RESEARCH ARTICLE

Seasonal survival and migratory connectivity of the Eurasian Oystercatcher revealed by citizen science

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ABSTRACT

Migratory connectivity describes linkages between breeding and non-breeding areas. An ongoing challenge is tracking avian species between breeding and non-breeding areas and hence estimating migratory connectivity and seasonal survival. Collaborative color-ringing projects between researchers and citizen scientists provide opportunities for tracking the annual movements of avian species. Our study describes seasonal survival and migratory connectivity using data from more than 4,600 individuals with over 51,000 observations, predominantly collected by citizen scientists. Our study focuses on the Eurasian Oystercatcher (*Haematopus ostralegus*), a species that has experienced a substantial and ongoing decline in recent decades. Multiple threats have been described, and given that these threats vary in space and time, there is an urgent need to estimate demographic rates at the appropriate spatio-temporal scale. We performed a seasonal multi-state (5 geographical areas within The Netherlands) live- and dead-recoveries analysis under varying model structures to account for biological and data complexity. Coastal breeding populations were largely sedentary, while inland breeding populations were migratory and the direction of migration varied among areas, which has not been described previously. Our results indicated that survival was lower during winter than summer and that survival was lower in inland areas compared with coastal areas. A concerning result was that seasonal survival of individuals over-wintering in the Wadden Sea, an internationally important site for over-wintering shorebirds, appeared to decline during the study period. We discuss the outcomes of our study, and how citizen science was integral for conducting this study. Our findings identify how the demographic rates of the oystercatcher vary in space and time, knowledge that is vital for generating hypotheses and prioritizing future research into the causes of decline.

Keywords: citizen science, migratory connectivity, multi-state, partial migration, program mark, seasonal survival

Kennis over seizoensoverleving en connectiviteit van migrerende Scholeksters dankzij burgerwetenschap

UITTREKSEL

Trekwegverbindingen beschrijven het verband tussen broedgebieden en overwinteringsgebieden. Het volgen van vogels tijdens de trek tussen broedgebieden en overwinteringsgebieden, noodzakelijk om seizoensoverleving en trekwegverbindingen te bepalen, is een grote en voortdurende uitdaging. Samenwerking tussen professionele onderzoekers en burgerwetenschappers bij kleurringprojecten maakt het vastleggen van deze jaarlijkse trekbewegingen mogelijk. In deze studie beschrijven we seizoensoverleving en trekwegverbindingen voor de Scholekster (*Haematopus ostralegus*) op basis van gegevens over meer dan 4600 individuen en 51,000 aflezingen, vooral door burgerwetenschappers. Onze onderzoeksoort de Scholekster vertoont al enkele decennia een sterke en aanhoudende afname. De verschillende bedreigingen variëren in ruimte en tijd, waardoor het noodzakelijk is om demografische parameters op de juiste tijd- en ruimte schaal te beschrijven. Vanwege de complexiteit van de data en de onderliggende biologie hebben we op verschillende manieren een model met meervoudige toestanden, zoals vijf geografische regio's, gemaakt om de overleving te analyseren. Kustpopulaties bleken grotendeels sedentair, terwijl de in het binnenland broedende populaties altijd migreerden. Voor de binnenlandvogels hing de richting van de trek af van de geografische locatie van het broedgebied en dit is nog niet eerder beschreven. De overleving was lager in de winter dan in de zomer en kustvogels overleefden beter dan binnenlandbroeders. Een verontrustende bevinding is dat de seizoensoverleving van de in de Waddenzee overwinterende Scholeksters lijkt af te nemen. De Waddenzee is internationaal van groot

belang voor overwinterende wadvogels. In de discussie gaan we in op de betekenis van de resultaten alsook het feit dat deze studie niet mogelijk zou zijn geweest zonder de grote inzet van vele burgerwetenschappers. We beschrijven hoe demografische parameters variëren alsook samenhangen in ruimte en tijd. Deze kennis is nodig om hypothesen te genereren over de oorzaken van de achteruitgang en om toekomstig vervolgonderzoek aan de oorzaken van de achteruitgang te prioriteren.

Sleutelwoorden: burgerwetenschap, meervoudige toestanden, programma MARK, seizoensoverleving, trekwegverbindingen

INTRODUCTION

Populations of a number of migratory bird species have declined rapidly in recent decades and developing effective conservation plans is of key importance. Understanding migratory connectivity, that is, the linkage between spatially disjoint breeding and non-breeding areas (Webster et al. 2002), has become a focus of research to map migratory pathways (Iwamura et al. 2014), identify threats at the appropriate spatial and temporal scale (Stanley et al. 2015, Allen and Singh 2016), and therefore prioritize actions that will optimally conserve the species (Martin et al. 2007, Flockhart et al. 2015). Estimating migratory connectivity is also vital for understanding the population dynamics of a species, especially when demographic rates like survival vary between breeding and non-breeding areas (Sillett and Holmes 2002, Rockwell et al. 2017, Rushing et al. 2017). Unfortunately, most species are data-deficient in terms of estimating season-specific demographic rates, especially when considering migratory connectivity among populations.

Movements of migratory birds have traditionally been monitored using metal-ringing schemes but recovery rates are often low and nearly non-existent for many species during winter. Geolocators and associated technologies like satellite transmitters offer opportunities for understanding individual-level movements, but due to their limited sample size and geographical spread, offer limited insights into a population's migratory connectivity (Laughlin et al. 2013, Hallworth and Marra 2015). Avian species that are large enough to carry individually recognizable tags, such as color-rings, provide opportunities for determining population demographics across large geographical areas and across the entire annual cycle. Observations of color-ringed birds can be obtained in the field without the need to capture the bird (after tagging) or finding it dead (Rock 1999, Salewski et al. 2007). Data can also be collected over much wider spatial scales and is not restricted to areas with bird-ringing programs, improving the probability of encounter in less densely populated or remote areas (Meissner and Bzoma 2011). Individually recognizable tags also provide an opportunity to engage citizen scientists, especially ornithologists who are already involved in citizen science programs like bird atlases and breeding bird surveys (Dickinson et al. 2012, Tulloch et al. 2013).

Although there are a number of potential biases inherent in color-ringing programs (Bearhop et al. 2003), long-term color-ringing projects have identified migratory routes and stopovers, season-specific survival estimates, and how these may vary over time (Madsen et al. 2002, Pigniczki et al. 2016, Wood et al. 2017).

Most studies of migratory connectivity have focused on species with disparate breeding and non-breeding ranges. However, determining migratory connectivity is also important at regional scales in partially migratory systems, especially where migratory and resident individuals overlap during the non-breeding season. Threats experienced during the non-breeding season may have carry-over effects and impact the demographic rates of individuals in the breeding season (Norris et al. 2004), and carry-over effects may also occur between the breeding and the non-breeding seasons (Sedinger and Alisauskas 2014). Hence, even in partially migratory systems there is a need to estimate migratory connectivity and to quantify the degree to which resident and migratory individuals overlap during the breeding and non-breeding seasons.

Eurasian Oystercatchers (*Haematopus ostralegus*) in The Netherlands present a model system for studying the population consequences of migratory connectivity for species with a partially migratory strategy, especially as few studies have quantified the species migratory characteristics (Hulscher et al. 1996, Ens and Underhill 2014). Of notable importance, the Eurasian Oystercatchers have experienced a substantial Europe-wide decline in recent decades (Roodbergen et al. 2012, van de Pol et al. 2014). The declining trends have also been observed in The Netherlands, an internationally important region containing ~30% of the breeding and 21% of the over-wintering population (van de Pol et al. 2014). The cause of the decline may be due to several threats that vary in space and time (van de Pol et al. 2014). During summer, agricultural intensification impacts inland breeding birds while an increasing incidence of flooding events is a threat to coastal breeding birds (van de Pol et al. 2014). During winter, climate change, human disturbance or competition with shellfisheries impacts both breeding and wintering birds (van de Pol et al. 2014). The relative impact of these threats, and how these impacts accumulate across the annual cycle, will depend upon where an individual is in space and time, that is, where an individual breeds and winters, and hence the need to determine migratory connectivity.

A substantial effort has been made in recent years to engage with citizen scientists and develop a ringing scheme that is predominantly led by volunteers. The initiative began in 2008 with "The Year of the Oystercatcher," organized by NGOs BirdLife Netherlands and Sovon (Ens et al. 2011), and has continued expanding to the date of this study. The initiative meant that oystercatchers were ringed across a much wider spatial scale in The Netherlands and that resightings occurred year-round, information that is vital for quantifying the seasonal movements of the oyster-catcher. In this study, we use color-ringing data from more than 4,600 individuals, with over 51,000 resightings, and in combination with dead recoveries, to estimate seasonal movements within The Netherlands and to obtain season- and state-specific survival estimates. The results from this study will be important for estimating migratory connectivity between breeding and non-breeding areas and identifying spatio-temporal patterns in survival. This knowledge will be vital for generating hypotheses about how threats across space and time affect the Eurasian Oystercatcher and thus developing effective conservation actions.

METHODS

Study Species and Populations

The Eurasian Oystercatcher is a wading and meadow bird that is distributed along the coastline of Europe and may also breed up to a few hundred km inland (Hulscher et al. 1996). It is a long-lived species with average adult annual survival of ~90% (Durell 2007, Duriez et al. 2012). As per many other long-lived species, fecundity is quite low with an average fledgling rate of 0.33 fledglings per pair and an average age of first breeding of 6.5 yr (Ens and Underhill 2014). Both sexes are alike (i.e. exhibit little sexual dimorphism), although it may be possible to distinguish males and females using biometric measurements, but care should be taken when comparing measurements across years or areas (Zwarts et al. 1996, van de Pol et al. 2009). Site fidelity to breeding ranges is considered high, and fidelity to winter ranges is also high, especially for adults, although individuals may move to other regions during cold spells (van de Pol et al. 2014).

The Dutch oystercatcher population is partially migratory, with year-round residents along the coast in the Wadden Sea and the Dutch Delta, but inland areas are only occupied during the breeding season. A turnover of individuals also occurs among seasons, for example, an unknown proportion of the Dutch breeding population over-winters in the UK, Belgium or France, while others migrate from more northerly breeding areas like Fennoscandia or Russia to winter in The Netherlands. During this study, oystercatchers were fitted with color-rings in more than 30 locations within The Netherlands, including the Wadden Sea and the Dutch Delta, and during the breeding season in several inland locations (Figure 1).

Figure 1 displays the 5 geographical states that were used to estimate survival, resightability probability and seasonal transitions among geographic areas within The Netherlands. The 5 states consist of 3 distinct areas: the Dutch Delta, the Wadden Sea and inland areas. The Delta area largely includes the river deltas with tidal flows, adjoining land areas and the waterways leaving Rotterdam. The Wadden Sea includes all the Wadden Sea islands in The Netherlands and coastal areas including those ~1 km inland from the coast. The inland areas consisted of all other regions of The Netherlands, and it should be noted that despite being named inland, this state did include some coastal areas.

We determined the 5 geographical states based on expected variation in survival and migratory transitions, and partly due to heterogeneity in resighting probabilities. The 2 principal coastal areas of the Wadden Sea and the Delta were separated due to expected variation in survival resulting from past activities related to human activities like shellfisheries and habitat loss (Duriez et al. 2009, van de Pol et al. 2014). The decision to split the Wadden Sea between east and west was driven by the spatial and temporal heterogeneity of ringing and resighting efforts. The East Wadden includes the islands of Schiermonnikoog and Ameland, where continued research projects have been running since the start of this project in 2008. The research projects were primarily active during summer resulting in a large difference in the number of individuals resighted between summer and winter (Figure 2a, b). Although the West Wadden has had a number of research projects in the past, for example, on the island of Texel (Verhulst et al. 2004, Oosterbeek et al. 2006), research projects on Texel have been low intensity since 2008 and most observations were by volunteers rather than researchers. We divided the inland states between north and south due to the expected variation in transition probabilities, since early analyses indicated that oystercatchers breeding inland in southern Netherlands were more likely to migrate to the Delta while oystercatchers breeding inland in northern Netherlands were more likely to migrate to the Wadden Sea. Dividing inland areas between the north and south enabled us to determine these differing migratory patterns. No clear boundaries were evident between northern or southern breeding oystercatchers, therefore we used the provincial boundaries of The Netherlands where the northern borders of Gelderland, Utrecht and South Holland split the south from the north (Figure 1).

Ringing and Recovery

Although oystercatchers have been color-ringed for decades, our study period begins with the effort to engage citizen
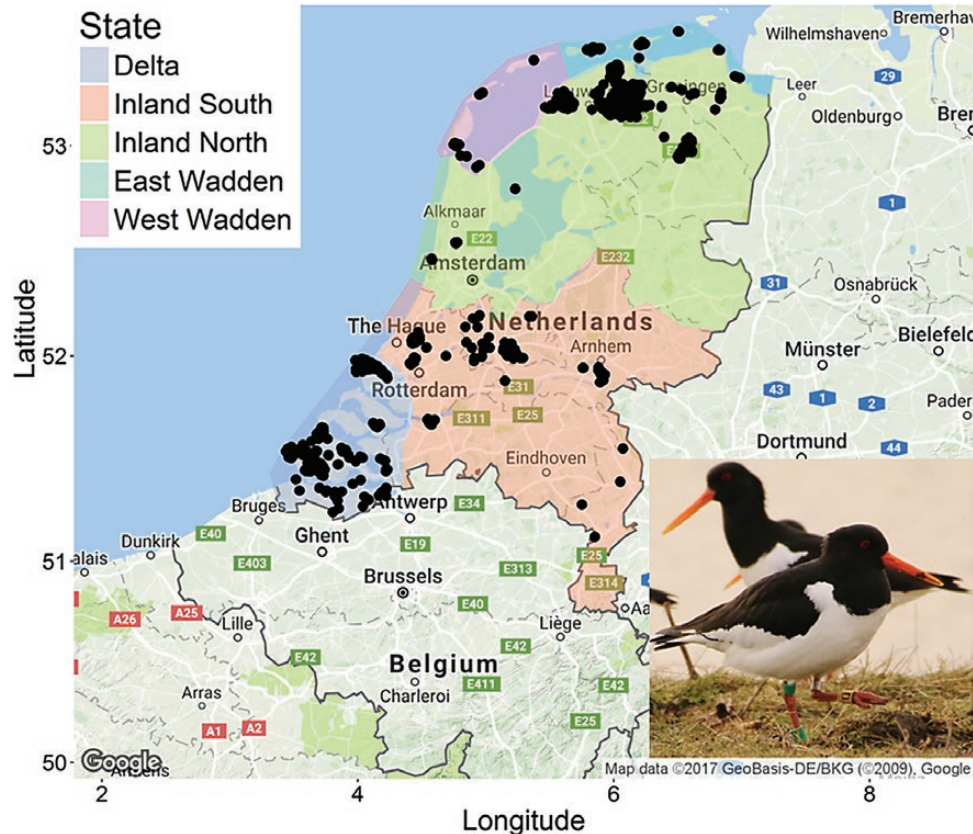
FIGURE 1. The Netherlands split into the 5 geographical states used in this study. The black points are color-ringing locations of Eurasian Oystercatchers (*n* = 3030 ringed individuals, example of color-ringed oystercatcher inset). Photo courtesy of Andrew M. Allen.

scientists in ringing programs across The Netherlands. Oystercatchers have been marked from 2008 to the present with individually recognizable color-rings containing letters or numbers (Figure 1). The color rings were fitted to both the left and right leg; a color marker was also attached along with a standard metal ring used by EURing (European Union for Bird Ringing; Figure 1). Individuals have been marked in both organized captures, for example, using mist nets, cannon nets or traps on the nest, and opportunistically by volunteers, for example, trapping individuals on the nest during the breeding season. All captures, and subsequent observations of color-rings, were entered into an online portal called Wadertrack (www.wadertrack.nl), which was launched in 2008. Wadertrack keeps a record of all the individuals that a citizen scientist has seen, and the citizen scientist is able to view the ringing data as well as all the historical and subsequent observations of that individual, providing an important stimulus for generating and maintaining interest to report color-ring data. The metal ring data and subsequent recoveries are managed by Vogeltrekstation (the Dutch Centre for Avian Migration and Demography), the administrative centre for bird ringing in The Netherlands. In our study, we only used dead recoveries for birds that had also been marked with a color-ring.

In this study, we focus on migratory connectivity and survival of adults, which includes all individuals that were identified as aged 3 yr or more. Oystercatchers could be determined as adults by the absence of a white collar during the breeding season while juveniles and immature oystercatchers do have a white collar. During the non-breeding season, adult oystercatchers also have a white collar but are distinguished by a deep red iris and orange eye-ring whereas juveniles have a brown iris and no clear eye-ring and immatures have a pale red iris, which is initially a brown wash on the upper half before becoming dull red (Cramp 1983). Immatures also have a yellow eye-ring with a developing orange suffusion (Cramp 1983). Since 2008, there have been 3,030 individuals ringed as adults across the 5 study areas (Appendix Table 3). Almost all rings were fitted during the breeding season (April = 198, May = 1750, June = 987) and a small number outside the breeding season (March = 13, July = 39, August = 8, September = 17, December = 18). The number of adults ringed gradually increased over time with an overall average of 337 ringed adults per yr (2008–2010 = 286, 2011–2013 = 326, 2014–2016 = 397).

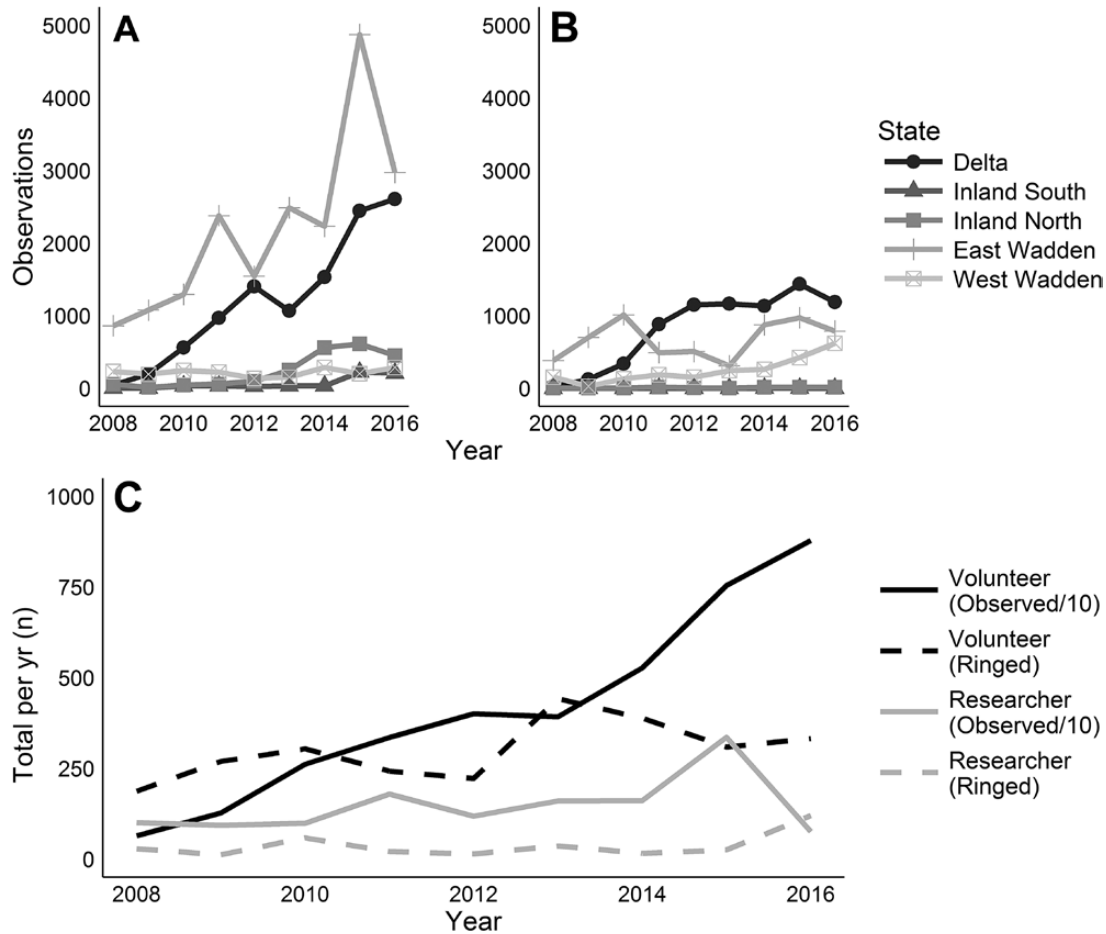In addition, a number of individuals had been marked with color-rings during research projects prior to this study.

FIGURE 2. Number of observations in (A) summer and (B) winter for the 5 geographical states used in this study, and (C) the number of Eurasian Oystercatchers observed (divided by 10) and ringed by citizen scientists and researchers between 2008 and 2016. Observations in the East Wadden contrasted between summer and winter. Observations from both inland areas were extremely low during winter.

The earlier studies were focused on specific geographic areas, such as the studies on the Wadden Sea islands of Schiermonnikoog (van de Pol et al. 2006) or Texel (Rutten et al. 2010) and also larger geographic areas such as a study investigating the effect of shellfisheries on the survival of oystercatchers in the Wadden Sea (Verhulst et al. 2004). A number of individuals from these previous studies were seen during the current study period. A total of 492 individuals were seen in the first study period of summer 2008, which we group as pre-2008a (Appendix Table 3). Another 1,106 individuals that were ringed prior to 2008 were seen in later periods, which we group as pre-2008b (Appendix Table 3). The first observation during the current study period, of those individuals ringed prior to 2008, equates to the individuals entering the marked population. In addition, for individuals ringed as juveniles or sub-adults prior to 2008, if they were adults by the start of the study in 2008, we included them as adults in our analysis. Including these individuals increased the sample size to 4,629 individuals with 51,001 observations.

Data Preparation

We performed several checks to determine the quality of the data. We removed observations that occurred before an individual was ringed, or with inaccurate co-ordinates, for example, locations occurring in open water or observations with clear rounding errors (e.g., 53°N and 5°E). We also cross-referenced resightings of color-rings with dead recoveries to not only inspect incorrect sightings, but also potential errors in dead recoveries. In addition, we investigated observations which were more than 20 km from an oystercatcher's median summer or winter location. A distance of 20 km is relatively short in terms of oystercatcher movements but 99.5% of observations were within this distance. The data preparation resulted in the removal of 185 observations from the dataset. The data preparation was in addition to ongoing data management actions within Wadertrack, where administrators inspect unusual observations, for example, observations that are spatially disjoint from all prior records. Observers were also encouraged to include photographs of observations so

that the individual's unique code could be verified. Since 2008, 168 observers have submitted 3,308 photos that support the records used in this study (41% of observers and 6.5% of records). We also quantified the contribution that citizen scientists made to data collection. We estimated the proportion of individuals ringed and observed by citizen scientists, and we also estimated the average distance between observations to better understand the spatial spread of observations.

We assigned all observations to one of the 5 geographical states used in the analysis (Figure 1), and these were divided by season, namely summer and winter. The summer (or breeding) period included all observations from April, May and June, and the winter (or non-breeding) period included all observations from September, October, November, December and January. We chose a longer winter census period because fewer resightings were made during winter months (Figure 2b). The census design violates the assumption of instantaneous sampling in mark-recapture studies and hence mortality may occur between sampling occasions. However, research has indicated that estimates may be robust in continuous sampling designs and may increase the precision of estimates due to larger sample sizes (O'Brien et al. 2005). We also determined the breeding and non-breeding seasons using the migratory, or transitional, phases of the oystercatcher's annual cycle. The annual cycle consists of 2 transitional phases when oystercatchers are migrating between breeding and non-breeding areas. Individuals are highly variable in the timing of migration, with spring migration occurring in February and March. The autumn migration is during July and August. We excluded the transitional phases from the analysis given the uncertainty of whether individuals were in the breeding or non-breeding area. Some individuals were seen multiple times in a single season, and occasionally in 2 or more different areas. We assigned the geographical state according to the area with the highest number of observations. We only observed a few instances ($n = 30$) where the number of observations were equal for 2 areas (in the same season). We determined whether the individual had performed an early or delayed migration, for example, some individuals had an observation in the Wadden Sea area and Inland during winter ($n = 14$), hence we used the Wadden Sea observation since this was likely a delayed migration. If there was no clear indication of delayed migration ($n = 16$), we examined the observation history to determine where an individual was during a prior summer or winter and used the observation that matched the observation history.

Many observations of color-ringed individuals were made outside of The Netherlands. Foreign observations were generally quite low in number ($n = 253$) and spread over a wide geographical area, ranging from Spain to Norway (see Appendix: Figure 5 for the seasonal and geographical spread of international observations). Given the seasonal movements of oystercatchers and the low number of foreign observations, we considered 2 model designs in our analysis. The first included a sixth state for all international resightings, hereon termed "Abroad". The second model design included an "Unobservable" state in the model (Kendall and Nichols 2002, Kendall 2004, Schaub et al. 2004). Kendall and Nichols (2002) describe an example of an unobservable state in the case of a metapopulation, whereby entire patches or breeding colonies are inaccessible or unknown and hence animals in these locations are unobservable. Kendall and Nichols' (2002) description of unobservable states fits the design of our study in that any individual who leaves The Netherlands becomes unobservable for practical purposes. Unobservable individuals may also move to inaccessible/unknown areas within The Netherlands, such as some of the rarely visited islands of the Wadden Sea. Including either the unobservable state, or the abroad state, meant that we could incorporate temporary emigration (Kendall and Nichols 2002, Schaub et al. 2004, Henle and Gruber 2017), a process that is known to occur given the partial migratory nature of oystercatchers, and the seasonal design of our study.

Statistical Analysis

We applied a multi-state live and dead recoveries (MSLD) model within Program Mark (White and Burnham 1999), but developed our models using package RMark (Laake 2013) in R 3.4.1 (R Core Team 2017). The time interval was 0.5 (i.e. 6 mo), to account for the seasonal structure of our model, and the study period was 9 yr (2008–2016), thus providing a total of 18 time intervals. The encounter histories were prepared using the LD format, thus every time interval had 2 entries whereby the L codes for the recapture or resighting and the D codes for a dead recovery. The recapture or resighting of an MSLD model denotes the state of the individual and was coded according to its geographical location, A = Abroad, D = Delta, S = Inland South, N = Inland North, W = West Wadden and E = East Wadden (Figure 1). The dead recovery was only coded as dead (1) or not (0) and did not contain information about where the bird was found (Cooch and White 2018).

Models that included an unobservable state had the resighting probability of U fixed to 0 to indicate that a state is unavailable for resighting (Schaub et al. 2004). Since it is also not possible to estimate survival for U, we constrained the survival of U to equal the average seasonal survival rates of the other states. In contrast to the model structure containing an unobservable state, we estimated the parameters of the Abroad state for resighting probability and survival in the model structure that included the international observations.

The number of ringed individuals, and subsequent resightings, was generally quite low for the inland regions, especially Inland South. The low sample sizes meant that survival parameters of inland areas could not be estimated for some time steps (i.e. season in a given year). To simplify the model structure, and because we did not expect variation in survival between Inland North and South, we constrained the survival of Inland South and North to be equal. We did not constrain the resighting or transition probabilities of Inland North and South to be equal. In addition, based on prior research, almost all individuals breeding in inland areas migrate to coastal areas to overwinter (Duriez et al. 2012). Therefore, almost no observations were returned from inland areas during winter. We fixed winter resighting probabilities to 0 and removed the few vagrant winter inland resightings from the dataset (n = 11, Figure 2b). To account for transitions that do not occur, we fixed the transition probabilities for inland areas such that the probability of remaining in either of the inland areas from summer to winter was 0. We examined all migratory transitions that were biologically possible and fixed the transition to 0 if there were no, or few (<3), occurrences of the transition during the entire study period.

We considered 4 temporal variables in our analysis. We created an additional variable in the design data to include seasonal survival (summer/winter). Resightings occurred fairly continuously within seasons, and the time steps of our model were 6 mo, hence summer survival (breeding season) denotes survival from the mid-point of summer to the mid-point of winter and winter survival (non-breeding season) denotes survival from the mid-point of winter to the mid-point of summer. Seasonal survival provides a summer and winter survival estimate for the entire study period, with no annual variation. The second temporal variable was time, which estimated a parameter for every time interval of the study (n = 18, 9 yr * 2 seasons). The third variable was temporal independence, that is, model parameters did not vary over time nor season and were constant for the entire study. The fourth variable was a temporal trend, which is a continuous trend over time with an intercept and a slope rather than a separate parameter for every time interval. We estimated the trend over the entire study period, and also estimated separate trends for summer and winter.

We ranked models according to Akaike's information criterion with a penalty for including additional parameters at low sample size (AICc; Burnham and Anderson 2002). We report the unadjusted AICc, that is, the AICc is based on the number of specified parameters rather than an adjusted AICc which is based on the number of estimated parameters. We also inspected the deviance of the model and the number of identifiable parameters. Given the large number of states (n = 5 or 6), with 18 time periods (9 yr, 2 seasons), a model with full time-varying survival, resighting, transitions and dead recovery probabilities may raise issues with parameter identifiability. To check parameter identifiability, we cloned the data 100 times and inspected model results (Cooch and White 2018). Parameter estimates should improve if non-identifiable parameters were due to small sample sizes, while standard errors of identifiable parameters should remain a proportion of the original model's standard errors (Cooch and White 2018). If parameters remain non-identifiable, this indicates that the data is not suitable for estimating the parameter, or that the parameter may be confounded (Cooch and White 2018).

RESULTS

Citizen Scientist Observations

Citizen scientists made a significant contribution to our ability to model survival and migration of oystercatchers within The Netherlands. Since volunteer programs were initiated in 2008, citizen scientists have provided 74% of observations to date and the number of observations have increased by ~26% annually (Figure 2c). Observations were reported by 409 observers on Wadertrack, of which 359 were citizen scientists and 50 were professional researchers. Citizen scientists have also been responsible for almost 90% of all birds ringed since 2008 (Figure 2c). Citizen scientists drastically increased the spatial coverage of both ringing operations and observations, and were also more likely to search for ringed oystercatchers over a larger area. The average distance between a citizen scientist's observations and their median location was 8.2 km compared with 3.7 km for researchers. Observer error may also be relatively low due to the enthusiasm of certain volunteers, whom can be expected to be experienced in reading rings. The top 35 citizen scientists, all of whom had made more than 100 observations, were responsible for 92% of citizen scientist observations.

Multi-State Live and Dead Recovery Model

The top performing model for both model structures (i.e. containing either a foreign or unobservable state) included time-varying survival and resighting probability while transition probabilities varied by season with a temporal trend (Table 1; Supplementary Material A). The results of both model designs were similar, and the most noticeable differences were transitions from Abroad to the Delta, which was not estimated when using an unobservable state, and a difference in autumn survival of inland birds of 0.05 which we expand upon below. Hence, we only present the results of the model containing the international observations, but the full model result tables are provided in Supplementary Material A. In addition, the top performing model contained a large number of parameters, therefore we also

TABLE 1. Model results for the top 15 mark-recapture live and dead recoveries analysis based on AICc, and a NULL model, using mark notation for the model structure of survival (*S*), resighting (*p*), transition (*Psi*) and dead recovery (*r*) probabilities. Models may include a spatial component of stratum (*str*) and/or a temporal component (time, season, time trend [*T*]). The absence of either the spatial or temporal components indicates that these were held constant, whereas "dot" indicates that both space and time were constant. nPar is the number of specified parameters in the model and nEst is the number of estimated parameters. ΔAICc reports the difference between the model AICc and the AICc of the top performing model.

Rank	Survival	Resighting	Transition	Recovery	nPar	nEst	ΔAICc	Deviance
1	S.str.time	p.str.time	Psi.season.T	r.str.season	209	193	0.00*	61,394.7
2	S.str.time	p.str.time	Psi.season.T	r.time	218	202	110.9	61,432.0
3	S.str.time	p.str.time	Psi.season.T	r.season	202	189	125.2	61,479.0
4	S.str.season	p.str.time	Psi.season.T	r.str.season	145	140	146.7	61,616.8
5	S.str.season.T	p.str.time	Psi.season.T	r.str.season	150	146	152.3	61,612.3
6	S.str.time	p.str.time	Psi.season	r.str.season	185	169	156.6	61,545.2
7	S.str.season	p.str.time	Psi.season.T	r.time	154	149	160.9	61,612.7
8	S.str.time	p.str.time	Psi.season	r.time	194	174	201.1	61,571.4
9	S.str.season	p.str.time	Psi.season	r.str.season	121	112	230.1	61,748.9
10	S.str.time	p.str.time	Psi.season	r.dot	177	162	230.9	61,635.8
11	S.season	p.str.time	Psi.season	r.time	130	120	233.8	61,734.4
12	S.season.T	p.str.time	Psi.season.T	r.time	159	145	237.0	61,678.6
13	S.str.time	p.str.season.T	Psi.season.T	r.str.season	149	128	615.6	62,077.6
14	S.str.time	p.str.season	Psi.season.T	r.time	151	134	628.4	62,074.2
15	S.str.season.T	p.str.season.T	Psi.season.T	r.str.season	99	91	719.2	62,292.7
NULL	S.dot	p.dot	Psi.dot	r.dot	4	4	15,578.2	77,422.7

*The AICc of the top performing model was 69,086.65

compared the results with a much-simplified model. The simplified model contained state-specific, seasonal trends, in survival and resighting probability instead of a full time-varying model, which reduced the parameter count by more than half (Table 1; Supplementary Material B).

An average of 92% of parameters were estimated across all models and 92% of parameters were also estimated in the top performing model (Table 1). Cloning the data 100 times did not increase the number of estimated parameters in the top performing model (92% parameters estimated) and parameters not estimated were either near the boundary of 1, such as survival in the West Wadden (see Survival below), had low sample sizes, such as survival and resighting probability estimates in the Abroad state, or few dead recoveries in some seasons or years (Supplementary Material A).

Resighting and dead recovery. The resighting probability varied by season and time across all 5 geographical areas (Figure 3). The highest resighting probabilities were during summer in the East Wadden (x = 0.69) and the Delta (x = 0.82) although inland summer resighting probabilities increased sharply towards the end of the study period (Figure 3a). The winter resighting probability in the East Wadden (x = 0.31; Figure 3b) was notably lower than summer while the resighting probabilities were more similar in the West Wadden between winter (x = 0.19) and summer (x = 0.27). The probability of dead recoveries could not be estimated for some time periods, but estimated parameters had an average of 0.27 in winter and 0.10 in summer. The complete results, including standard errors and confidence intervals, for resighting

and dead recovery probabilities, are shown in Supplementary Material A.

Transitions. Although a large number of transitions were biologically possible, several transitions either never occurred or rarely occurred and hence these were fixed to 0 during the model fitting process (*n* = 32; Table 2). Most individuals that were ringed or resighted in the Wadden Sea during summer were residents and remained in the Wadden Sea through to the next time step of winter (Table 2). Oystercatchers breeding in the Delta had a 0.05 probability of transitioning Abroad during autumn while a small number also migrated to the West Wadden. The inland areas had differing migratory patterns between Inland North and South (Table 2; Appendix: Figure 6). During autumn, oystercatchers from Inland South largely migrated to the Delta or Abroad while oystercatchers from Inland North migrated to the East and West Wadden (Table 2; Appendix: Figure 6). In addition, the probability of an oystercatcher from Inland South migrating to the Delta and the West Wadden increased during the study period while the probability of migrating Abroad decreased (Appendix: Figure 6). Oystercatchers from Inland North had an increasing trend for the probability of migrating to the East Wadden and a decreasing trend for the probability of migrating to the West Wadden (Appendix: Figure 6). Oystercatchers also migrated from Abroad to the East and West Wadden during autumn, although these were a small proportion of the ringed population since the probabilities of transitioning from the Wadden Sea to Abroad during spring was low (Table 2; Appendix: Figure 6). The spring transitions consisted of oystercatchers returning to the breeding areas although the probability of
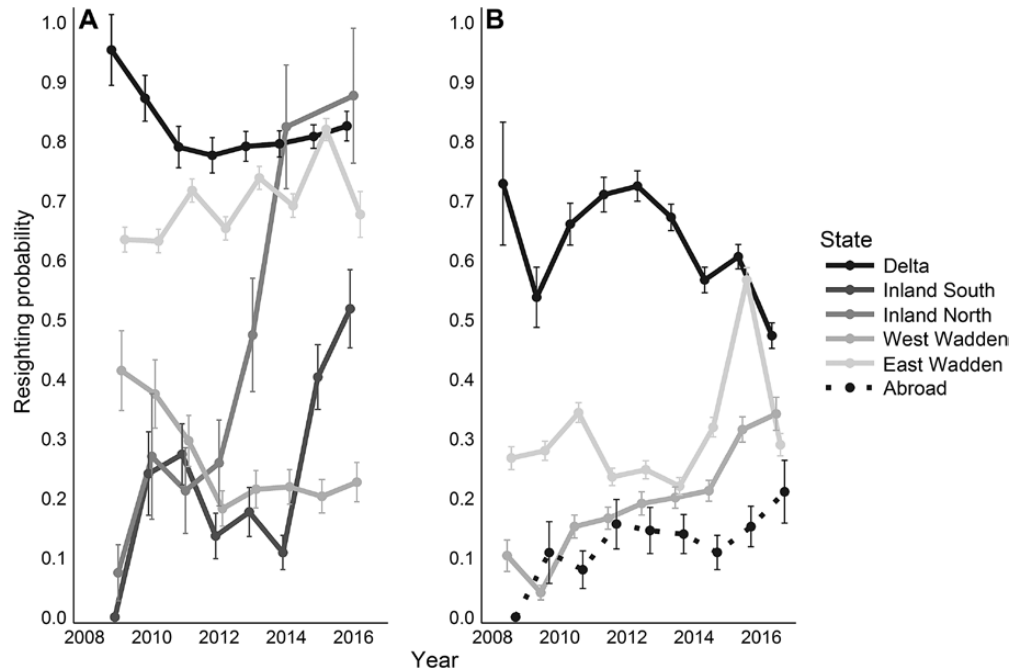
FIGURE 3. Resighting probability, including error bars for the standard error, for the top-performing model for (A) summer and (B) winter. Resighting probabilities were fixed to zero for Inland South and North during winter since all individuals transitioned out of this state at the end of the breeding season.

TABLE 2. Transition matrix for both the autumn and spring migration. The origin is shown in the first column while the destination is shown in the other columns, hence all rows sum to 1. InlandS = Inland South, InlandN = Inland North, WestWad = West Wadden and EastWad = East Wadden. An asterisk (*) indicates that the parameter was fixed. The transitions indicate the mean across the study period while the standard deviation (shown in brackets) relate to the standard deviation across the study periods to provide an indication of the degree of change in transition rates, rather than the standard error of the model estimate. Dashes (-) are values that were not estimated because the parameter was fixed and a caret (^) indicates that the parameter was estimated by subtraction.

Origin	Transition	Delta	InlandS	InlandN	WestWad	EastWad	Abroad
Delta	Autumn	0.94^ (-)	0.00* (-)	0.00* (-)	0.01 (0.003)	0.00* (-)	0.05 (0.002)
InlandS	Autumn	0.22 (0.021)	0.00* (-)	0.00^ (-)	0.03 (0.014)	0.00* (-)	0.75 (0.034)
InlandN	Autumn	0.00 (0.001)	0.00^ (-)	0.00* (-)	0.87 (0.008)	0.12 (0.005)	0.01 (0.001)
WestWad	Autumn	0.00* (-)	0.00* (-)	0.00* (-)	0.99^ (0.000)	0.01 (0.000)	0.00* (-)
EastWad	Autumn	0.00* (-)	0.00* (-)	0.00* (-)	0.01 (0.001)	0.99^ (0.001)	0.00* (-)
Abroad	Autumn	0.00 (0.000)	0.00* (-)	0.00* (-)	0.65 (0.060)	0.28 (0.07)	0.07^ (0.051)
Delta	Spring	0.94^ (0.005)	0.06 (0.005)	0.00 0.000	0.00* (-)	0.00* (-)	0.00 (0.000)
InlandS	Spring	0.00* (-)	1.00^ (0.000)	0.00* (-)	0.00* (-)	0.00* (-)	0.00* (-)
InlandN	Spring	0.00* (-)	0.00* (-)	1.00^ (0.000)	0.00* (-)	0.00* (-)	0.00* (-)
WestWad	Spring	0.01 (0.001)	0.00 (0.002)	0.26 (0.002)	0.65^ (0.014)	0.00 (0.001)	0.08 (0.009)
EastWad	Spring	0.00* (-)	0.00* (-)	0.01 (0.002)	0.00 (0.000)	0.97^ (0.001)	0.02 (0.002)
Abroad	Spring	0.11 (0.026)	0.87 (0.023)	0.02 (0.005)	0.00* (-)	0.00* (-)	0.00^ (0.000)

transitioning was different due to the varying size of the color-ringed population in each geographical state.

Survival. Summer survival (from breeding to non-breeding season) averaged 0.95 across all areas and was highest in the Wadden Sea areas (x = 0.97, SE = 0.01) and lowest inland (x = 0.85, SE = 0.07; Figure 4a). In contrast, winter survival (non-breeding to breeding season) was lowest in the East and West Wadden (x = 0.90, SE = 0.03 and x = 0.91, SE = 0.03, respectively), compared with 0.95 in the Delta and 0.92 Abroad (SE = 0.04 and 0.02, respectively). Temporal trends

in survival in the Delta and Wadden Sea areas were similar in the summer, but differences emerge in the winter survival patterns. Compared with the Delta, in most years survival was lower in both the West and East Wadden and the East Wadden appears to have a declining trend in winter survival estimates (Figure 4b; Supplementary Material B). The winter of 2012/2013 had a notable decline in the winter survival of oystercatchers in the West Wadden (Figure 4b). Summer survival of oystercatchers in inland areas was much lower than other areas during the early years of the study (2008 and
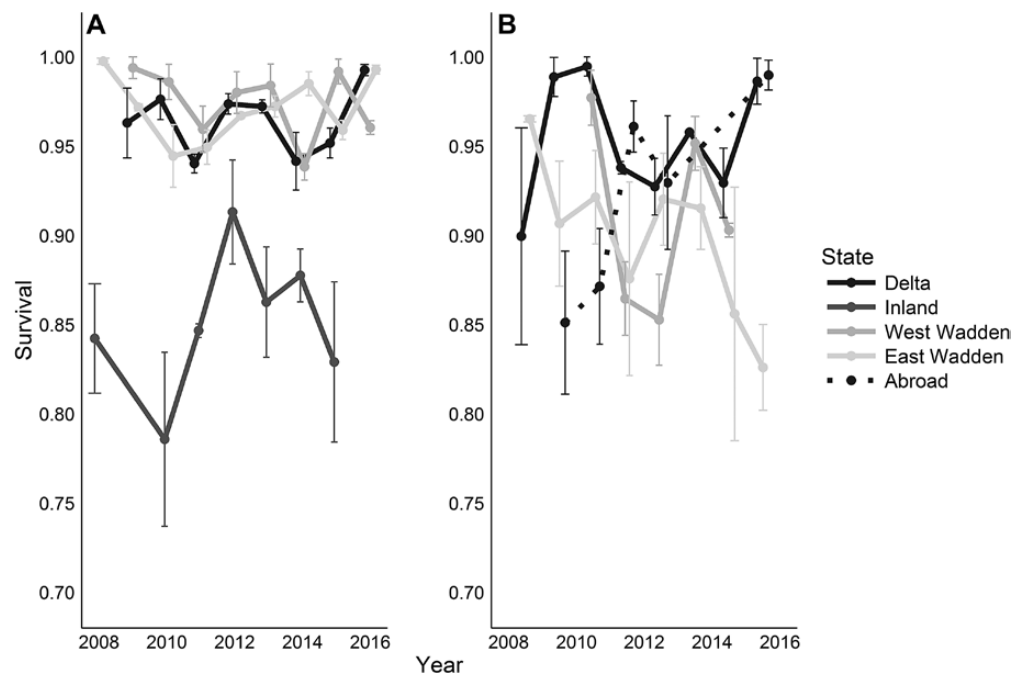
FIGURE 4. Survival estimates, including error bars for the standard error, for the top performing model for (A) summer (i.e. breeding season; mid-point of summer to mid-point of winter) and (B) winter (i.e. non-breeding season; mid-point of winter to mid-point of summer). No estimates were made for summer survival in the Abroad state, nor winter survival Inland, which is why no values are shown.

2009), and although survival increases in later years it remains below other areas (Figure 4a).

DISCUSSION

We quantified partial migratory patterns and season- and state-specific survival probabilities for Eurasian Oystercatchers among 5 regions of The Netherlands. Individuals that bred in the Wadden Sea and the Delta areas were largely sedentary and were joined by several other breeding populations that over-winter in these areas. An unexpected result was the diverging pattern of migration for inland birds and a large number of individuals from southern inland areas transitioned to the Delta or Abroad while individuals from Inland North largely transitioned to the Wadden Sea. Summer survival was higher than winter survival, especially within the Wadden Sea which had the largest differences between seasons. Winter survival appeared to decline in the East Wadden during the study period, however no noticeable trends were apparent in summer survival. Summer survival of inland areas was notably lower than other regions of The Netherlands. Furthermore, our results emphasize the contribution that citizen scientists make to mark-resighting projects, not only by enabling high resighting probabilities in both summer and winter, but also by increasing the number of ringed individuals which occurred over a much larger geographical area compared with previous research-focused projects.

Citizen Science

Most studies to date have reported survival estimates from metal banding schemes, especially when reporting data from large geographical scales or across seasons, meaning that sample sizes during the non-breeding season are generally low and it has been difficult to estimate survival for specific regions or movements between areas (Duriez et al. 2009, 2012, Robinson et al. 2010). A few studies of oystercatchers have reported results from color-ringing projects although these have often had a much narrower geographical focus and only report on annual or single-season survival (van de Pol et al. 2006, Durell 2007). Color-rings enable resightings of individuals without the need to handle an individual after ringing, meaning that birdwatchers and volunteers can contribute to data collection (i.e. act as citizen scientists). The current citizen science project has involved several years of outreach to stimulate involvement in the oystercatcher project. The citizen science project was initiated in 2008 with the "Year of the Oystercatcher", a year during which Sovon and Birdlife Netherlands focused their attentions on the oystercatcher. Outreach actions have been ongoing since the projects initiation, for example, an annual oystercatcher weekend when volunteers share their research experiences and time is also dedicated

to searching for color-ringed individuals. The success may also be due to the high number of color-ringed individuals in the population, hence the efforts of citizen scientists to find individuals are more easily rewarded. Ongoing developments also make it simpler to report oystercatchers that have been seen with rings, for example, Wadertrack and more recently a smartphone app (BirdRing; www.birdring. nl) that helps citizen scientists correctly report the ring combination and report the observation instantly in the field. Observers are also instantly rewarded with the full life-history of observations for the individual due to the link between the Wadertrack and the European color-ring birding (www.cr-birding.org) databases.

The continued outreach to engage with citizen scientists has enabled more than 51,000 observations of color-ringed oystercatchers during the 9-yr study, which allowed us to parameterize a more complex model that quantified survival and migration over finer spatial and temporal scales. Furthermore, annual observations have increased by ~26% each year which will aid future analyses (Figure 2a, b). Impressively, nearly 74% of observations and 90% of the birds ringed were by citizen scientists. Combining research data with less structured citizen science data does require careful consideration in later research, for example, the seasonal heterogeneity in resighting probabilities. The East Wadden includes Schiermonnikoog, which has an ongoing and long-running research program but researchers are mostly present during summer resulting in a stark contrast between summer and winter resighting probabilities (Figure 3). The research efforts in the East Wadden contrasted with the Delta where most observations were by volunteers and resighting probabilities were generally quite stable from summer to winter. Nevertheless, citizen scientists provided observations across broad spatial scales and enabled high resighting probabilities in many regions.

Migration

We reveal clear partial migratory patterns with predominantly sedentary breeding populations in the coastal areas of the Delta and the Wadden Sea while inland breeding populations were fully migratory. Although inland populations were previously known to be migratory (Duriez et al. 2012), we found diverging migratory patterns of northern and southern inland areas which had not been reported previously (Table 2). In addition, there were large transition probabilities to Abroad, which supports our approach for considering a design that either included a foreign state, or included an unobservable state to account for temporary emigration (Kendall 2004). The diverging migratory patterns highlight the need for quantifying migratory connectivity in the region given that inland breeding birds show relatively diffuse connectivity by wintering in the Wadden Sea, the Dutch Delta or in areas outside of The Netherlands,

and hence may be exposed to differing threats during the winter period. Our results also supported a model structure that included a seasonal time trend. The strongest trends were in the inland areas (Appendix: Figure 6). The trends were likely due to the number of individuals ringed inland compared with the total ringed population, whereby inland birds represented 3% of ringed oystercatcher at the end of 2008 but 26% by the end of 2016. Hence, the trends in migratory patterns were likely not a change in oystercatcher behaviour, but these changes were nonetheless important to incorporate in a multi-state model with a seasonal structure.

An interesting result was that individuals from Inland South had a high probability of transitioning Abroad during autumn. It should be noted that this result is based on a low number of international observations (<0.5% of all observations). However, models including either an unobservable or a foreign state detected this transition. One reason that Inland South individuals may have a high probability for transitioning abroad is that conditions in Dutch coastal areas may not be optimal, which may be due to competition (Dokter et al. 2017), reduced food stocks (Duriez et al. 2012), or that the wintering populations of bivalve feeders are already near capacity with resident individuals and long-distance migrants (Duriez et al. 2009, Kraan et al. 2009, van Roomen et al. 2012, Ens et al. 2014), which may result in higher rates of migration to more southern destinations. For example, 58 individuals that were ringed inland were observed outside of The Netherlands during winter but only 2 of these were observed north of The Netherlands, while all others were seen in Belgium, France or other southerly destinations (Appendix: Figure 5). Inland breeding birds had a low probability of being resighted abroad during winter, and another possibility is that inland breeding oystercatchers were migrating to parts of The Netherlands that were not monitored during winter, for example, the East Wadden had a much lower winter resighting probability and several islands were inaccessible. Stimulating volunteers to monitor some of these areas would help improve migratory estimates. Establishing collaborations with organizations in Belgium, France and Spain might help to increase resightings of individuals wintering abroad. Increasing the number of international resightings would also enable an expansion of the model to include European-level estimates of migratory connectivity, which would be vital for determining whether certain assumptions like comparable survival between observed and unobserved states are valid, and to determine how drivers of migration vary within Europe.

It is also evident that some birds migrate from abroad, or an area where they are not observed (i.e. an unobservable state), to the Wadden Sea to over-winter. The probability of an individual transitioning to the Wadden Sea to

over-winter was higher in the model design that included an unobservable state compared with one that included an Abroad state. One explanation is that almost no resightings were made of oystercatchers Abroad during summer (Appedix A: Figure 5), indicating that more resighting efforts are needed in breeding localities outside The Netherlands. In addition, the transition probabilities of individuals over-wintering in the Wadden Sea from Abroad may be underestimated since most individuals were ringed during summer, hence breed in The Netherlands and are sedentary. The pre-2008 dataset included 303 individuals that had been ringed during winter, and these individuals may migrate to northern localities outside The Netherlands to breed. Of the 303 individuals that were observed during the current study period, 128 were only seen during winter, 82 during summer and 93 in both seasons, hence 42% of the individuals ringed during winter may be transitioning abroad during spring. Increasing ringing operations during winter would improve estimates about the number of migratory individuals over-wintering in the Wadden Sea. However, winter operations are often led by researchers because of the technical procedures required to catch the birds, such as mist nets or cannon nets (Verhulst et al. 2004), which contrast with the breeding period when individuals can be caught relatively easily on the nest by researchers and licensed volunteers (Ens et al. 1992).

Survival

Our results highlighted how survival varied not only among regions but also between seasons. Summer survival estimates for inland areas were particularly low compared with the other regions, and also with previous studies (Duriez et al. 2012, Roodbergen et al. 2012). We would need to consider the migratory patterns to determine annual survival, for example, inland breeding birds that over-winter in the Delta would have an average annual survival of 0.81 (0.85*0.95) while inland breeding birds over-wintering in the East Wadden would only have an average annual survival of 0.77 (0.85*0.91; Figure 4a). Our results are similar to those reported by Duriez et al. (2012) for the 1990s (81% for migrants and 82% for residents), although the authors did not distinguish between migrants from inland or northerly breeding populations in their study. Annual survival of inland breeding birds contrasted with resident coastal breeding individuals, especially from the Delta where annual survival was 0.91 (0.96*0.95, Figure 4a), and thus highlights the importance of quantifying migratory connectivity, given how annual survival rates were influenced by where individuals breed and over-winter.

A challenge when interpreting summer survival of inland breeding birds is to disentangle when mortality occurs. Including an unobservable state resulted in lower summer survival estimates for inland birds (0.80) compared with a model

structure that included an abroad state (0.85; Supplementary Material A). Model designs with an unobservable state include the assumption that survival in the unobservable state equals survival in other states (Kendall 2004). It may be that winter survival for the unobservable state was actually lower and this difference was therefore transferred to the estimates of inland autumn survival. For example, a source of winter mortality may be due to hunting in France (Duriez et al. 2012, van de Pol et al. 2014). Given that a potentially large proportion of inland breeding oystercatchers migrate to France, and that the additional mortality from hunting may have a high impact for such a long-lived species (van de Pol et al. 2014), the inland population may be disproportionately affected by hunting. Winter survival in the Abroad state was estimated as 0.92, which was lower than winter survival in the Delta and higher than the Wadden Sea, although the results were quite uncertain with wide confidence limits. Further research is needed to verify survival outside of The Netherlands and to identify European-level estimates of migratory connectivity, and hence improve flyway management for the oystercatcher (Boere and Piersma 2012, Clausen et al. 2017). Additional research is also needed to identify why inland survival estimates are lower and whether this mortality occurs during winter or summer.

Some additional considerations may be needed when interpreting the summer survival estimates of inland breeding oystercatchers. Samples sizes were generally much lower inland, especially during the early years of the project (Figure 2a). Combining the summer survival estimates for inland areas improved parameter identifiability during these early years although the confidence intervals remained fairly large. It is also important to note that our survival estimates were apparent survival. Although site fidelity is generally found to be quite high in breeding oystercatchers (Heg et al. 2003, Bruinzeel 2007), it is uncertain how this may apply to inland breeding oystercatchers which breed in more temporally heterogeneous agricultural landscapes. The dynamic nature of agricultural landscapes may result in lower rates of site fidelity, increasing the challenge of finding birds in subsequent years which may subsequently appear as mortality in a mark-resighting model (Sandercock et al. 2002, Sandercock 2003). Finally, almost all inland birds were ringed by citizen scientists, hence some apparent mortality may also be due to ring loss although our analyses indicated that rates of ring loss were low for inland breeding birds (Conn et al. 2004, Allen et al. personal observation).

Our results indicated a declining trend of winter survival for the Wadden Sea areas. Winter survival at the start of study was comparable with other studies reporting survival from the Wadden Sea (~0.95, Duriez et al. 2012) but the rates declined to much lower levels by the end of our study. Annual survival rates have previously been reported in the range of 0.85–0.95 (Roodbergen et al. 2012, Ens and Underhill 2014), which also agrees with our results, although annual survival

rates may have fallen below 0.85 by the end of our study (summer * winter; Figure 4). The declining survival rates may have important implications for the global population of Eurasian Oystercatchers given its importance as an over-wintering area (van de Pol et al. 2014). A number of studies have highlighted how mechanical shellfisheries had serious consequences for the survival of shorebirds wintering in the Wadden Sea (Verhulst et al. 2004, Duriez et al. 2009, Kraan et al. 2009). Although mechanical shellfisheries have been severely restricted (van de Pol et al. 2014), the shellfish stocks may need time to recover, and hence the positive effects for shorebirds may be delayed. Shellfish recovery may also be hampered by a number of factors such as an increase in non-mechanical shellfisheries (Nehls et al. 2009), competition with the invasive Pacific oyster (*Crassostrea gigas*; Waser et al. 2016) and reports of poor recruitment success of cockles and other bivalves due to climate change and predation (Beukema and Dekker 2005). Furthermore, Dokter et al. (2017) described how razor clams (*Ensis directus*), a food source for oystercatchers, became fully depleted during the course of winter in the Balgzand area of the Wadden Sea (Ens et al. 2015).

The challenges associated with the principal prey items of oystercatchers point towards a worrying food landscape in the Wadden Sea, which appears to be supported by our estimates of declining winter survival. It should also be noted that some of the declining survival estimates may be due to ring wear, which appeared to be higher in the Wadden Sea due to the longer period of ringing operations (Allen et al. personal observation). Ring wear may explain up to 1% of perceived mortality; however, prior analyses indicate that it is likely to be less than this (Allen et al. personal observation). Similarly, we estimated that the average annual rate of ring loss was 2.5%; however, more than half of individuals with a missing color-ring were recognizable, meaning that the impact of ring loss on survival estimates in this study will likely be lower, and may instead have only a slight impact on both survival and resighting probability (Allen et al. personal observation).

Conclusions

Oystercatchers in The Netherlands are partially migratory in The Netherlands with seasonally and spatially variable demographic rates. Inland breeding populations were migratory, wintered in multiple coastal locations, and had the lowest apparent survival rates. In contrast, birds breeding in coastal areas were generally sedentary and had higher survival probabilities in summer compared with winter. Winter survival probability for all individuals in the Wadden Sea declined during our study. These findings highlight how an understanding of migratory connectivity can inform conservation of Dutch oystercatcher populations. Our findings are also important for generating hypotheses for future research about the contributions that spatio-temporally varying threats make towards the

oystercatcher decline, such as the causes for low survival of inland breeding oystercatchers. A deeper understanding of the causes will be vital for developing conservation actions at the appropriate temporal and spatial scale (Marra et al. 2011, Hostetler et al. 2015).

SUPPLEMENTARY MATERIAL

Supplementary material is available at *The Auk: Ornithological Advances* online.

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APPENDIX TABLE 3. Total number of individuals included in the study according to where an individual was ringed (or first seen). Ringed post-2008 were ringed during the current study period, pre-2008 (a) were ringed prior to 2008 but were seen during summer 2008, pre-2008 (b) were ringed prior to 2008 but were only seen after summer 2008. Although these individuals were known to be alive, they only entered the **"marked"** population of this study when they were first seen during this study period.

	Total	Delta	Inland South	Inland North	East Wadden	West Wadden
Ringed post-2008	3030	1064	283	993	623	67
Pre-2008 (a)	492	0	0	23	391	78
Pre-2008 (b)	1106	29	0	23	753	301

APPENDIX FIGURE 5. Resightings outside of The Netherlands for Eurasian Oystercatchers included in the current study. Resightings are color-coded according to the season they were observed: Spring = February, March; Summer = April, May, June; Autumn = July, August; Winter = September, October, November, December, January. Note that seasons are based on oystercatcher movements rather than weather-determined seasons. The geographical area (state) where the individual was ringed is denoted by the shape of the symbols. The top-left inset displays individuals resighted in northern Europe while the bottom-left inset displays individuals resighted in southwestern Europe.

APPENDIX FIGURE 6. Results of the transition matrices shown in Table 2, mapped on the study area to help visualize the migratory connectivity of oystercatchers within The Netherlands and also within areas outside The Netherlands (Abroad state). The inset graphs display examples of the seasonal time trends for transitions from summer to winter including (a) Inland South to Delta, (b) Inland South to Abroad, (c) Inland North to West Wadden and (d) Inland North to East Wadden.