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Original Articles

Factors affecting detection probability: Insights from banding data in a long-term continent-wide monitoring program

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ABSTRACT

Bird banding studies are essential for providing critical data on species population demographics and movements, as important components for understanding their ecology and conservation and management applications. However, analysing sightings of banded individuals is often complicated by untested assumptions of the species' behaviour or visibility of the bands, leading to biased populations estimates, especially in large-scale long-term studies. In this study we investigate factors influencing detection rates of colour-banded Eurasian cranes (*Grus grus*), from a monitoring program spanning 35 years, involving 5049 marked individuals using four different types of bands (ELSA, 'Finnish', 'Spanish' and alphanumeric) with 172,725 resightings along migratory flyways. Data were compiled from European national banding schemes and the internet-based Crane Observation Ring Archive (iCORA). We used capture-mark-recapture mixture models to study the variation in detection probability from differences in the type of bands used, time since marking, year of observation, natal origin and an additional parameter to account for unexplained resighting heterogeneity. All band types showed high detection probabilities in their first years (as high as 80 %) but declined significantly over time, with detection

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rates halving within 20 years. Although starting with the lowest detection probability, alphanumeric bands remained relatively stable over time. There was a general increase in detection probability over the 35-year study period, which can be attributed to enhanced observation efforts, addition of pictures to reports and improved coordination of reports. Detection also varied by natal country, each population's migratory routes, which were related to differences in monitoring efforts and habitat conditions along the flyways. Our findings emphasize the importance of band type, observation effort, migration pattern and environmental factors in determining detection probabilities, but also the importance to account for unexplained heterogeneity with a mixture model. This study is crucial for the study of demographic parameters within the European crane population and future evidence-based population management.

1. Introduction

Methods that enable the repeated identification of individuals within a population are fundamental tools for ecological research. The ability to track individuals over time is critical not only for the study of life history traits, population size estimation, and the assessment of demographic rates and migration patterns (Badger et al., 2020; Beissinger and McCullough, 2002; Brusa et al., 2020; Souc et al., 2023; Vinks et al., 2021), but also for assessing specific management and conservation questions related to these aspects of species' ecology (Gervasi et al., 2017; Iwai, 2022; León-Ortega et al., 2016). Consequently, the use of physical tags or marks is a common approach in animal studies. For example, uniquely coded rings or coloured plastic bands are frequently applied to the legs of birds (Baillie and Schaub, 2009; Calvo and Furness, 1992). Given their extensive use in population studies, it is important to evaluate the effectiveness of markings such as leg bands, to reliably identify individuals over time, particularly in long-lived species (Breton et al., 2006a; Szymanski et al., 2020; Touzalin et al., 2023).

Capture-recapture statistical methods are widely used to analyse repeated observations of marked individuals to estimate demographic parameters (Sandercock, 2019, 2006). However, accurately estimating key parameters such as survival, immigration and emigration depends on properly accounting for detection probability (Abadi et al., 2013; Cubaynes et al., 2010), which refers to the likelihood of observing an individual when it is present in the system under study. This is critical, as tracking changes in population size and structure over time and identifying factors regulating demographic rates require models that can effectively determine whether unobserved individuals are dead or alive. Estimating detection probability is further complicated by factors influencing the likelihood of resighting different individuals, resulting in heterogeneity in detection probabilities (Oliver et al., 2011; Prévot-Julliard et al., 1998). Failure to account for such variation can lead to biased estimates of survival, reproduction, or abundance (Abadi et al., 2013; Cubaynes et al., 2010).

The resighting of marked animals is influenced not only by their visibility but also by monitoring effort and the ability of observers to correctly identify marked individuals when encountered (Johansson et al., 2020). Consequently, variation in detection can arise due to differences in animal behaviour, habitat type, location, observer effort, experience, and band type (Pradel and Sanz-Aguilar, 2012). A key assumption of standard capture-recapture methods is that the bands or markings used for individual identification are neither lost, overlooked nor incorrectly recorded; violations of this assumption can significantly affect population parameter estimates (Johansson et al., 2020; Szymanski et al., 2020). However, leg-bands and other markings may not maintain the same level of reliability over time, due to physical loss (Breton et al., 2006b; Szymanski et al., 2020; Touzalin et al., 2023), material degradation, or readability issues (Breton et al., 2006a; Thorup, 2000). As a result, declining detectability of individuals over time due to reduced band reliability may introduce significant bias, thereby negatively impacting estimates of both survival and detection rates (Breton et al., 2006b; Touzalin et al., 2023).

This challenge is further compounded in long-term studies spanning extensive geographical areas, which may involve the use of multiple band types, codes, colours, or materials that are favoured in different regions or at different periods. It is therefore critical to consider these variations in band type when analysing detection probabilities, as they can introduce non-random variation in resighting rates (Juillet et al., 2011; Smout et al., 2011). Such regional or temporal changes in banding methods have the potential to generate misleading geographic or trend estimates of demographic parameters. This issue has been highlighted in double-marking studies (Breton et al., 2005; Juillet et al., 2011; Roche et al., 2014), which demonstrate how marker loss over time affects detection rates, and shows that adjusting for this temporal change yields more accurate demographic estimates (Juillet et al., 2011; Roche et al., 2014).

The Eurasian crane (*Grus grus,* hereafter referred to as 'crane') is a long-lived bird that migrates between breeding areas in Northern Europe and Asia and wintering areas in southern Europe and Asia and northern Africa (del Hoyo et al., 1996; Prange and Ilyashenko, 2019). The species is of particular interest to ecologists and conservation biologists because of its cultural significance, population recovery in many European countries over the last decades and negative impact on agriculture (Alonso et al., 2016; Austin et al., 2018; Salvi, 2015). Over the past 30–40 years, the European population went through a rapid recovery following protection efforts (Alonso et al., 2016; Ilyashenko, 2016) and is recently estimated at 590,000 individuals (Prange and Ilyashenko, 2019). In conjunction with this, a coordinated banding scheme across Europe was initiated in 1985 to primarily investigate its migration routes and several aspects of its ecology. Since the beginning of the crane banding programme, different types of bands have been used at different times and with different regional emphases (Alonso and Alonso, 1999; Alonso et al., 2018; Nowald, 2010; Prange and Ilyashenko, 2019). Thus, while the combination of banding and extensive observation efforts across 14 European countries provides a robust foundation for investigating various aspects of the crane ecology, it is crucial to understand and account for how heterogeneity in band types influences variation in individual detection. Only by addressing this can accurate estimates of population trends, life-history traits, and migration patterns be reliably determined.

In this study, we employ capture-recapture modelling using capture and resighting data from 1985 to 2021 to investigate detection probabilities associated with different band types used in marking cranes. Specifically, we examine how various band types influence detection rates, assess the impact of band readability and degradation on detection probabilities and analyse the effects of temporal variation in observation effort. Understanding and accounting for variation in detection rates is a critical first step towards obtaining accurate survival estimates and advancing knowledge of the demographic and life-history parameters of this species. The overarching objectives of this study are to explore variation in detection probability within the context of long-term, large-scale capture-recapture studies and to provide critical insights for both current and future research on cranes, as well as to offer guidance for banding programs in other species. A follow-up study specifically focusing on the results on survival probabilities is currently in preparation to study crane demography (Gicquel et al., in prep).

2. Methods

2.1. Study area and species

2.1.1. General information

The Eurasian crane is a large, long-distance migratory species with a breeding range across northern and eastern Europe (Prange, 2005; Prange and Ilyashenko, 2019). During the breeding season, these cranes primarily inhabit boreal wetlands, peat bogs, and open forested landscapes in countries such as Norway, Sweden, Finland, Estonia, Latvia, Lithuania, Germany, the Czech Republic, and Poland, where they establish territorial breeding sites. Migration occurs along three main flyways: the Western European, Central (or Baltic-Hungarian), and Eastern routes (Leito et al., 2015). Cranes from northern and central Europe – including Scandinavia, Germany, and Poland – predominantly follow the Western European flyway, wintering in France and the Iberian Peninsula, with some reaching North Africa (Alonso et al., 2016; Hansson et al., 2024; Salvi, 2016). The Central flyway is primarily used by cranes from the Baltic countries and Finland, with Eastern Hungary as a crucial stopover and wintering site; some birds may continue south to Italy or North Africa (Mingozzi et al., 2013; Végvári, 2015). The Eastern flyway encompasses populations from Finland, Estonia, Latvia, Lithuania, Belarus, Russia, and Ukraine, which migrate to wintering grounds in Greece, Turkey, Israel, and Ethiopia (Leito et al., 2011; Ojaste et al., 2020). Cranes demonstrate high site fidelity, often returning to the same breeding, stopover, and wintering areas annually, influenced by habitat stability and resource availability.

2.1.2. Crane capture and banding

In this study, cranes were banded in 11 European countries, reflecting their wide distribution range (Table A.1, Appendices). The countries where juvenile cranes hatched and were banded include Germany, Sweden, Finland, Norway, Latvia, Estonia, Lithuania, and the Czech Republic. In addition, data from cranes hatched and ringed in the framework of a crane reintroduction project in the United Kingdom were used. For individuals that have been banded outside of the breeding range within their first year, we managed to determine their natal country based on subsequent spring migration (if information was available).

Most cranes were hand-captured at their natal areas at an estimated age of 6–8 weeks by a short-distance run from a vehicle or a hide, and only a minor fraction were captured at the wintering areas: 42 juveniles were captured in Spain during winter using oral tranquilizers (alpha-chloralose) and rocket nets (Alonso et al., 2018), and four juveniles were captured in France. In addition to the national scheme metal ring on the tarsometatarsus, cranes were marked either with an alphanumeric band or a unique combination of three coloured plastic bands on one or both tibiotarsi. Since 1988, country codes with three coloured plastic bands on the left tibia and individual codes with three bands on the right tibia were used. Seven different colours of plastic rings were available: white, yellow, red, blue, green, black, and brown. Marked juveniles were released immediately after banding.

2.1.3. Crane resightings

Resightings were registered across the whole geographic range of cranes, both at the breeding and wintering range and also at the numerous stop-over sites along the three main flyways. The geographical distribution of the resightings is depicted in Fig. 1, and more information can be found in Table A.1 in the Appendices.

2.2. Band types

Cranes were marked with four distinct band types throughout the study period: Alphanumeric, Spanish, Finnish, and European Laser-Signed Advanced "ELSA" (Table A.2, Appendices). Alphanumeric bands were first introduced in the 1980 s and remained in use through the 1990 s and early 2000 s. These bands featured letter-number combinations in white on a red background. Over time, however, the background colour faded, making them increasingly difficult to read (see Fig. 2). Moreover, reading the alphanumeric codes from a distance proved challenging. In response, a three-colour band combination system, wherein each crane received a unique colour code, was introduced in 1988. These "Spanish" bands, constructed with two UV resistant PVC layers and coloured directly within the plastic material (Gravograph,

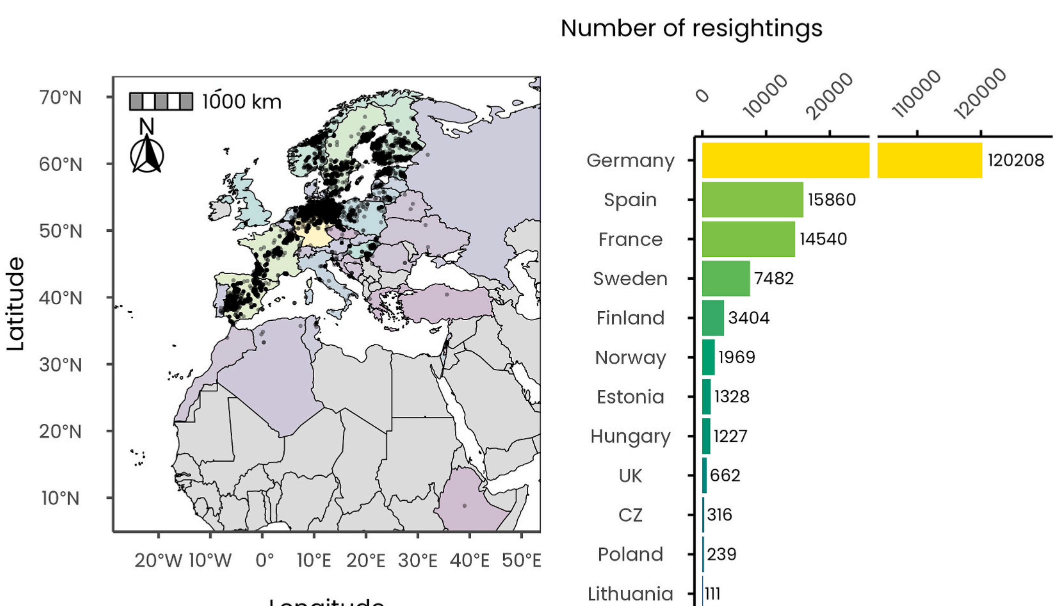

Fig. 1. Geographic distribution and number of banded crane resightings across Europe and neighbouring regions between 1985 and 2021. The map highlights areas with reported resightings (dots), while the bar chart provides the exact number of resightings for each country with more than 100 resightings. Colours indicates number of resightings in each country, and correspond between the map and bar chart. The number of resightings in purple highlighted countries summed to 328 (all together). Czech Republic and United Kingdom abbreviated CZ and UK respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 2. Different band types have been used during the study period 1985–2021. Left image shows an old alphanumeric band 'F36′ (© H. Wilken). Middle image shows plastic coloured bands (Spanish type; the upper red ring on the left tibia of the crane is a metal ring with the number of the national ringing office inscribed on it) (© L. Kaletta). Right picture shows the 'ELSA' bands (© J. Månsson). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2024), allowed for easier identification of individuals from a distance using telescopes or cameras. "Finnish" coloured bands were implemented from 1990, those bands were either made from plastic or metal, but this information was not consistently reported in the database. Between 1988 and 2001, two types of coloured bands (Spanish and Finnish-made) were used to band cranes in Spain, Sweden, Germany, Norway, Estonia, Finland, and Israel (Alonso and Alonso, 1999; Alonso et al., 2018). In 2001, a new band type, the European Laser-Signed Advanced (Fiedler et al. 2002), was introduced and distributed by NABU Crane Center (Crane Conservation Germany – Kranichschutz Deutschland) to all European crane ringers (Nowald, 2010). This band type is made from injection moulded polyoxymethylene. Several additional countries joined the banding efforts using this system, including the Czech Republic, France, United Kingdom, Latvia, Lithuania, Hungary, and Russia.

2.3. Database management

Before entering each observation of a colour-banded crane into national observation databases, coordinators from national working groups verified the accuracy, and confirmed the reported band combination. When banded cranes were observed outside of their natal country, they were reported to the respective banding country's national coordinator. This continental collaborative approach ensured a standardised and coordinated system for marking cranes across countries, contributing to the creation of a unified European crane banding database. This was coordinated from 1989 to 2008 by the Spanish Crane Working Group, which provided the rings to Germany, Poland, France, Portugal, Spain and Israel with a website (https://www.ecwg.org) to report sightings of marked cranes (details in Alonso et al., 2018). In 2009, Crane Conservation Germany launched iCORA (Internet-based Crane Observation Ring Archive; Heinicke et al. 2016). The iCORA platform facilitates reporting sightings of marked cranes and provides access to individual capture and resighting histories. The integration of data from national and scientific projects, alongside community-led initiatives such as the Amigos de Gallocanta association, has resulted in a continent-wide, long-term dataset. This extensive dataset contributes significantly to studies on demographic and life-history parameters, providing a comprehensive understanding of crane population ecology.

2.4. Data processing

We compiled data on all banding and resighting events from the combined datasets, including dates, localities, and geographical coordinates. Multiple consecutive observations from the same or nearby locations were considered a single resighting using the date and location of the first observation. The final dataset included 6,352 individual cranes banded in 14 countries and 181,692 resightings from 42 countries (in Europe, Africa and Asia) between 1985 and 2021. Records containing detectable errors and inaccuracies (e.g., unidentifiable colour-band combinations or uncertain crane identities) were excluded. We also omitted individuals banded as adults with unknown ages. After processing, the final dataset comprised 5,049 cranes banded as juveniles in 11 countries (with nine natal countries, and eleven and two cranes banded at their winter quarters in Spain and France, respectively), with a total of 172,725 resightings (Fig. 1).

2.5. Modelling

We collapsed banding and resighting observations into annual 'capture histories' for each of the 5,049 individual cranes, representing their initial banding and subsequent observations over the 37-year study period (1985–2021). To determine the most appropriate analytical approach, we first tested the data's goodness of fit (GOF) using the R package *R2ucare* (Gimenez et al., 2018b), an R version of the U-CARE software (Choquet et al., 2009). The tests revealed evidence of trap dependence (Test 2.CT), transience (Test 3.SR), and overdispersion (Tests 2.CL and 3.SM) (Table B.1, Appendices). Consequently, we applied models using the mixture extension 'CJSMixture' of the Cormack–Jolly–Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) using the *RMark* package (Laake, 2013) in the software R (v. 4.3.1, R Core Team, 2023), combined with program MARK (White and Burnham, 1999), to estimate the survival probability (ϕ) and the detection probability (p) of cranes. Mixture models are recognised as an effective method for accounting for heterogeneity of unknown origin, with two mixture groups generally being sufficient (Pledger et al., 2003).

The survival parameter (ϕ) was modelled using age, time and natal origin, with:

(1) age: modelled by three life stages: juvenile (0 year old), subadult (1–3 years old), and adult *(*4 + years old*)*. Juvenile is implicitly included in the model as the reference category (intercept). To allow within-group age effects, we incorporated: *Subadult* and *Adult* as categorical (binary) variables (0/1, indicating presence in the respective age class). *Age* is a continuous variable capturing the linear effects of age within each life stage.This approach allows for distinct survival estimates for juveniles while maintaining a linear and gradual change in survival rates within the sub-adult and adult age classes,
(2) time (*T*): following a temporal linear trend,
(3) *natal country*: assuming a difference in survival rates for cranes of different origin, reflecting different environmental effect, and also accounting for difference arising from the use of different migratory flyways.

Detection probability (p) was modelled as a function of biologically and methodologically relevant covariates that could influence the likelihood of detecting an individual. The factors considered were:

(1) *colourband*: categorical variable to account for differences in detection probability based on the type of bands used, as they may vary in visibility and readability,
(2) time since marking *(tsm)*: fitting a linear trend accounting for decrease in detection rates arising from degradation of colourbands,
(3) time (T): fitting a linear temporal trend of detection probability to account for increasing observation over the years,
(4) *natal country*: accounting for a potential variations in detection due to differences in observation effort across countries and migratory flyways,
(5) *mixture*: accounting for unexplained heterogeneity in detection probability among individuals by dividing individuals into two detection groups (high detectability vs low detectability).

In addition to the null model and single-effect models, we tested various combinations of variables to assess whether multiple factors influence survival and detection additively or interactively. Additive models examined whether multiple covariates independently contributed to variation in survival or detection probabilities, such as testing whether survival varied by age class and time or whether detection probability was influenced by band type and time since marking. Interaction models explored whether the effect of one factor depended on another, for instance, whether age-specific survival trends changed over time or whether the impact of band type on detection probability varied with time since marking. Additionally, for detection probability, models incorporating a mixture effect were included to account for latent heterogeneity by classifying individuals into high vs. low detectability groups, with the parameter *pi* remained constant. By structuring the model set in this way, we aimed to evaluate key biological and methodological factors while balancing model complexity and interpretability (see Table B.2, Appendices).

Given the period and extent of use for each band type, specific parameter components were fixed based on the banding history in each country. For instance, ELSA bands were introduced in 2001, meaning cranes banded with ELSA could not have been detected before that year and could not be detected after 21 years of age (Tables A.1 and A.2, Appendices). To account for overdispersion, which can bias more complex models by favouring complexity and narrowing confidence intervals, the Variance Inflation Factor ($\hat{c}$, calculated from the most general model: 8.58) was adjusted using the *adjust.chat* function in *RMark*. We then reviewed the adjusted model list based on QAICc rankings (Table B.3, Appendices). We performed model-averaging of the two top-ranked models (QAICc $\leq$ 2) after $\hat{c}$ adjustment. Standard errors and confidence intervals in the figures reflect model averaging of the predictions of the two supported models. Given the small sample size from Lithuania, we also ran the top models excluding the Lithuanian cranes. However, this did not affect the survival or detection estimates (see Table C.1, Appendices).

3. Results

The model obtained from the model averaging of the top two models according to the QAICc indicates that detection probability varied according to band type (*colourband*), time since marking (*tsm*), the interaction between a *colourband* x *tsm*, a linear temporal trend (T), *natal country*, and the two mixture groups (Table 1; Table B.3, Appendices). Two mixture groups, used to account for unobserved heterogeneity in detection, were identified. The first group, representing 45 % of the cranes in the dataset, had a mean detection probability of 0.30 [0.20–0.42], while the second group, representing the remaining 55 %, exhibited a higher mean detection probability of 0.72 [0.60–0.82].

Table 1
Parameter beta estimates of the two best fitting models (see Table B.3) for estimating survival and detection probability of banded cranes between 1985 and 2021. Respective QAICc weight for model 1 and model 2 are 0.55 and 0.45. Key variables include age classes:juveniles (intercept), sub-adults, adults; time since marking (*tsm*) in years, temporal trend (T), *natal country* and band types (*colourband*), for parameters (Par.) of mixture (pi), survival (Phi) and detection (p).

		Model 1		Model 2	
Par.	Variable	Estimate	SE	Estimate	SE
pi	Intercept	−0.18	0.06	−0.20	0.06
Phi	Intercept	3.92	0.21	3.94	0.21
	Age	−0.10	0.05	−0.12	0.05
	Subadult	0.03	0.32	−0.01	0.33
	Adult	−1.18	0.47	−1.30	0.47
	T	−0.09	0.01	−0.09	0.01
	Age: *T*	0.002	0.002	0.002	0.002
	Subadult: *T*	0.04	0.01	0.04	0.01
	Adult: *T*	0.09	0.02	0.10	0.02
p	Intercept	−2.32	0.39	−3.07	0.40
	Colourband − Finnish	1.74	0.18	2.22	0.23
	Colourband − Spanish	1.04	0.19	1.91	0.23
	Colourband − ELSA	1.10	0.21	1.79	0.25
	tsm	−0.21	0.01	−0.07	0.03
	T	0.09	0.01	0.10	0.01
	Natal Country − Estonia	−1.44	0.35	−1.45	0.35
	Natal Country − Finland	−1.66	0.36	−1.63	0.36
	Natal Country − Germany	0.43	0.35	0.43	0.35
	Natal Country − Latvia	−0.54	0.50	−0.59	0.50
	Natal Country − Lithuania	11.74	249.67	12.94	315.37
	Natal Country − Norway	0.81	0.37	0.82	0.37
	Natal Country − Sweden	−0.11	0.35	−0.11	0.35
	Natal Country − United Kingdom	2.17	0.48	2.09	0.46
	mixture 2	2.78	0.05	2.80	0.05
	Colourband – Finnish: *tsm*	0	0	−0.11	0.03
	Colourband – Spanish: *tsm*	0	0	−0.19	0.02
	Colourband – ELSA: *tsm*	0	0	−0.14	0.03

Moreover, in our dataset, 20 % of banded cranes were never resighted after banding. Overall, the average estimated survival is 0.90 [0.88–0.92] (estimated mean and 95 % CI).

3.1. Band types

Resighting or detection probability varied significantly among band types (Table 1; Fig. 3a). Cranes marked with ELSA bands exhibited the highest detection probability (0.65 [0.52–0.75]), followed by those with Finnish bands (0.57 [0.46– 0.66]), Spanish bands (0.51 [0.43–0.60]) and alphanumeric bands, which had the lowest detection probability (0.27 [0.13–0.47]).

3.2. Time since marking and interaction between band types

Detection probability was influenced by time since marking (*tsm*), with older cranes, marked for longer periods, exhibiting a slight decline in detectability (Table 1). The interaction between band type and time since marking also affected detection probability. While colour bands displayed varying patterns of detectability over time, all experienced a substantial reduction in detection probability, with detection rates approximately halving for all colour bands within 20 years (Fig. 3b). The notable exception was the alphanumeric bands, which maintained a relatively stable, albeit low, detection probability over time (Table 1; Fig. 3b).

3.3. Temporal change in detection rate

Crane detection probability increased over the study period (Table 1), starting from a relatively low probability of 0.25 [0.13–0.41] (mean and 95 % CI) in 1986 and progressively rising to a probability of

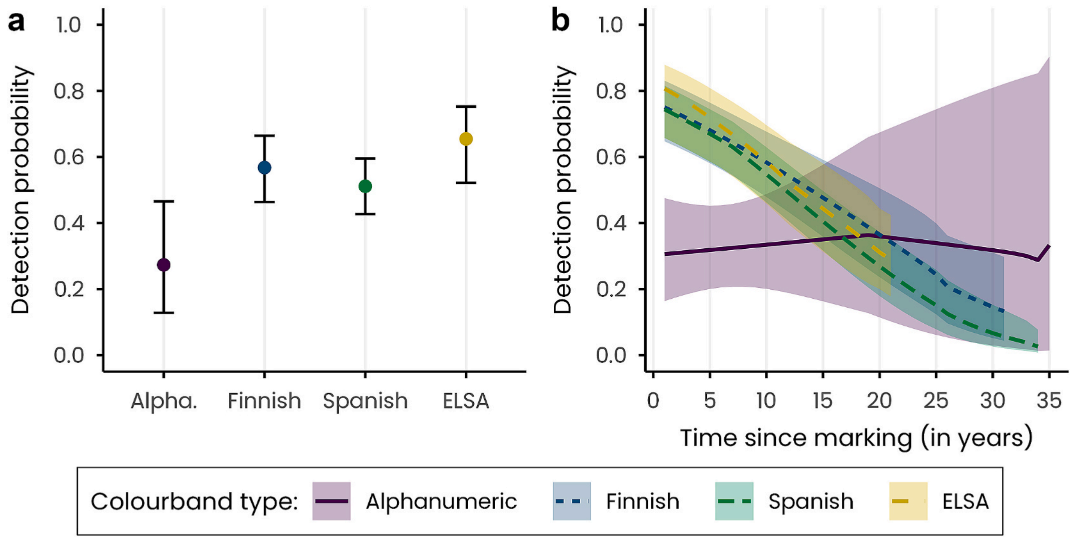

Fig. 3. Detection probability of cranes (a) banded with different types of bands and (b) in interaction with time since marking between 1985 and 2021. Points in (a) and lines in (b) are the estimated means with the whiskers and shaded areas representing the 95% CIs of the mean. All other variables were kept constant at their average values when predicting detection probability from the models.

0.53 [0.41–0.65] between 2015 and 2021 (Fig. 4). This trend parallels the annual increase in the number of observation days per year for marked cranes (Fig. D.1, Appendices).

3.4. Natal country

Detection probability also varied by the cranes' natal country. For instance, cranes from Finland (0.30 [0.21–0.42]) and Estonia (0.46 [0.36–0.55]) exhibited lower detection probabilities compared to those from Norway (0.77 [0.65–0.87]), Latvia (0.78 [0.46–0.96]), and the United Kingdom (0.97 [0.86–0.99]; Table 1; Fig. 5)."Moreover, cranes originating from Lithuania showed an exceptionally high mean detection probability (0.99 [0.00–1.00]); resulting from the small sample size and extreme variance in resightings between individuals (Table A.1, Appendices).

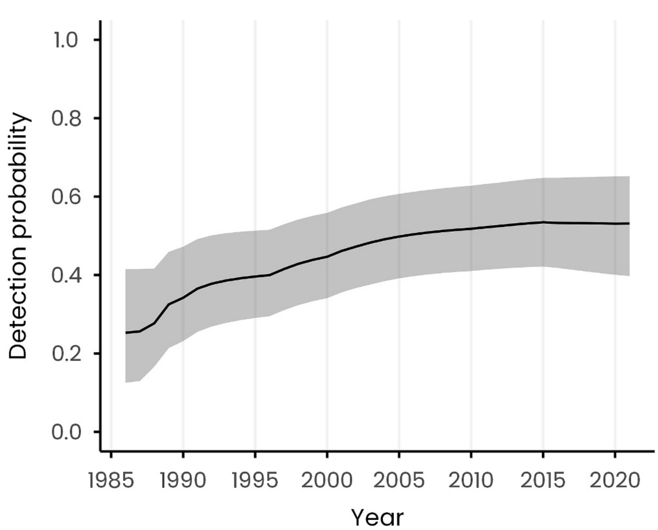

Fig. 4. Detection probability of colour banded cranes between 1985 and 2021 (line and shaded area is the mean and 95% CIs respectively). All other variables were kept constant at their average values when making predictions from the model.

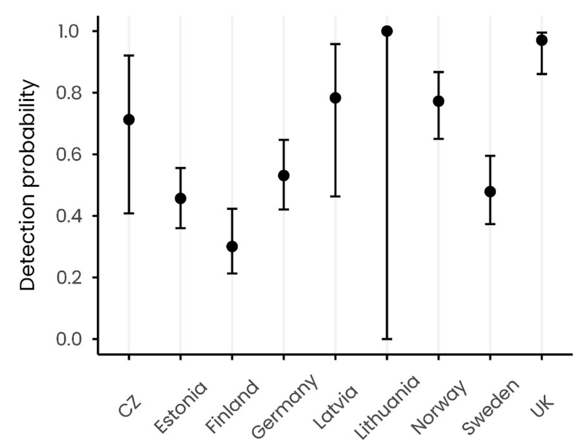

Fig. 5. Detection probability of colour banded cranes hatched in different European countries between 1985 and 2021. Points represent the estimated means and whiskers their associated 95% confidence intervals. CZ and UK are abbreviations for Czech Republic and United Kingdom respectively. All other variables were kept constant at average values when predicting detection probability from the models.

4. Discussion

Overall, our global detection estimates are largely consistent with previous findings. For instance, analysis of crane data from the EURING database (1936–2017) reported an average detection probability of 0.45 [0.44–0.46] (Bautista and Alonso, 2018), which aligns closely with our average estimate of 0.51 [0.40–0.62]. However, unlike this previous study, we demonstrate that the observation of banded cranes has been significantly influenced by at least three key factors: (1) band type and its longer-term readability, (2) regional and temporal variation in observation effort, and (3) an additional, as yet unexplained, source of heterogeneity. These findings are critical for informing future bird banding programs in general but also for improving data collection and the interpretation of demographic parameters in the specific case of Eurasian crane when studying population dynamics.

4.1. The influence of band type on short- and longer-term detection probability

The type of band used significantly influenced the detectability of banded cranes, likely due to differences in the visibility and durability of the materials. ELSA bands exhibited the highest average detection probability, followed by Finnish, Spanish, and alphanumeric bands. In general, detection probability decreases as the time since marking increased. This is raising concerns about the long-term durability and visibility of bands, due to their wear and tear, particularly for older cranes whose bands have likely become less detectable over time.

Initially, ELSA bands demonstrated the highest detection probability, around 80 % in the first year, whereas Finnish and Spanish bands started with moderate detection probabilities, not significantly lower than ELSA, but higher than alphanumeric bands. Despite those initial differences, detection probabilities of ELSA, Finnish, and Spanish bands declined at similar rates. Some observers reported that while Spanish bands were better than alphanumeric bands over time, the red and blue colours on these bands tended to fade (Lundgren, pers. comm.). Moreover, Finnish bands were prone to partial or complete loss after several years, with their colours also deteriorating with age. One key advantage of ELSA bands is their durability, with very few reported losses by observers. Their observed reliability is likely due to how they are manufactured (moulded polyoxymethylene providing high rigidity and wear resistance), and are attached to the legs of cranes (snap-fit with additional glue on edges).

In Dunlins (*Calidris alpina*), plastic ring colours were observed to fade after approximately six to eight years (Thorup, 2000). Another study comparing two types of alphanumeric band, plastic ('darvic', two-layered) and metal ('incoloy'), reported a reduction in the readability of the bands' inscriptions. This decline was attributed either to colour fading in plastic bands or to surface wear erasing the codes on metal bands, with a significant wear effect emerging after four to seven years (Breton et al., 2006a). These findings are consistent with our own observations, suggesting that the gradual decline in detection rates may be associated with the material durability of bands, whether plastic (e.g., Spanish) or metal (e.g., Finnish). This degradation could result from factors such as the fading of the colour or its peeling off the base layer, a phenomenon reported (but not verified) after several years (Lundgren, pers. comm.). It could also come from dirt on the surface of the band, especially for the ELSA bands that are not round but hexagonal and for which dirt can accumulate on the smooth sides (Torrijo, pers. comm.). A study on Piping Plovers (*Charadrius melodus*) indicated higher reporting rates for colour band combinations compared to alphanumeric flag codes (Roche et al., 2014). However, this study also noted a greater risk of reporting an incorrect colour band combination compared to incorrect alphanumeric codes. In our study, we observed that alphanumeric bands maintained a constant detection rate over time, albeit at a low level; and the wide confidence intervals make it difficult to interpret their detectability in the long-term. Low detection of alphanumeric-banded cranes may be due to the need for closer observation distances to read them accurately compared to colour bands. Moreover, few cranes were marked with alphanumeric bands. At that time the observation effort was also low, and two facts could explain the constant detectability rates of these few cranes over the years after marking: (i) the high fidelity of cranes to their breeding territories and to specific wintering sites (e.g. Hornborgasjön, Günz, Arjuzanx, Gallocanta, Hortobágy, Hula Valley), and (ii) the tendency of many observers to search more intensively for 'their local cranes' than for others. Colour bands, on the other hand, may be more prone to misreading due to confusion between certain colours (e.g. green vs. blue, white vs. yellow), which would be consistent with findings in Roche and collaborators (2014). According to observers in the present studies, difficulties to separate these colours were extra challenging if colours had faded. To minimize the risk of misreadings, some ringers are avoiding confusing colours at the same position of the colour combinations (Ticháčková, pers. comm.).

4.2. Regional and temporal differences in detection probability

The difference in detection due to the natal origin of cranes could be influenced by factors such as behaviour (Végvári et al., 2011), migration patterns (Leito et al., 2015, 2011), habitat use, or geographic distributions (Ojaste et al., 2020) impacting resighting outcomes. Cranes from countries with extensive monitoring efforts, whether at breeding sites, wintering grounds, or specific stopover points along migratory routes, tend to show higher detection probabilities. Indeed, observation effort varies along and between flyways, with the western flyway having generally a higher monitoring effort compared to the central and eastern flyways (Leito et al. 2011). In addition, some countries started to band cranes when the observation effort was already high, which might explain the high detection probabilities of these birds (e.g, Latvia, Lithuania, UK; see Table A.1, Appendices).

The nature of the local crane population might also play a role in their detection. A study focusing on the cranes banded in UK reported a detection probability of 0.99 (95 %CI [0.96– 0.99]) for their population (Donaldson et al., 2023), which is also similar to our value for this country. This very high detection probability can be attributed to the fact that this population is reintroduced and thus intensively monitored, and that these cranes do not perform long migrations. The detection was also very high in a reintroduced population of whooping cranes (*Grus americana*) (Servanty et al., 2014). In the case of the Sandhill crane (*Antigone canadensis*), detectability was shown to decrease with age, except for territorial individuals that can be observed more easily (Wheeler et al., 2019). Unsurprisingly, this suggests that higher and consistent monitoring efforts carried out at specific geographic areas significantly increase detection probabilities. This was probably the case of the reintroduced population in UK and probably also of some territorial crane pairs that were particularly intensively monitored in specific regions of Lithuania, Latvia, Norway, Sweden, Germany and Czech Republic (see Fig. 5).

The increase in detection probability over the study period can be largely explained by an increase in the number of observers, the improvement of optical equipment (e.g. telescopes and digital cameras), and probably also an increased awareness of the importance of reporting marked birds and improved facilities for reporting observations (iCORA website). Specifically accounting for advances in observational technologies was not possible because of a lack of data across both regions and time. According to our data, there has been a remarkable increase in observation effort over the 20 years following the start of crane marking in Europe (see Fig. D.1, Appendices). An earlier study of waterfowl species subject to hunting showed that an increase in reporting was associated with improved band quality and readability and implementation of reporting platforms (Arnold et al., 2020). An increase in citizen science activities, including reports of marked animals including birds, has been observed following the launch of public online platforms for reporting (Knape et al., 2022). An example of such a platform is eBird, which explicitly aims to collect bird sightings from citizens for research purposes (Sullivan et al., 2009). For cranes, the iCORA online reporting platform, launched in 2009, has made reporting easier and provides immediate feedback to observers, encouraging further reporting. Enhanced observer participation, driven by these efforts, underscores the crucial role of community involvement and technological advancements in avian research and conservation.

4.3. Additional factors driving current unexplained heterogeneity

Even though our study accounted for potential unexplained and unmodeled heterogeneity in detection by including mixtures, there remains the possibility that unaccounted heterogeneity – such as covariates related to variation in monitoring effort or general detection probability – could affect detection probability and thereby also estimates of for example life history traits. For instance, if critical covariates are incomplete or entirely lacking, it could result in biased estimates, potentially underestimating the true survival rates of the population. This is particularly concerning given that our dataset indicates that 20 % of individuals were never resighted after banding. These individuals could either be transients, i.e. individuals that emigrated out of the study area (see Genovart & Pradel, 2019), an aspect supported by the results of Test 3.SR (Table B.1, Appendices). However, given the extensive area covered by observers and the well-known migration routes and staging areas, it is most likely that these individuals died shortly after being banded and before being resighted for the first time, as for instance juveniles being preyed upon, or dying during their first autumn migration. The distinction between these two scenarios is crucial for accurate survival modelling, as misidentifying transients as residents could significantly skew the results. Future research should address these limitations by exploring in more detail the sources of detection variation, particularly spatial and individual heterogeneity, which may not have been fully captured in our study. For the spatial heterogeneity, this could be tackled by using a spatial capture-recapture model. As for individual heterogeneity, it is understood as any source of variation between individuals in demographic parameters that cannot be accounted for by temporal or spatial heterogeneity alone, and can be accounted for by adding a relevant individual covariate (Gimenez et al., 2018a). This may be partly explained by weather conditions that are known to affect detection rates. Unfortunately, incorporating weather data is not feasible in these models due to the annual scale of our dataset and the complexity of aggregating such data in relation to all observation sites from multiple countries.

4.4. Conclusions

Our study reveals significant variation in detection probability of banded cranes, which are influenced by factors such as band type, regional and temporal differences in observation effort, and additional unexplained heterogeneity. The detection probability provides insights into the durability or readability of the bands used to mark cranes, with different type of bands showing variable detection probability patterns over time. Overall, our results show that, with the exception of alphanumeric bands, all other band types are equivalent in their average detection and have a similar durability over time. This supports the continued use of ELSA bands for marking cranes in Europe. These results provide important information for future banding schemes of birds in general but also call for further studies investigating in more detail the long-term durability of different band types and how environmental factors could influence detection probabilities. Understanding the impact of factors such as habitat type, observer effort, and weather conditions on band visibility could lead to more accurate adjustments in survival models. Also, cranes in regions with greater monitoring efforts exhibit higher detection rates, suggesting that addressing regional variations through increasing observation efforts in some countries could enhance detection rate and accuracy estimates of life history traits in future studies.

The findings of this study hold significant implications beyond crane research. Accurate assessment of banding and, more generally, marking methods is crucial for reliable data collection in wildlife studies and understanding factors that influence detection probability can significantly improve monitoring efforts for wildlife and demographical studies in general.

CRediT authorship contribution statement

Morgane Gicquel: Investigation, Data curation, Writing – review & editing, Visualization, Writing – original draft, Formal analysis. **Juan C. Alonso:** Investigation. **Lovisa Nilsson:** Writing – review & editing, Funding acquisition, Supervision, Investigation, Conceptualization. **Matthew Low:** Writing – review & editing, Resources, Supervision. **Javier A. Alonso:** Investigation, Writing – review & editing, Conceptualization. **Dmitrijs Boiko:** Writing – review & editing, Data curation, Investigation. **Damon Bridge:** Writing – review & editing, Data curation. **Patrick Dulau:** Investigation, Data curation, Writing – review & editing. **Thomas Heinicke:** Investigation, Writing – review & editing. **Anne Kettner:** Writing – review & editing. **Yosef Kiat:** Writing – review & editing, Data curation. **Petras Kurlavičius:** Investigation, Writing – review & editing, Data curation. **Sigvard Lundgren:** Writing – review & editing, Data curation, Investigation. **Michael Modrow:** Investigation, Writing – review & editing, Data curation. **Günter Nowald:** Writing – review & editing, Data curation, Investigation. **Ivar Ojaste:** Investigation, Writing – review & editing, Data curation. **Alain Salvi:** Investigation, Writing – review & editing. **Jostein Sandvik:** Data curation, Investigation. **Markéta Ticháčková:** Data curation, Writing – review & editing. **Antonio Torrijo:** Data curation, Investigation. **Jari Valkama:** Investigation, Writing – review & editing, Data curation. **Zsolt Végvári:** Data curation, Writing – review & editing. **Johan Månsson:** Supervision, Project administration, Funding acquisition, Investigation, Conceptualization, Writing – review & editing, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.114020.

Data availability

The authors do not have permission to share data.

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