites in the Mediterranean stays superficially the same. By 2080, the Lusitanian site becomes Mediterranean North, which will have minimal impact on cranes. The shift in Estonia is from Boreal to Nemoral in 2050, and then to Atlantic North in 2080. Figure 5 shows the regions where winter temperatures in 2080 will be above freezing. In Central Europe this map is coincident with the current area where irregular stopovers occur. However, the most striking feature of the map is the potential shift in Western Estonia towards non-freezing conditions. This suggests the possibility of cranes being able to overwinter in the country by 2080. The Pannonian Zone is only close to zero in January and, under recent climate regimes, will probably no longer be frozen at this time. However, Western Estonia is adjacent to the Nemoral and Boreal Zones, which may lead to longer periods of frozen conditions than would be expected for the Atlantic North Zone. However, overall, the data shown in Fig. 5 confirm the potential for further expansion of cranes in Europe, because conditions are likely to become more favourable for the species.

In contrast, the sites in the Atlantic Central and Pannonian Zones are expected to be stable. Another major influence on crane migration patterns is likely to be the shift within the Mediterranean Zone to hotter and drier classes, which could lead to drying out of shallower wetlands. The link to irrigated land, as discussed below, could counter this effect. In addition, Class 8, currently only present in North Africa, has similar temperature ranges to Classes 6 and 7, but has much lower rainfall. This could be amplified if the agricultural sector increases its use of water for irrigation. This may be unlikely in Spain and Southern France because of the already extensive use of irrigation from existing reservoirs, but could be a major problem in Africa. Sepp (pers. comm.) has recently observed this same process in Ethiopia. There is also a problem with the increasing use of aquifer water, e.g. in Israel, which is causing the drying out of springs adjacent to the Dead Sea; another site used by migrating cranes. It is generally expected that the process of desertification is likely to continue, because of the changes in climate that are already taking place.

Table 3 Mean temperatures in the EnZs and EnSs

Stopover or wintering	Site code	T_{mean} (°C)											
		January	February	March	April	May	June	July	August	September	October	November	December
	ALN	−9.70	−9.02	−6.20	−2.31	3.46	8.43	10.94	9.65	5.26	0.32	−5.34	−8.43
⊙	*BOR*	−9.41	−8.94	*−4.38*	*0.87*	*7.44*	12.58	14.91	13.09	*8.09*	*2.67*	*−3.43*	−7.60
⊙	*NEM*	−4.49	−4.03	*−0.20*	*5.80*	*11.91*	15.39	17.06	16.38	*11.58*	*6.54*	*1.08*	−2.66
◐	*ATN*	*1.87*	*2.14*	*4.12*	6.51	10.29	12.99	14.99	14.96	*12.15*	*8.74*	*4.93*	*2.86*
	ALS	−2.61	−1.71	1.19	4.69	9.51	12.72	15.04	14.96	11.53	7.05	1.74	−1.40
	CON	−2.23	−0.89	3.18	8.17	13.41	16.43	18.21	17.98	13.80	8.75	3.05	−0.56
	CON1	−2.64	−0.66	3.76	8.73	13.86	16.66	18.19	18.09	14.27	9.07	2.96	−1.12
	CON2	−2.61	−1.58	1.70	5.49	10.48	13.62	15.71	15.62	11.96	7.42	2.00	−1.42
⊙	*CON3*	−3.66	−2.54	*1.75*	*7.84*	*13.47*	16.49	18.03	17.70	*13.11*	*7.87*	*2.04*	−1.69
	CON4	−2.00	−0.71	3.25	7.58	12.76	15.65	17.51	17.37	13.37	8.39	2.88	−0.44
⊙ ◐	*CON5*	*−0.06*	*0.99*	*4.18*	*8.30*	*13.29*	16.34	18.22	18.09	*14.17*	*9.37*	*4.38*	*1.28*
	CON6	−0.37	0.75	4.06	7.38	12.06	15.09	17.28	17.18	13.62	8.96	3.78	1.01
	CON7	−2.08	−0.57	3.52	7.84	12.93	15.86	17.72	17.54	13.55	8.73	2.92	−0.73
	CON8	−1.57	0.17	4.18	9.08	14.24	17.23	18.90	18.84	14.98	9.83	4.00	0.18
⊙	*CON9*	−1.71	−0.23	*3.86*	*8.85*	*14.13*	17.14	18.93	18.67	*14.46*	*9.33*	*3.72*	0.10
	CON10	−3.35	−1.84	2.97	8.92	14.28	17.29	18.97	18.62	14.03	8.78	2.58	−1.45
	CON11	−1.58	0.14	3.99	8.72	13.86	17.14	18.97	18.97	15.17	10.09	4.22	0.19
	CON12	−0.17	1.85	5.84	10.21	15.23	18.41	20.30	20.21	16.38	11.14	5.31	1.29
◉	*ATC*	*3.54*	*4.16*	*6.54*	8.63	12.43	15.22	17.57	17.53	*14.62*	*10.80*	*6.56*	*4.53*
◉	*PAN*	*−0.80*	*1.22*	*5.50*	10.93	16.25	19.63	21.38	21.14	*16.97*	*11.41*	*5.27*	*1.07*
◉	*LUS*	*6.03*	*7.12*	*8.87*	10.45	13.78	16.99	19.59	19.69	*17.31*	*13.41*	*9.15*	*6.98*
	ANA	−0.10	1.03	3.36	6.80	9.90	12.50	14.53	14.41	12.06	8.48	4.27	1.27
◉ ●	*MDM*	*4.00*	*5.15*	*7.46*	10.31	14.68	19.15	22.36	22.35	*18.70*	*13.57*	*8.45*	*5.27*
◉ ●	*MDN*	*4.89*	*6.08*	*8.36*	11.19	15.44	19.49	22.43	22.41	*19.03*	*14.15*	*9.20*	*6.08*
●	*MDS*	*8.86*	*9.94*	11.86	14.19	18.11	22.50	25.52	25.71	22.61	17.83	13.07	*10.04*

The cells with italicized values display areas occupied by cranes during their wintering or spring/autumn migration. Stopover and/or wintering sites and their symbols and site codes are given on Figs. 3 and 5

Table 4 Average percentage of stopover, stopover and regular wintering, and wintering sites of Eurasian cranes (*Grus grus*) in the projected EnZs of Metzger et al. (2008) according to the CGCM2–A2 scenario

	Stopover			Regular stopover and irregular wintering			Stopover and wintering			Wintering		
	1990	2050	2080	1990	2050	2080	1990	2050	2080	1990	2050	2080
ALN	–	–	–	–	–	–	–	–	–	–	–	–
BOR	21.1	0.6	–	–	–	–	–	–	–	–	–	–
NEM	49.3	51.5	13.4	–	–	–	–	–	–	–	–	–
ATN	–	–	31.4	50.0	50.0	50.0	–	–	–	–	–	–
ALS	–	–	–	–	–	–	–	–	–	–	–	–
CON	29.6	47.9	47.2	50.0	50.0	–	–	–	–	–	–	–
ATC	–	–	8.0	–	–	50.0	28.6	28.6	28.6	–	–	–
PAN	–	–	–	–	–	–	42.9	42.9	42.9	–	–	–
LUS	–	–	–	–	–	–	14.3	0.7	–	–	–	–
ANA	–	–	–	–	–	–	–	–	–	–	–	–
MDM	–	–	–	–	–	–	12.9	7.9	2.7	37.1	35.7	24.8
MDN	–	–	–	–	–	–	1.3	19.9	25.7	0.9	–	–
MDS	–	–	–	–	–	–	–	–	0.1	62	64.3	75.2

ALN Alpine North, *BOR* Boreal, *NEM* Nemoral, *ATN* Atlantic North, *ALS* Alpine South, *CON* Continental, *ATC* Atlantic Central, *PAN* Panonian, *LUS* Lusitanian, *MDM* Mediterranean mountains, *MDN* Mediterranean North, *MDS* Mediterranean South

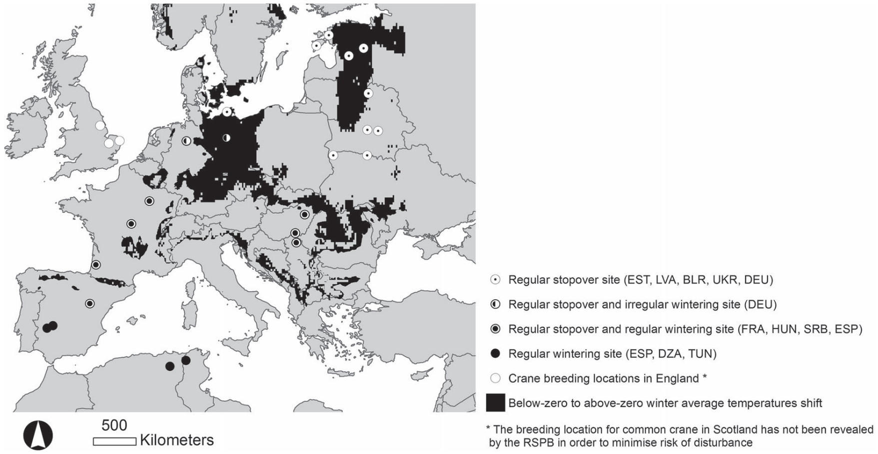

Fig. 5 Shift map displaying the evolution from below −0 to above −0 winter average temperatures by 2080 (according to CGCM2–A2 climate change scenario)

Models of potential breeding sites in relation to habitat change and conservation networks

The probable distribution of crane breeding habitats was modelled as shown in Fig. 6. The model was further analysed in the context of current and potential land use changes and in comparison with current territorial cover of conservation measures (strict nature protection and green infrastructure).

Fig. 6 Suitability map of potential nesting sites of the Eurasian crane (*Grus grus*) in Estonia calculated from the predicted probability map using the 32 % threshold value

Table 5 shows that the majority of protected area designations are for bogs and forests and that most cranes are in areas dominated by land not covered by designation as protected area. Nevertheless, the increasing crane population outside protected areas demonstrates that the cranes are able to prosper without designation of individual sites, although they are protected by law from hunting. Thus, in common with many other countries, the protected area designation process covers specific types of sites and often omits large sections of the countryside. The modelling therefore shows that the success of the birds is independent of site protection.

Discussion

In Estonia, the potential loss of wetlands, and hence land use changes, could override conservation measures, as most potential crane breeding sites are outside protected areas; although since 2004 the situation has been relative stable (Raet et al. 2010). However, the continued upward trend of the crane population suggests that, if there is no sudden change in land use, the existing ecological network of interrelated wetlands and fields will maintain the current status of the species, or even enable a population increase. The main problem would be the expansion of crops, but at present the European Commission (2010) states that the present condition of the grain market indicates that there is only likely to be reallocation of crops inside established cereal areas rather than expansion. Under these conditions, it is unlikely that drainage for agriculture will take place. The lack of change in the ecological network in Estonia has been an important factor influencing the continued success of the cranes; although this cannot be attributed to a positive environmental conservation

Table 5 Percentage of relevant CORINE land cover classes in the potential crane breeding sites of the Eurasian crane (*Grus grus*) in Estonia in sites with conservation (cons) measures, green infrastructure (GI), without any conservation designation (no-cons) and without green infrastructure (no-GI)

CODE_2006	Crane breeding areas Landcover	%	Cons	GI	No-cons	No-GI
3242	Coniferous forest (transition bog)	14.4	24.2	18.6	8.1	5.0
4121	Bog	12.3	26.1	16.4	3.3	3.2
4112	Fen, marshes	4.9	10.6	6.8	0.1	0.5
3241	Coniferous forest (transitional mineral soil)	6.6	4.6	7.7	7.9	4.1
312	Coniferous forest	12.5	11.0	14.5	13.7	8.2
313	Mixed forest	11.3	4.7	11.4	15.6	11.1
311	Broad-leaved forest	6.2	2.6	5.9	8.5	6.9
243	Land principally occupied by agriculture, with significant areas of natural vegetation	4.3	1.5	2.2	*6.2*	***9.1***
231	Pastures	7.7	0.5	1.9	12.4	20.7
211	Non-irrigated arable land	9.6	0.9	5.5	15.2	18.8
	Other	10.2	13.2	9.2	9.2	12.4

policy, but rather to a lack of resources for the continued agricultural intensification that has taken place elsewhere in Western Europe. The analysis in the present paper shows that protected site designation has played a relatively minor role. Therefore, if financial returns in the agriculture sector improve, it is possible that the current abundance of suitable sites may be threatened. However, the abandoned fields that were formally in agricultural use, although generally on soils of low fertility, are likely to be the first to be converted back into crops (Kukk et al. 2010).

Climate change may also lead to changes in agricultural crops, e.g. maize is likely to become more widespread and other crops could also change in their distribution patterns. As a result, longer staging periods are possible in the northern stopover sites of cranes, with more food resources may becoming available or even during wintering. Longer staging periods with higher numbers of cranes during migration will increase damage to cereal fields, as is the case currently in Western, South-Western and Central Europe. According to recent studies, (Alonso et al. 1994, 2008; Prange 2010; Leito et al. 2011; Alonso et al. 2014; Munillo 2014; Prange 2014), there is evidence that the Eurasian crane is a species with high flexibility for changing flyways and migration patterns. However, immature birds are likely to contribute more to a potential northward shift in the wintering range of cranes. Furthermore, the current population in the UK is residential within a non-freezing winter region, which may be indicative of future patterns and is consistent with the potential change shown in Fig. 6 (Nowald et al. 2012, 2013; Great Crane Project 2014).

Because of this flexibility, the cranes are likely to be able to modify their current flyways and overwintering sites. The cranes are currently staying longer in the northern stopover sites in mild autumns and winters, probably due to climate change.

Other birds, e.g. the Little Egret (*Egretta garzetta*) have also expanded their distribution rapidly (Holt et al. 2012). The bird was hunted to extinction in the seventeenth century in Britain. Since then, the first recorded pair bred in 1996, and there are currently approximately 4,500 birds throughout Britain. It has been suggested that this increase is attributable to climate change (Maclean et al. 2008), but such a rapid expansion is more likely to be due to a combination of a number of other factors, such as lack of competitors in their favoured habitats. There is also the analogous history of the Black Stork in Spain (*Ciconia nigra*) as described by Alonso (2006) and Cano et al. (2014); the species has expanded because of increases in suitable foraging habitats, such as rice fields, reservoirs and ponds. In addition, more birds are breeding outside the south, which means that more birds require wintering areas. Climate change is also often considered to have a role in the decline in the migration of the White Stork (*Ciconia ciconia*) (University of East Anglia 2013), although other factors such as the availability of rubbish tips are also considered to be important (Tortosa et al. 2002).

The initial examination of the climate change scenario suggested that Eurasian cranes are not under threat and could be favoured in possible new climate regimes; indeed the map of potential expansion shows that a large new area could become available for stopovers. However, in the south of Spain, the likely shift to hotter and drier classes could pose a threat, although cranes already overwinter in similar conditions in North Africa. The climate baseline was 1990, so further work is required not only to bring the baseline up to date but also to examine the potential impact of new scenarios.

Conclusion

The increase in crane numbers in Estonia is largely independent of site protection, but requires a policy initiative to protect the existing network of wetlands. Relevant habitats have remained stable in Estonia, and are not expected to change elsewhere under current economic conditions. In the north, potential shifts in climate could favour cranes, but in the south of Spain the drying out of wetlands and desertification could pose a threat to the current population.

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

Running Title: From northern Europe to Ethiopia: long-distance migration of Common cranes

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The majority of Common cranes (*Grus grus*) breeding in northern Europe are short- to middle-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 3950 to 5360 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.

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* L.) 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 1000 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 satges, 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. The 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 during 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 3822 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 1505 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 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 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 3400–5870 km for the Finnish crane sub-population and from 2040–5350 km for the Estonian sub-population. The total distance flown varied from 3520–6527 km and 2177–5862 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 5860 km and the total distance flown up to 6876 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 2800 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 2400 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 barriers is approximately 3850 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 2600 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 (2420 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 970–1240 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 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 2420 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 3030–5060 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 (2420–5110 km from Belarus/Hungary/Ukraine/Israel to Ethiopia) took 6–15 days, with the cranes making only overnight stops. Crossing the 2420–2700 km-wide desert area in northeast 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 1727 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. 4C). In addition, there were similar relationships between the mean flight distance and migration stages (Fig. 4D). 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 652–1130 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 (Fig. 1). The arrival of the Finnish cranes to the wintering grounds in Israel or Ethiopia (a difference in distance of 2420 km) and the Estonian cranes in Turkey or Ethiopia (a difference in distance of 2830 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 1010 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 (Pekarski 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 (2420 km between Israel and Ethiopia), which supports the idea of their strongly selecting for favourable weather conditions. 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 6178 km on the East European migration route was only four days longer than the longest migration (28 days covering 1800 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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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. Shaded rows are the totals for each country. 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. 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	1909	477.3	43.4
FIN	Einari-10	45	3	42	3	1763	587.7	39.2
FIN	Goljatti-10	47	9	38	3	4487	498.6	95.5
FIN	Sipriina-10	93	7	86	3	2479	354.1	26.7
FIN	Outo-11*	66	13	53	3	6178	475.2	93.6
FIN	Ruvas-11*	58	17	41	3	6527	383.9	112.5
FIN	Mansikka-12*	83	10	73	3	3520	352.0	42.4
EST	Tom-09	63	12	51	4	4430	369.2	70.3
EST	Rasina-10*	65	9	56	3	2177	241.9	33.5
EST	Ahja2-11*	80	11	69	4	2747	249.7	34.3
EST	Lootvina-11	73	9	64	2	4027	447.4	55.2
EST	Ahja3-12	82	4	78	3	1388	347.0	16.9
EST	Hauka1-12	80	12	68	4	3672	306.0	45.9
EST	Kadaja-12	88	5	83	3	2278	455.6	25.9
EST	Hauka2-13	57	6	51	4	2337	389.5	41.0
EST	Ahja4-13*	83	19	64	5	5862	308.5	70.6
EST	Ahja5-16*	127	21	106	4	6674	317.8	52.6
EST	Mustakurmu-17	79	10	69	2	3620	362.0	45.8

Figure captions

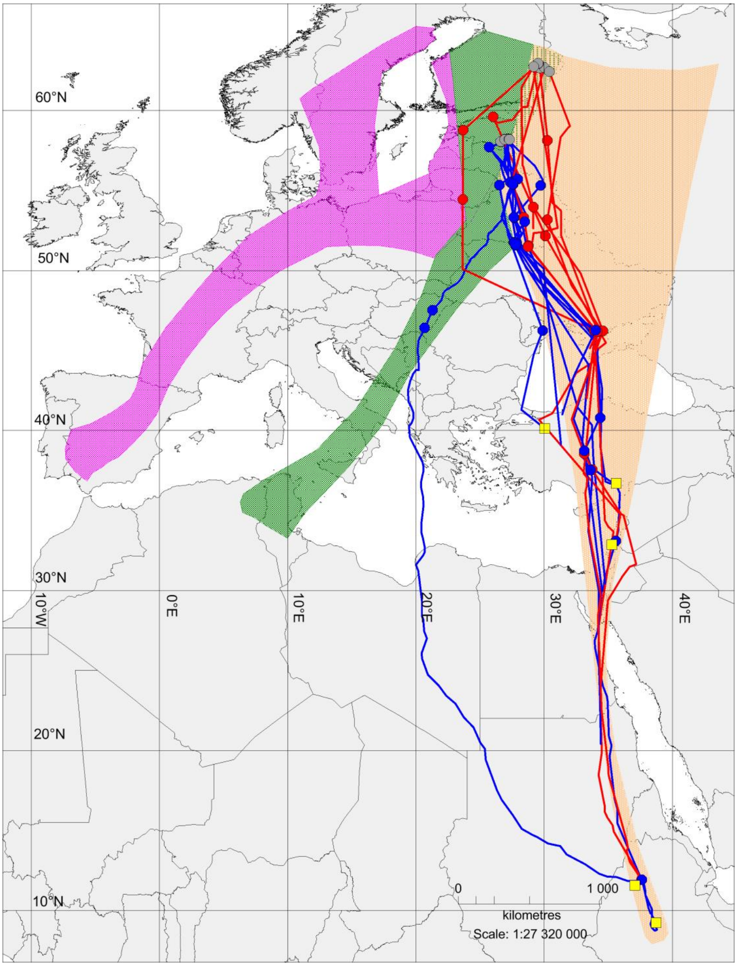
Fig. 1. Migratory routes of the Common cranes studied along the East European flyway. Grey circles denote the tagging sites in Finland and Estonia, and yellow squares indicate the overwintering areas. Red and blue lines and circles indicate the flight tracks and staging sites of the Finnish and Estonian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

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.

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

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

681 Ojaste Fig. 1



682

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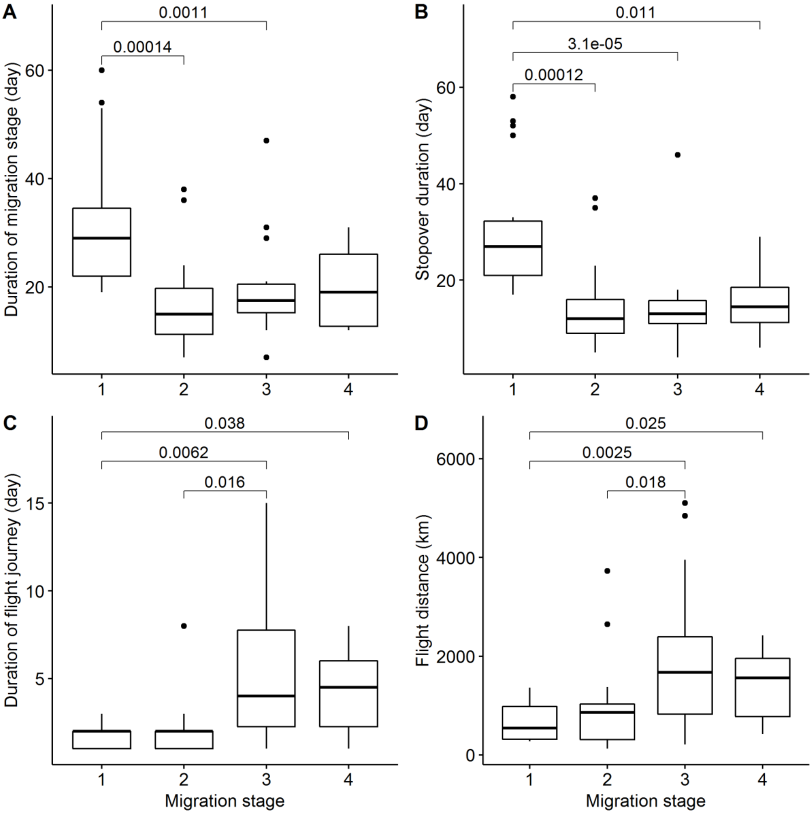
684 Ojaste Fig. 2



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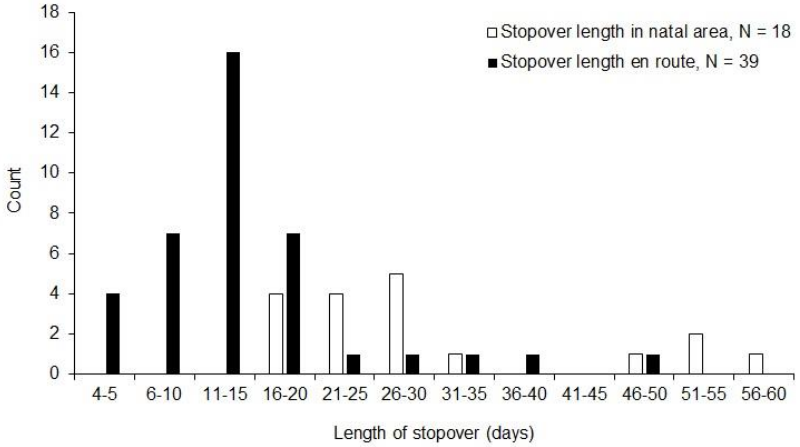
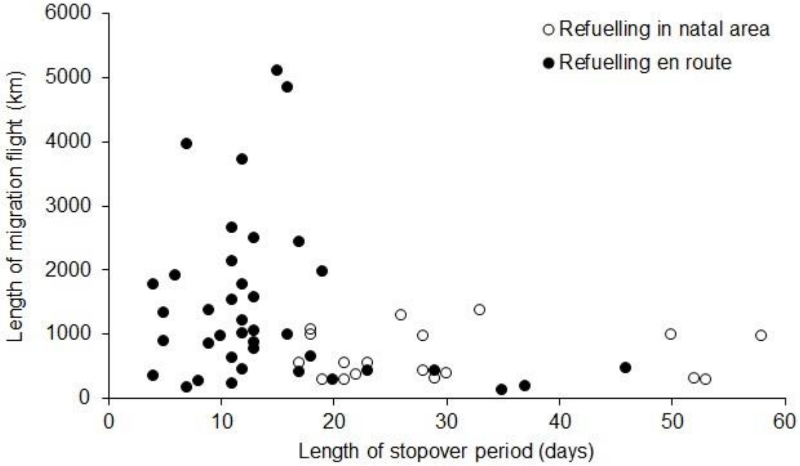
686

Ojaste Fig. 3


☐ Stopover length in natal area, N = 18
■ Stopover length en route, N = 39
Count
18
16
14
12
10
8
6
4
2
0
4-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
41-45
46-50
51-55
56-60
Length of stopover (days)

690 Ojaste Fig. 4



691

CURRICULUM VITAE

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Last name: Ojaste
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Address: Mõisatalli 26, Vahi alevik, Tartu vald,
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Email: ivar.ojaste@emu.ee
Academic degree: Research Master's Degree (MSc, 2007) "Home range use by families of Eurasian Crane (*Grus grus*)"

Education:

2006–2019	Estonian University of Life Sciences, *PhD* studies in Environmental Science and Applied Biology
2004–2006	Estonian University of Life Sciences, MSc studies in Environmental Protection
1999–2004	Estonian University of Life Sciences, BSc studies in Exploitation and Protection of Natural Resources
1991–1994	Luua Forestry School, studies in Forest Specialist
1981–1989	Taebla Gymnasium

Foreign languages: English, Russian

Professional employment:

2018– …	Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Chair of Environmental Protection and Landscape Management, Junior Researcher
2012– …	Estonian Ornithological Society, Technical staff
2012–2019	Estonian Naturalists Society, Administrator
2009–2012	Environmental Board, conservation biologist
2006–2009	State Nature Conservation Centre, Chief Species Protection Specialist
2002–2006	Administration of Silma Nature Reserve, vice-director

Research interest: Biosciences and Environment; 1.4. Ecology, Biosystematics and -physiology; CERCS SPECIALITY: B280 Animal ecology

Professional training:

2015 International PhD-Course “Ecology of animal migration”, Centre for Animal Movement Research, Lund University

Participation in research projects:

2015–2018 8-2/T15096PKMH “Sookure elupaiga ja rändeteede kasutamise strateegia (1.08.2015−30.06.2018)”, Kalev Sepp, Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences.

2017 PM170161PKMH “Sookure rändevõrgustiku uurimine satelliitjälgimise abil lindude rände uudse teooria väljatöötamiseks (1.04.2017−31.12.2017)”, Aivar Leito, Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences.

2008–2013 SF0170160s08 “Animal ecology, systematics and conservation (1.01.2008−31.12.2013)”, Olavi Kurina, Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences.

2004–2007 ETF6005 (ETF6005) “Relationship between numbers and distribution of waders and soil biota in coastal and floodplain meadows (1.01.2004−31.12.2007)”, Aivar Leito, Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences.

Additional information:

Has reviewed manuscripts for the following journal: Ornis Fennica.

Supervised dissertations:

2013 Teet Paju, Master’s Degree, (sup.) Tiit Randveer; Ivar Ojaste; Meelis Leivits, Raiete mõju metsise (*Tetrao urogallus*) populatsioonile, Estonian

	University of Life Sciences, Institute of Forestry and Rural Engineering.
2011	Piret Mägi, Master's Degree, (sup) Ivar Ojaste; Tiit Lukki, Metsamajanduse mõju metsise (Tetrao urogallus L.) mängude asustatusele (Impact of modern forestry on lek population of Capercaillie (Tetrao urogallus L.)), Tallinn University, Institute of Mathematics and Natural Sciences, Department of Natural Scinces.
2009	Indrek Põder, Research Master's Degree, (sup) Ivar Ojaste; Aivar Leito, Sookure Grus grus pesitsusaegse kodupiirkonna struktuur ja elupaigaeelistused Ida-Eestis (The breeding home range structure and habitat preferences of the Eurasian Crane Grus grus in East-Estonia), Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Department of Environment Protection.

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Teaduskraad: Magistrikraad (MSc, teaduskraad, 2007) keskkonnakaitse erialal. Lõputöö teema: "Sookure *Grus grus* kodupiirkonna kasutus", (juh) Aivar Leito, Eesti Maaülikool

Haridustee:

2006–2009	Eesti Maaülikool, Põllumajandus- ja Keskkonnainstituut, keskkonnateaduse ja rakendusbioloogia doktoriõpe
2004–2006	Eesti Maaülikool, Põllumajandus- ja Keskkonnainstituut, keskkonnakaitse magistriõpe
1999–2004	Eesti Põllumajandusülikool, bakalaureuseõpe loodusvarade kasutamise ja kaitse erialal
1991–1994	Luua Kõrgem Metsakool, metsamajanduse tehnik
1981–1989	Taebla Keskkool, keskharidus

Võõrkeeled: Inglise, vene

Teenistuskäik:

2018–…	Eesti Maaülikool, Põllumajandus- ja Keskkonnainstituut, Keskkonnakaitse ja maastikukorralduse õppetooli nooremteadur
2012–…	Eesti Ornitoloogiaühing, liigikaitse ekspert
2012–2019	Eesti Looduseuurijate Selts, teadussekretär
2009–2012	Keskkonnaamet, looduskaitse bioloog
2006–2009	Riiklik Looduskaitsekeskus, liigikaitse peaspetsialist
2002–2006	Silma Looduskaitseala Administratsioon, direktori asetäitja

Teadustöö põhisuunad:

Bio- ja keskkonnateadused; 1.4. Ökoloogia, biosüstemaatika ja -füsioloogia; CERCS ERIALA: B280 Loomaökoloogia; PÕHISUUND: Lindude pesitsus- ja rändeökoloogia

Enesetäiendus ja koolitused:

2015	Rahvusvaheline doktorantide kursus “Loomade rände ökoloogia”, Lundi Ülikool

Osalemine uurimisprojektides:

2015–2018	8-2/T15096PKMH“Sookureelupaigajarändeteede kasutamise strateegia (1.08.2015−30.06.2018)”, Kalev Sepp, Eesti Maaülikool, Eesti Maaülikool, põllumajandus- ja keskkonnainstituut.
2017	PM170161PKMH “Sookure rändevõrgustiku uurimine satelliitjälgimise abil lindude rände uudse teooria väljatöötamiseks (1.04.2017−31.12.2017)”, Aivar Leito, Eesti Maaülikool, põllumajandus- ja keskkonnainstituut.
2008–2013	SF0170160s08 “Loomade ökoloogia, süstemaatika ja kaitse (1.01.2008−31.12.2013)”, Olavi Kurina, Eesti Maaülikool, Põllumajandus- ja keskkonnainstituut.
2004–2007	ETF6005 (ETF6005) “Ranna- ja luhaniitude kurvitsaliste arvukuse ja leviku seos mullaelustiku komponentidega (1.01.2004−31.12.2007)”, Aivar Leito, Eesti Maaülikool, Põllumajandus- ja keskkonnainstituut.

Lisainfo:

Retsenseerinud käsikirju järgmistele ajakirjadele: Ornis Fennica.

Juhendatud väitekirjad:

2013	Teet Paju, magistrikraad, (juh) Tiit Randveer; Ivar Ojaste; Meelis Leivits, Raiete mõju metsise (*Tetrao urogallus*) populatsioonile, Eesti Maaülikool, Metsandus- ja maaehitusinstituut.
2011	Piret Mägi, magistrikraad, (juh) Ivar Ojaste; Tiit Lukki, Metsamajanduse mõju metsise (Tetrao urogallus L.) mängude asustatusele, Tallinna

	Ülikool, Matemaatika ja Loodusteaduste Instituut, Loodusteaduste osakond.
2009	Indrek Põder, magistrikraad (teaduskraad), (juh) Ivar Ojaste; Aivar Leito, Sookure Grus grus pesitsusaegse kodupiirkonna struktuur ja elupaigaeelistused Ida-Eestis, Eesti Maaülikool, Põllumajandus- ja keskkonnainstituut, keskkonnakaitse osakond.

LIST OF PUBLICATIONS

1.1. Scholarly articles indexed by Web of Science Science Citation Index Expanded, Social Sciences Citation Index, Arts & Humanities Citation Index and/or indexed by Scopus (excluding chapters in books)

Haase, M.; Höltje, H.; Blahy, B.; Bridge, D.; Henne, E.; Johansson, U.S.; Kaldma, K.; Khudyakova, E.A.; King, A.; Leito, A.; Mewes, W.; Mudrik, E.; **Ojaste, I.**; Politov, D.V.; Popken, R.; Rinne, J.; Stanbury, A.; Tofft, J.; Väli, Ü.; Schmitz Ornés, A. (2019). Shallow genetic population structure in an expanding migratory bird with high breeding site fidelity, the Eurasian Crane, *Grus g. grus*. Journal of Ornithology, xxx−xxx.10.1007/s10336-019-01688-1 [Accepted].

Ojaste, I.; Leito, A.; Suorsa, P.; Hedenström, A.; Sepp, K.; Leivits, M.; Sellis, U. & Väli, Ü. (2019). From northern Europe to Ethiopia: long-distance migration pattern of Common cranes (*Grus grus*). Ornis Fennica, xxx−xxx [Accepted].

Lõhmus, A., Leivits, M., Pēterhofs, E., Zizas, R., Hofmanis, H., **Ojaste, I.**, Kurlavičius, P. (2017). The Capercaillie (*Tetrao urogallus*) – An iconic focal species for knowledge-based integrative management and conservation of Baltic forests. Biodiversity and Conservation, 26 (1), 1−21.10.1007/s10531-016-1223-6.

Leito, A.; Bunce, R. G. H.; Külvik, M.; **Ojaste, I.**; Raet, J.; Villoslada, M.; Leivits, M.; Kull, A.; Kuusemets, V.; Kull, T.; Metzger, M. J.; Sepp, K. (2015). The potential impacts of changes in ecological networks, land use and climate on the Eurasian crane population in Estonia. Landscape Ecology, 30 (5), 887−904.10.1007/s10980-015-0161-0.

Leito, Aivar; Truu, Jaak; Õunsaar, Maris; Sepp, Kalev; Kaasik, Are; **Ojaste, Ivar**; Mägi, Eve (2008). The impact of agriculture on autumn staging Eurasian Cranes (*Grus grus*) in Estonia. Agricultural and Food Science, 17 (1), 53−62.

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1.3. Scholarly articles in Estonian and other peer-reviewed research journals with a local editorial board

Tilgar, V.; **Ojaste, I.**; Saag, P. (2015). Metsise (*Tetrao urogallus*) stressitase seoses sõjaliste harjutustega. Hirundo: Eesti Ornitoloogiaühingu ajakiri, 1, 1−9.

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Leito, Aivar; **Ojaste, Ivar**; Sellis, Urmas. (2011). Eesti sookurgede rändeteed. Hirundo : Eesti Ornitoloogiaühingu ajakiri, 2, 41−53.

Ojaste, I.; Vikat, K.; Leivits, A.; Valker, T. (2003). Kurvitsaliste sügisränne Põgari rannaniidul. Linnurada, 32−48.

Lõhmus, A.; Kalamees, A.; Kuus, A.; Kuresoo, A.; Leito, A.; Leivits, A.; Luigujõe, L.; **Ojaste, I.**; Volke, V. (2001). Kaitsekorralduslikult olulised linnuliigid Eesti kaitsealadel ja tähtsatel linnualadel. Hirundo: Eesti Ornitoloogiaühingu ajakiri, 37−167.

Leivits, A.; **Ojaste, I.**; Tammekänd, I.; Lelov, E.; Randla, T.; Vilbaste, E.; Leibak, E. (2001). Ülevaade Leidissoo haudelinnustikust aastal 2000. Linnurada, 3−18.

Lõhmus, A.; Kalamees, A.; Kuus, A.; Kuresoo, A.; Leito, A.; Leivits, A.; Luigujõe, L.; **Ojaste, I.**; Volke, V. (2001). Kaitsekorralduslikult olulised linnuliigid Eesti kaitsealadel ja tähtsatel linnualadel. Hirundo: Eesti Ornitoloogiaühingu ajakiri, 4, 37−167.

2.2. Monographs (registered in ETIS before 01.07.2014)

Leito, A.; Keskpaik, J.; **Ojaste, I.**; Truu, J. (2006). The Eurasian Crane in Estonia. Tartu: Eesti Loodusfoto.

Leito, A.; Keskpaik, J.; **Ojaste, I.**; Truu, J. (2005). Sookurg. Tartu: Eesti Loodusfoto.

3.2. Articles/chapters in books published by the publishers not listed in Annex

Leito, A.; **Ojaste, I.**; Truu, J.; Keskpaik, J.; Palo, A. (2004). Sookure pesitsemine Eestis. Eesti Looduseuurijate Seltsi aastaraamat (157−189). Tartu: Eesti Looduseuurijate Selts.

3.4. Articles/presentations published in conference proceedings not listed in Section 3.1

Leito, Aivar; **Ojaste, Ivar**; Põder, Indrek (2013). Dependence of Cranes on Arable Lands and the Crop Damage Problem in Estonia. Proceedings of the VIIth European Crane Conference: breeding, resting, migration and biology: 7th European Crane Conference; Stralsund, Germany; Oct. 14-17, 2010. Editors Abbr Nowald, Günter; Weber, Alexander; Fanke, Jane; Weinhardt, Elke; Donner, Norman. Crane Conservation Germany, 155−158.

Leito, Aivar; **Ojaste, Ivar**; Põder, Indrek; Sellis, Urmas (2013). The breeding Homerange and First Autumn Migration of two Offspring from a Cranebrood in 2009. Proceedings of the VIIth European Crane Conference: breeding, resting, migration and biology: 7th European Crane Conference; Stralsund, Germany; Oct. 14-17, 2010. Editors Abbr Nowald, Günter; Weber, Alexander; Fanke, Jane; Weinhardt, Elke; Donner, Norman. Groβ Mohrdorf, Germany: Crane Conservation Germany, 151−154.

Leito, Aivar; **Ojaste, Ivar**; Põder, Indrek (2013). Monitoring of the Eurasian Crane in Estonia: Methods and Last Results. Proceedings of the VIIth European Crane Conference: breeding, resting, migration and biology: 7th European Crane Conference; Stralsund, Germany; Oct. 14-17, 2010. Editors Abbr Nowald, Günter; Weber, Alexander; Fanke, Jane; Weinhardt, Elke; Donner, Norman. Groβ Mohrdorf, Germany: Crane Conservation Germany, 141−145.

Palm, V.; **Ojaste, I.**; Leito, A.; Elts, J. (2013). The Dependence of Spring Arrival and Breeding Success of the Eurasian Crane in Estonia on Climate Variables. PROCEEDINGS of the VIIth European Crane Conference - Breeding, resting, migration and biology. Editors Abbr Nowald, G., Weber, A., Fanke J., Weinhardt E., Donner, N. 146−150.

5.2. Conference abstracts that do not belong to section 5.1

Ojaste, Ivar; Leito, Aivar; Suorsa, Petri; Leivits, Meelis; Palm, Vello; Sepp, Mait; Meitern, Helve; Sellis, Urmas (2014). Migration tactics in the Eurasian crane (*Grus grus*) families in reaching Ethiopian over-wintering sites as revealed by satellite telemetry. VIII European Crane Conference Scientific Abstracts of Oral and poster contributions: VIII European Crane Conference; Gallocanta, Spain; 10-14.11.2014. 36−37.

Leivits, Meelis; Tammekänd, Indrek; Tammekänd, Jaak; **Ojaste, Ivar**; Leivits, Agu (2011). Effect of forest drainage on the size of Capercaillie (*Tetrao urogallus*) leks in Estonia: A key attribute for long-term habitat loss. Abstracts: 8th Conference of the European Ornithologists' Union 27–30 August 2011, Riga. _Editors Abbr Fusani, L; Coppack, T.; Strazds, M. Riga: Latvian Ornithological Society, 226−226.

Leivits, Agu; Leito, Aivar; **Ojaste, Ivar**; Leivits, Meelis; Merivee, Murel (2010). Site-based monitoring and assessment breeding bird communities of the protected mires in Estonia: the effect of recreational disturbance on habitat use of birds. Bird Numbers 2010. Monitoring, indicators and targets. Book of abstracts.: 18th Conference of the European Bird Census Council 22-26 March, Caceres (Extremadura, Spain). Editors Abbr Bermejo, A. Madrid: SEO/BirdLife, 59−60.

Palm, Vello; **Ojaste, Ivar**; Leito, Aivar; Elts, Jaanus (2010). The dependence of migration phenology and breeding success of the Eurasian Crane in Estonia on climate variables. 7th European Crane Conference; Stralsund, Sweden; 14.-17.10.2010. Editors Abbr Nowald, Günter; Donner, Normann. Stralsund, 46−46.

Leito, Aivar; **Ojaste, Ivar**; Keskpaik, Jüri (2003). Recent estimation of population size, color-ringing, radio- and satellite-marking of the Common Crane in Estonia. Vth European Crane Conference: Vth European Crane Conference, 10-13 April 2003, Sweden. 34−35.

Leito, Aivar; Nowald, Günter; Alonso, Javier; **Ojaste, Ivar** (2003). Marking of the Common Crane in Estonia. Vth European Crane Conference. Preface, Programme, Abstracts: Vth European Crane Conference, 10-13 April 2003, Sweden, 34.

6.3. Popular science articles

Valker, T.; **Ojaste, I.** (2003). Osmussaare haudelinnustik 2003. a. Linnurada, 3−17.

Leivits, A.; Dragon, T.; Gerloff, A.; **Ojaste, I.**; Randla, T.; Soppe, A.; Tammekänd, I.; Valker, T.; Vilbaste, E. (2002). Ülevaade Läänemaa Suursoo maastikukaitseala haudelinnustikust aastal 2001. Linnurada, 1, 3−25.

Ojaste, I.; Luigujõe, L.; Leito, A.; Leito, T.; Kuresoo, A.; Pehlak, H. (1999). Kesktalvine veelinnuloendus Lääne-Eestis jaanuaris 1999. Linnurada, 1, 44−48.

Ojaste, I. (1998). Hullo lahe laidude haudelinnustik. Linnurada, 2, 8−20

VIIS VIIMAST KAITSMIST

KAIE METSAOTS
HOLISTIC DEVELOPMENT OF THE OIL SHALE REGION AS AN INDUSTRIAL HERITAGE, RECREATIONAL, SPORTS AND TOURISM DISTRICT
PÕLEVKIVIREGIOONI TERVIKLIK ARENDAMINE TÖÖSTUSPÄRANDI-, PUHKE-, SPORDI- JA TURISMIPIIRKONNANA
Professor **Kalev Sepp**
27. juuni 2019

GUNNAR MOROZOV
CARBON AND NITROGEN FLUXES IN BIRCH AND GREY ALDER STANDS GROWING ON DIFFERENT SITES
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Professor **Veiko Uri**
21. august 2019

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EFFECTS OF SYNTHETIC AND BIOLOGICAL PESTICIDE EXPOSURE ON HONEY BEES AND BUMBLE BEES
SÜNTEETILISTE JA BIOLOOGILISTE PESTITSIIDIDE MÕJUD MEEMESILASTELE JA KIMALASTELE
Professor **Marika Mänd, Reet Karise**
26. september 2019

PEETER PADRIK
FACTORS INFLUENCING THE QUALITY OF SEMEN FROM ESTONIAN HOLSTEIN AI BULLS, AND RELATIONSHIPS BETWEEN SEMEN QUALITY PARAMETERS AND IN VIVO FERTILITY
EESTI HOLSTEINI TÕUGU SUGUPULLIDE SPERMA KVALITEET, SEDA MÕJUTAVAD TEGURID NING SEOS IN VIVO VILJAKUSEGA
Professor **Ülle Jaakmaa,** Professor **Olev Saveli**
01. november 2019

TARMO NIINE
IMPACT OF GASTROINTESTINAL PROTOZOAN INFECTIONS ON THE ACUTE PHASE RESPONSE IN NEONATAL RUMINANTS
SEEDEKULGLAT TÕVESTAVATE ALGLOOMADE MÕJU MÄLETSEJALISTE ÄGEDA JÄRGU VASTUSELE NEONATAALPERIOODIL
Professor **Toomas Orro** ja doktor **Brian Lassen**
21. november 2019

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