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Estimating the size of the Dutch breeding population of Continental Black-tailed Godwits from 2007–2015 using resighting data from spring staging sites

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Over the past 50 years, the population of Continental Black-tailed Godwits *Limosa limosa limosa* breeding of the East Atlantic Flyway has been in steep decline. This decline has previously been documented in trend analyses and six Netherlands-wide count-based population estimates, the last of which was completed in 1999. We provide an updated population size estimate and describe inter-annual fluctuations in the population between 2007 and 2015. To generate these estimates, we integrated a mark-recapture survival analysis with estimates of the densities of colour-marked individuals at migratory staging sites with known proportions of Continental and Icelandic *L. l. islandica* Black-tailed Godwits within a Bayesian framework. The use of these analytical techniques means that, in contrast with earlier efforts, our estimates are accompanied with confidence intervals, allowing us to estimate the population size with known precision. Using additional information on the breeding destination of 43 godwits equipped with satellite transmitters at Iberian staging areas, we found that 87% (75–95% 95% CI) of the nominate subspecies in the East Atlantic Flyway breed in The Netherlands. We estimated that the number of breeding pairs in The Netherlands has declined from 47,000 (38,000–56,000) pairs in 2007 to 33,000 (26,000–41,000) in 2015. Despite a temporary increase in 2010 and 2011, the population declined by an average of 3.7% per year over the entire period from 2007–2015, and by 6.3% from 2011–2015. We conclude that investing in an intensive demographic programme at a regional scale, when combined with targeted resightings of marked individuals elsewhere, can yield population estimates at the flyway scale.

Key words: population estimate, survival probability, mark-recapture, Bayesian framework, trend

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Staging Black-tailed Godwits in Extremadura, Spain, almost ready to depart to their breeding grounds (1 February 2010).

Estimates of population sizes are fundamental to conservation and management issues, as they indicate whether a species should be listed as of conservation concern (Dawson *et al.* 2011, Donald & Fuller 1998, IUCN 2016). Estimates of population sizes over multiple years also help to document trajectories of change, which can play a role in risk assessments (Keith *et al.* 2015). Yet, estimating the population sizes of widespread populations is often an arduous task, and estimates are often imprecise. The most common method for estimating wader population sizes is to count congregating individuals at as many locations as possible during the same period of time each year (e.g. mid-winter; Underhill & Prys-Jones 1994, Yates & Goss-Custard 1991). This approach has a disadvantage, though, as individuals can be double-counted, flocks can be missed altogether (Rappoldt *et al.* 1985), and site-use can be underestimated when turnover is high (Ganter & Madsen 2001, Loonstra *et al.* 2016). A common alternative method for counting birds, are 'atlas-projects'. These projects, however, are often restricted to estimating only a limited part of a species' total population size (Donald & Fuller 1998, Szabo *et al.* 2012).

There is yet another method to estimate population

size that does not necessitate complete coverage of a species' range and is grounded on a clear set of assumptions based on the mark-resight framework (Otis *et al.* 1978). This method involves a four-step process: (1) marking individuals with unique combinations of colour rings, (2) collecting data on the survival of these colour-marked individuals so that the remaining numbers of marked individuals at a given time point can be estimated, (3) determining the density of those colour-marked individuals at sites where they randomly mix with others from the larger population, and (4) dividing the total number of colour-marked birds by the proportion of colour-marked birds observed among all individuals (Gunnarsson *et al.* 2005, McClintock & White 2012, Spaans *et al.* 2011). Mark-resight models have been used to estimate the population size of staging or stopover populations (Frederiksen *et al.* 2001, Lyons *et al.* 2015, Matechou *et al.* 2013), these models are less often used to estimate total population size (but see Gunnarsson *et al.* 2005, Lourenço *et al.* 2010b, Spaans *et al.* 2011), or used to estimate population size over time (but see Ganter & Madsen 2001).

One of the limitations constraining the broader use of this method, especially in long-term studies, is that

the number of marked birds alive at a given moment is not precisely known and must be separately estimated with a mark-recapture survival analysis (White & Burnham 1999), unless the detection probability is equal to one. We therefore developed a model that estimates the number of marked birds alive at a given moment in time using a Cormack-Jolly-Seber (CJS) model. To estimate the total population size, the CJS model was integrated with a binomial model for counts of marked and unmarked birds. This is best done in a Bayesian framework, which enables the likelihood estimates from both models to be joined, making the final estimates of population size more precise than they would be if they were analysed separately (Abadi *et al.* 2010, Doak *et al.* 2005).

We employ this method to generate yearly estimates of the total population size of Continental Black-tailed Godwits *Limosa limosa limosa* breeding in The Netherlands over the period from 2007–2015. As a result of agricultural intensification, godwit reproductive success (Kentie *et al.* 2013, 2015, Schekkerman *et al.* 2008) and breeding population size have dropped dramatically over the past 50 years (Gill *et al.* 2007). Black-tailed Godwits are now labelled as ‘near-threatened’ by the IUCN (2016), even though the Icelandic subspecies *Limosa limosa islandica* is still increasing in numbers (Gill *et al.* 2007). The most recent estimate of the Dutch breeding population was generated from the 1999 Dutch Breeding Bird Atlas (Hustings *et al.* 2002) – a new edition is currently being compiled (Schekkerman *et al.* 2012) – and that only estimate of the total continental godwit population size is from 2009 (Lourenço *et al.* 2010b). Given the rates of decline previously documented in continental godwits (Gill *et al.* 2007), updating these estimates is critical to ongoing conservation efforts.

To estimate the size of the Dutch breeding population of Black-tailed Godwits, we used birds marked on the breeding grounds in our core study area in south-west Friesland from 2004 onwards in combination with subsequent resightings of these individuals throughout The Netherlands to estimate their yearly survival probabilities. To couple these with estimates of the density of colour-marked individuals at sites with known proportions of continental and Icelandic godwits (Lopes *et al.* 2012), from 2007 onwards we counted marked and unmarked godwits at staging areas in Spain and Portugal. Finally, we used data gathered from individual godwits tagged with satellite transmitters at the same Iberian staging areas (e.g. Senner *et al.* 2015) to estimate the proportion of these godwits that bred in The Netherlands. Taken together, this allowed us to

generate precise annual estimates of the size of the Dutch-breeding populations of continental godwits and to assess trends that can be used to guide future godwit-related conservation and management activities.

METHODS

Study species and study areas

Continental Black-tailed godwits (hereafter: ‘godwits’, and ‘Icelandic godwits’ when referring to the Icelandic subspecies) are long-distance migrants that spend the nonbreeding season in West Africa and southern Spain (Hooijmeijer *et al.* 2013, Márquez-Ferrando *et al.* 2014). During northward migration, large numbers of godwits stage in Extremadura (39°01'N, 5°58'W) and Doñana Wetlands (37°06'N, 6°10'W), Spain, and coastal Portugal (38°55'N, 8°55'W), where they feed efficiently on leftover rice kernels on agricultural fields (Lourenço *et al.* 2010a, Lourenço & Piersma 2008, Santiago-Quesada *et al.* 2009). From early March



Black-tailed Godwits staging in Extremadura, Spain, flying up after foraging in a rice field near Yelbes (9 February 2016).

onwards, godwits arrive on their breeding grounds (Lourenço *et al.* 2011), where during the course of March and April they establish their territories and lay a clutch of four eggs.

Godwits are faithful to previous breeding sites and partners (Kentie *et al.* 2014). Their chicks are precocial and leave the nest within 24 hours after hatching (Schekkerman & Boele 2009). After the cessation of parental care, adult godwits leave The Netherlands from early June onwards (with unsuccessfully breeding individuals leaving earliest; Hooijmeijer *et al.* 2013). Juveniles prepare for migration slightly later, and often gather in flocks in July and even August (Schekkerman *et al.* 2014). Not all young godwits return to the breeding grounds in their second calendar year, and some arrive only after the breeding period, probably as prospectors (Kentie *et al.* 2014). However, it is not yet known whether these prospecting individuals are using staging areas during the same time period as do godwits that move on to the breeding grounds for the entire breeding season.

As part of a long-term demographic study, we marked individual godwits with colour rings in south-west Friesland, The Netherlands (52°55'N, 5°5'E; Kentie *et al.* 2014). Additional godwits were marked during the breeding season elsewhere in The Netherlands. Adults were captured on the nest and uniquely marked with four plastic colour rings, a coloured flag, and a numbered metal ring. Pre-fledging chicks captured at greater than 10 days of age were large enough to wear a colour-ring combination: these comprise 47% of the 3499 individuals used in the analysis (Table 1). Smaller chicks were given an engraved lime flag, but were not included in the analysis. See Kentie *et al.* (2013) for more details on capture procedures.

Density samples

Starting in 2007, we monitored rice fields in Extremadura, Spain, and the Tejo and Sado estuaries in Portugal for colour-marked godwits in January and February of each year (Lourenço *et al.* 2010b, Masero *et al.* 2011). From late winter 2010 we also began surveying Doñana National and Natural Park and its surrounding area in southern Spain for colour-marked godwits (Márquez-Ferrando *et al.* 2014). The numbers of godwits occurring here at these times of year are considerable: approximately 25,000 in Extremadura (Masero *et al.* 2011), 45,000 in Portugal (Lourenço *et al.* 2010b), and 28,000 in Doñana (Márquez-Ferrando *et al.* 2014). During the surveys we scanned the godwits whose legs were clearly visible. For each scan, we noted the number of godwits scanned and the number

of godwits with a colour-ring combination from our colour-marking scheme. If a flock was large, we sometimes made multiple scans of the flock, but from different vantage points to minimize the risk of noting individuals more than once.

From 2011 onwards, management in and around the Giganta rice fields in the Tejo area changed, leaving the fields inundated with water throughout the godwit staging period (J.A. Alves pers. comm.). These changes led to greater use of the area by Icelandic godwits. Such an influx likely 'diluted' the density estimates of marked continental godwits at the site, because it was not possible to exclude the Icelandic subspecies during the density measurements. For this reason, in our analyses we did not incorporate samples from the Tejo taken after 2011. As individuals with a colour-ring combination containing a lime flag included birds marked at the staging sites, and therefore consisted partly of Icelandic godwits, we excluded those as well.

Percentage of staging godwits breeding in The Netherlands

In 2013–2015 we fitted satellite transmitters to 60 adult female godwits that were captured in mist nets at nocturnal roosts within Spanish (Extremadura: $n = 45$) and Portuguese (Tejo: $n = 15$) staging sites (see Senner *et al.* 2015). We deployed solar-powered PTT-100s (9.5 g) from Microwave Technology Inc. that were attached with a leg-loop harness made of 2 mm nylon rope; in total, the attachment weighed c. 12 g for an average loading factor of $3.43 \pm 0.22\%$ (\pm SE) of an individual's mass at the time of capture. We specifically targeted large, female godwits, as they were best able to accommodate the size of the transmitter. The location of each individual during the breeding period was used to determine the proportion of godwits staging in Iberia that bred in The Netherlands.

Integrated model

We integrated the models estimating the number of marked birds alive with those estimating the density of marked birds during the staging period into one Bayesian model. To estimate the number of marked birds alive, we first estimated juvenile and adult survival with an age-dependent CJS based on resightings at the breeding grounds. Nearly all godwits survive the period between staging and breeding (Senner *et al.* in prep.), which justifies the use of yearly survival estimated during the breeding period. Because we suspected high trap-dependence when including all godwits marked in The Netherlands outside of our core godwit study area, we estimated survival only with

birds marked in our core study area in southwest Friesland, but included resightings of those individuals from across The Netherlands. Godwits equipped with satellite transmitters were excluded from this analysis because their survival rate may be lower than that of colour-marked individuals (Hooijmeijer *et al.* 2014, Senner *et al.* in prep.).

We first tested our mark-resighting data for Goodness-of-Fit in U-CARE (Choquet *et al.* 2009). Because we already included age structure within our model, we only tested for capture-heterogeneity (test2.ct; Pradel *et al.* 2005), which was significant ($\chi^2_9 = 17.8$, $P = 0.04$). We therefore included individual random effects for resighting probability p in our CJS model. We allowed p to vary between years and included an additive age effect with two age classes, because not all godwits return in their second calendar year (Kentie *et al.* 2014). For apparent survival (ϕ), we also included two age classes in the model and treated year as a random effect separately for each age class. By using year as a random effect, we were able to use the survival estimate of the final year of the study (Kéry & Schaub 2012). We believe that our estimate approaches true survival for the following reasons: godwits are highly site-faithful (Kentie *et al.* 2014, van den Brink *et al.* 2008), before and after breeding they forage and roost within or near our study area, and we used resightings from across The Netherlands.

Next, we used a binomial model to estimate a yearly proportion of marked individuals in flocks at each of the staging areas. This proportion was then

used to estimate the total population size using the equation $N_t \sim K_t / pband_t$, where N_t is the total population size at time t , K_t is the number of marked birds alive at time t , and $pband_t$ is the proportion of marked birds seen at time t . We used the number of colour-marked godwits per year, including godwits marked in The Netherlands outside our core study area, and multiplied these by our yearly survival rates to estimate the marked population in year t . Because not all second calendar year godwits may use the staging areas at the times we took our density samples, we corrected for the occurrence of young marked birds. To do so, we included within the Bayesian framework a binomial model which estimated the proportion of second calendar year birds resighted at the staging sites. Of chicks marked before 2015, we resighted 26 individuals between 2009 and 2016 which were in their second calendar year, and 42 which were in their third calendar year. We corrected for the mortality between second and third calendar year birds, by using the mean adult survival estimated by the model. Because of the necessity to correct for mortality with age, we abstained from using older age classes. Last, we estimated the population size of Dutch-breeding godwits by integrating the proportion of godwits with satellite tags that bred in The Netherlands, and corrected for the proportion of Icelandic godwits (6.5%, $n = 278$; Lopes *et al.* 2012), both included as binomial models, and assumed that the proportion of second calendar year godwits passing through the staging areas were breeding birds.

We ran JAGS (Plummer 2003) in the R statistical platform (v. 3.2.3; R Core Team 2014) with the R2jags package (Su & Yajima 2015) to perform Markov Chain Monte Carlo (MCMC) simulations for parameters estimation. We used uninformative priors for all parameters. We ran three parallel chains of 50,000 iterations with a burn-in of 10,000 and kept every 6th observation. We checked the R-hat for convergence of the model (in all but one cases < 1.01 , with the random part of year dependent survival equalling 1.05). Estimations are presented as the posterior means with a 95% credibility interval.

RESULTS

From 2004–2015 we colour-marked 3499 godwits, of which we used 1891 godwits marked in southwest Friesland to estimate yearly adult and juvenile survival probabilities (Table 1). Adult survival was high (0.94, 0.85–1.00 95% CI) in the first year of the study, and the

Table 1. Number of marked Continental Black-tailed Godwits with our colour ring scheme (excluding those with a lime flag colour), and number marked in southwest Friesland.

Year	Number ringed with our scheme		Number ringed in southwest Friesland	
	n adults	n young	n adults	n young
2004	66	28	66	24
2005	57	13	57	9
2006	104	55	46	22
2007	143	102	124	46
2008	131	112	115	68
2009	218	124	134	38
2010	201	147	117	53
2011	119	189	65	41
2012	233	181	181	58
2013	350	322	267	106
2014	241	363	162	92

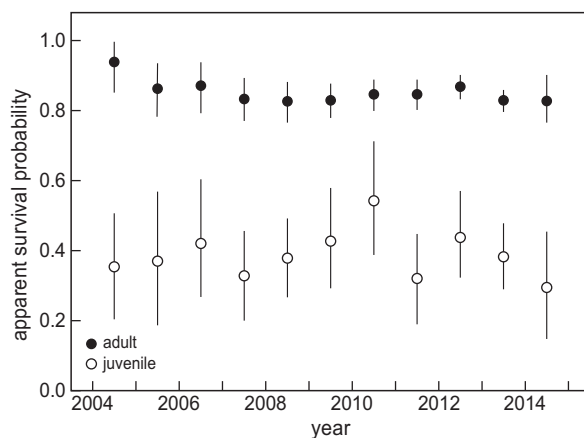


Figure 1. Apparent survival probability of adult and juvenile Black-tailed Godwits obtained from the CJS in the Bayesian model. Posterior means and 95% credibility intervals are shown.

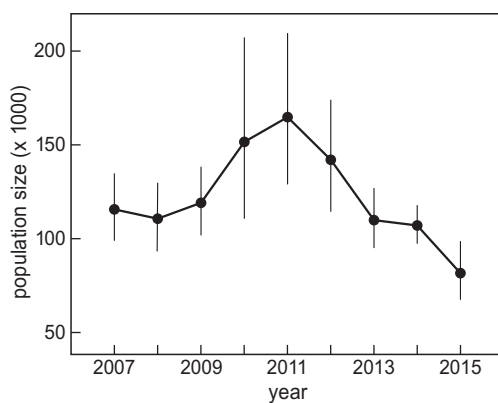


Figure 2. Population size of Black-tailed Godwits *Limosa limosa* of the East-Atlantic Flyway based on colour ring densities on the staging sites. These estimates include godwits from de Icelandic subspecies *Limosa limosa islandica* using Iberian rice fields, which we assume to be 6.5% of the population size.

mean adult survival over the whole period was 0.85 (0.84–0.87; Figure 1). Juvenile survival probability ranged between 0.30 in 2014 and 0.54 in 2010 with relatively large credibility intervals (Figure 1), and the mean juvenile survival was 0.34 (0.33–0.45). The random year effect of juvenile survival was $SD = 0.47$ (0.09–1.00), and the random year effect of adult survival was $SD = 2.71$ (1.71–4.31). The averaged mean posterior resighting probability was 0.82 (0.80–0.85) for adults and 0.30 (0.21–0.39) for second calendar year birds (Table S1). The individual resighting random effect was $SD = 1.34$ (1.12–1.56). For all parameter estimates see the Supplementary Material.

Of the 60 godwits fitted with satellite transmitters at the Iberian staging sites, 13 transmitters or godwits died before migration or did not migrate further, and 39 females established breeding territories in The Netherlands. Moreover, two individuals appeared to be Icelandic godwits. Excluding these two, 87% (75–95%) of the tagged birds were Dutch breeding birds.

In total, we checked 420,206 godwits for colour-rings at Spanish and Portuguese staging sites (Table 2). The density of colour-ringed godwits increased from 1/500 godwits in 2007 to 1/77 godwits in 2015. The fraction of godwits in their second calendar year passing through the staging sites in January and February was 0.53 (0.36–0.74). The estimated population size of godwits, including Icelandic godwits using the Iberian rice fields, increased from 115,305 (98,304–134,265) individuals in 2007 to 164,010 (128,479–209,253) in 2011, before decreasing to 81,793 (66,973–98,309) in 2015 (Figure 2). The annual growth rate from 2007–2015 was 3.7%, with the fastest decline occurring from 2011–2015 at 6.3% per year. The Dutch breeding population in 2015 was estimated at 33,140 (26,031–41,303) breeding pairs.

Table 2. Number of Continental Black-tailed Godwits checked for colour rings at the staging sites in Spain and Portugal.

Year	Total birds checked
2007	136,623
2008	65,222
2009	70,196
2010	11,030
2011	16,395
2012	17,914
2013	24,952
2014	67,638
2015	10,236

DISCUSSION

We estimated the total population size of Continental Black-tailed Godwits in the East-Atlantic Flyway, by estimating survival probabilities of colour-marked individuals and then using the density of surviving colour-marked individuals observed at staging areas in Spain and Portugal. We could correct for the fraction of the *islandica* subspecies, which are staging on the Iberian rice fields and fish ponds, within the model. Although we found that 87% of continental godwits staging in Iberia breed in The Netherlands and that adult survival was relatively high from 2007–2015, during the course of our study, the Dutch-breeding population declined

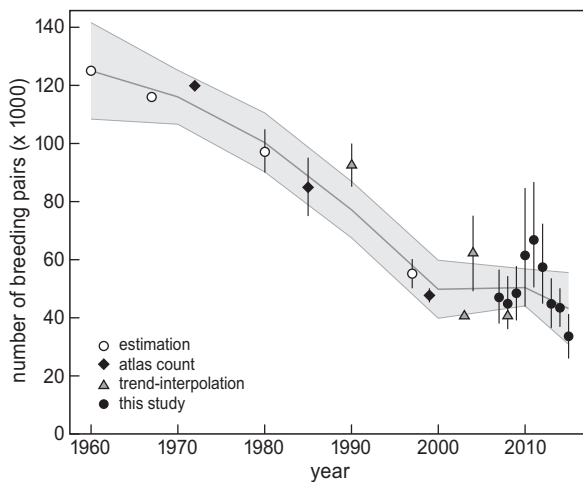


Figure 3. Number of breeding pairs of Continental Black-tailed Godwits in The Netherlands, based on estimations, atlas counts, interpolations, and this study (references: Bekhuis *et al.* 1987, Bijlsma *et al.* 2001, Hustings *et al.* 2002, Mulder 1972, Osieck & Hustings 1994, Teixeira 1979, Teunissen *et al.* 2005, Teunissen *et al.* 2012, van Dijk *et al.* 2005). When available, minimum and maximum estimation or 95% CI are plotted. The lines are fitted with a local polynomial regression fitting (LOESS) in R, and represent the mean and the 95% CI of the point estimates of the number of breeding pairs.

by 3.7% per year, and this decline accelerated from 2011–2015 to a rate of 6.3% per year. In total, we estimated that nearly 33,000 pairs of godwits currently breed in The Netherlands, which is less than one third of the number of pairs that bred there in the 1970s (Figure 3). In combination with the already steady declines that have occurred over the past four decades, these recent, rapid declines suggest that drastic measures are necessary to stop the disappearance of one of the most iconic meadow bird species breeding in The Netherlands.

One of the findings in our study is that in the midst of a steady population decline, the size of the breeding population actually increased from 2009 to 2011, before again declining from 2011–2015. The causes of this increase could potentially result from two separate processes. On the one hand, the increase might have been caused by an increasing proportion of Icelandic godwits using Iberian rice fields, as the Icelandic godwit population has steadily grown over the past three decades (Gill *et al.* 2007). We assumed a constant proportion of Icelandic godwits of 6.5% at Iberian staging sites based on a DNA study of godwits caught in the rice fields of Extremadura between 2005 and 2008 (Lopes *et al.* 2012). That study found no increase in the proportion of Icelandic godwits, and the percentage

they found resembled the proportion of Icelandic godwits in rice fields estimated on the basis of ring resightings (10%; Alves *et al.* 2010, 7.7%; Masero *et al.* 2011). Two of the godwits we fitted with satellite transmitters appeared to be Icelandic godwits (4.3%, 1.2–14.2% CI), however, we targeted continental godwits thus this proportion will be too low. However, if the peak in godwit numbers in 2011 was only caused by an increase in the proportion of Icelandic godwits at Iberian staging sites, their proportion should have been 30% or higher. This we consider unlikely.

The increase did correspond with high reproductive success in at least part of the population's breeding range in 2010 (Kentie 2015). Nevertheless, if the population increase was explained entirely by an increase in godwit reproduction, godwit pairs would have been required to produce on average 0.61 chicks per year that survived to become breeders per year in 2009 and 2010. Previous studies have found that godwit nest success averages c. 50% (Kentie *et al.* 2015), with a maximum of 69% on herb-rich meadows in 2008 (Kentie 2015), meaning that in an average year 30% of hatched chicks would have had to survive to the next year, or 22% in a year with high nest survival. The highest first-year survival, from nestling to second calendar year bird, in our research area was 24% (Kentie 2015), which occurred in herb-rich meadows in 2010. However, in the grassland monocultures, where the majority of godwits breed in The Netherlands, the highest first-year survival was 14%. After 2011, the decline in godwit numbers happened so rapidly that only complete reproductive failures would make this possible. We therefore conclude that a combination of changes in the proportion of Icelandic godwits and variation in continental godwit reproductive success is likely to explain the temporary increase, and note that the confidence intervals for the population estimates between 2010 and 2012 were rather large.

We estimate that there were 33,000 breeding pairs in The Netherlands in 2015. This estimate was based on two other estimates. First, with information gathered from godwits equipped with satellite tags at Iberian staging sites, we estimated that 87% of the continental population breeds in The Netherlands. This percentage falls within the range of previous findings, which were derived from comparisons of country-wide counts (Table 3). Second, we estimated that adult survival was around 85% throughout much of our study, which corresponds closely with previous estimates from other Dutch study areas (Roodbergen *et al.* 2008). Despite the close correspondence of these underlying estimates with those from other published

Table 3. Percentage of the East Atlantic Flyway Continental Black-tailed Godwits breeding in The Netherlands. To define the flyway population, we included godwits breeding in Belgium, United Kingdom, Germany, France, Spain, Italy, Luxembourg, Austria, Sweden and The Netherlands.

Year	Percentage	Source
1970	91%	Mulder (1972)
1985	91%	Piersma (1986)
1990	90%	Hötter <i>et al.</i> (1991)
1995	85%	Beintema <i>et al.</i> (1995)
2000	84%	Thorup (2006)
2015	87%	this study

studies, as well as the increased precision of our statistical estimates in relation to previous efforts, the upper and lower 95% CI of our estimate ranged from 26,000 to 41,000, indicating that our estimates still include some uncertainty.

More generally, with the Bayesian mark-resighting methodology presented here, we were able to estimate the numbers of Black-tailed Godwits using staging sites in Iberia with relatively tight confidence limits in most years. The benefit of this method is that the total flyway population can be estimated without the necessity of surveying individuals across the entire breeding range of Continental godwits. For populations that are not easily counted across breeding areas, but congregate at wintering or staging sites, such as many wader species, this method may thus have considerable advantages (Spaans *et al.* 2011). Moreover, when operating a demographic monitoring programme, this method makes it possible to track the population size on a yearly basis with relatively low additional effort, especially when compared with such intensive undertakings as breeding bird atlases. Nonetheless, there are potential drawbacks: for instance, our estimates of the Continental Black-tailed Godwit population would have been more precise if continental and Icelandic godwits did not mix in Iberia, or if we had temporal estimates of the mixture of continental and Icelandic godwits for the whole study period.

Conclusion

With a breeding population of 33,000 pairs in 2015, the Dutch godwit population has plummeted by nearly 75% since the first nation-wide estimate of 120,000 pairs in 1967 (Mulder 1972, Figure 3). In spite of this, the agricultural grasslands of The Netherlands remain the single most important stronghold for breeding Continental Black-tailed Godwits in the East Atlantic

Flyway population — they breed nowhere else in such large numbers (Piersma 1986, Thorup 2006) and are declining just as rapidly in most other countries in which they still breed (Gill *et al.* 2007, Thorup 2006). Furthermore, previous work has identified low levels of reproductive success to be the single most important factor driving the decline (Schekkerman *et al.* 2008, Kentie *et al.* 2013, Roodbergen *et al.* 2012), which shows that factors operating in The Netherlands are largely responsible for the declines that have occurred thus far. Although enormous amounts of money and effort have been expended to conserve continental godwits (Kleijn *et al.* 2010), our findings make clear that these have been ineffective or insufficient. Initiatives leading to drastically improved management are thus necessary to preserve one of the most iconic species of the Dutch countryside before it becomes relegated to a few small corners of its former range.

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SAMENVATTING

Hoewel we weten dat het aantal Grutto's *Limosa limosa limosa* in West-Europa de laatste 50 jaar hard achteruit is gegaan, stamt de laatste Nederlandse populatieschatting nog uit 1999. In dit artikel presenteren we nieuwe populatieschattingen voor de gehele continentale gruttopopulatie van West-Europa en voor de Nederlandse broedpopulatie afzonderlijk. Deze schattingen laten zien dat de Nederlandse populatie tussen 2007 en 2015 met 3,7% per jaar is afgenomen van 47.000 (95%-betrouwbaarheidsinterval: 38.000–56.000) tot 33.000 (26.000 – 41.000) broedparen in 2015. Om tot deze schatting te komen, hebben we gegevens afkomstig van Grutto's met kleuringen en zendertjes geïntegreerd in één analyse in een Bayesiaans statistisch model. Allereerst hebben we voor 2007 tot en met 2015 door middel van een *mark-recapture* overlevingsanalyse het aantal nog in leven zijnde Grutto's met kleurringen geschat. Daarna hebben we op pleisterplaatsen in Spanje en Portugal

tijdens de voorjaartrek elk jaar de fractie Grutto's met kleurringen geschat. We hebben daarbij gecorrigeerd voor het percentage IJslandse Grutto's *Limosa l. islandica* (waarvan de aantallen toenemen) dat gebruikmaakt van dezelfde pleisterplaatsen. Door deze getallen te combineren kon een populatieschatting worden gemaakt en kon tevens de nauwkeurigheid van die schatting worden aangegeven met betrouwbaarheidsintervallen. Met behulp van Grutto's die op de pleisterplaatsen werden uitgerust met satellietzenders, kwamen we erachter dat 87% (75–95%) van de West-Europese populatie in Nederland broedt. Deze nieuwe schatting laat bovendien zien dat het aantal broedparen in Nederland vanaf 1967 met 75% is afgenomen en dat de snelheid van de afname in de periode 2011–2015 sneller ging dan in de vier jaar daarvoor. We laten met deze analyse zien dat met behulp van een intensief regionaal ring- en monitoringprogramma in combinatie met het verzamelen van terugmeldingen van geringde vogels elders, betrouwbare schattingen kunnen worden gemaakt van populaties op de schaal van een hele trekroute. Aangezien eerder onderzoek aantoonde dat het lage broedsucces de oorzaak van de achteruitgang is, heeft Nederland als het belangrijkste broedgebied voor West-Europese Grutto's de grootste verantwoordelijkheid binnen Europa voor het in stand houden van deze populatie.

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SUPPLEMENTARY MATERIAL

Table S1. Parameter estimates (mean, standard deviation (SD), credibility interval (2.5% CI and 97.5% CI) and R-hat) from the Bayesian population model.

Parameter*	posterior mean	SD	2.5% CI	97.5% CI	R-hat
phi adult 2004–2005	0.939	0.038	0.854	0.997	1.001
phi adult 2005–2006	0.865	0.038	0.786	0.936	1.001
phi adult 2006–2007	0.871	0.037	0.797	0.940	1.001
phi adult 2007–2008	0.834	0.032	0.770	0.894	1.001
phi adult 2008–2009	0.826	0.029	0.767	0.883	1.001
phi adult 2009–2010	0.830	0.025	0.780	0.878	1.001
phi adult 2010–2011	0.847	0.023	0.800	0.890	1.001
phi adult 2011–2012	0.848	0.022	0.803	0.890	1.001
phi adult 2012–2013	0.869	0.018	0.833	0.903	1.001
phi adult 2013–2014	0.831	0.016	0.798	0.862	1.001
phi adult 2014–2015	0.828	0.036	0.764	0.904	1.004
phi juv 2004–2005	0.355	0.076	0.205	0.505	1.002
phi juv 2005–2006	0.370	0.095	0.181	0.565	1.001
phi juv 2006–2007	0.421	0.083	0.268	0.602	1.001
phi juv 2007–2008	0.330	0.068	0.199	0.461	1.003
phi juv 2008–2009	0.379	0.058	0.268	0.496	1.001
phi juv 2009–2010	0.427	0.071	0.296	0.578	1.002
phi juv 2010–2011	0.543	0.084	0.391	0.714	1.002
phi juv 2011–2012	0.323	0.069	0.188	0.454	1.001
phi juv 2012–2013	0.440	0.062	0.327	0.568	1.001
phi juv 2013–2014	0.383	0.048	0.29	0.479	1.002
phi juv 2014–2015	0.298	0.085	0.144	0.461	1.006
p adult 2005	0.901	0.038	0.813	0.960	1.001
p adult 2006	0.858	0.039	0.772	0.923	1.001
p adult 2007	0.816	0.040	0.730	0.887	1.001
p adult 2008	0.789	0.035	0.715	0.853	1.001
p adult 2009	0.717	0.035	0.646	0.782	1.001
p adult 2010	0.795	0.027	0.739	0.844	1.001
p adult 2011	0.691	0.030	0.630	0.749	1.001
p adult 2012	0.732	0.028	0.676	0.785	1.001
p adult 2013	0.871	0.017	0.836	0.903	1.001
p adult 2014	0.907	0.014	0.878	0.932	1.002
p adult 2015	0.957	0.029	0.891	1.000	1.005
p 2 nd calendar year 2005	0.411	0.110	0.215	0.638	1.001
p 2 nd calendar year 2006	0.311	0.081	0.172	0.485	1.001
p 2 nd calendar year 2007	0.248	0.064	0.141	0.388	1.001
p 2 nd calendar year 2008	0.215	0.051	0.128	0.327	1.001
p 2 nd calendar year 2009	0.156	0.037	0.093	0.237	1.001
p 2 nd calendar year 2010	0.219	0.047	0.137	0.320	1.001
p 2 nd calendar year 2011	0.140	0.032	0.086	0.209	1.001
p 2 nd calendar year 2012	0.165	0.038	0.101	0.247	1.001
p 2 nd calendar year 2013	0.327	0.058	0.221	0.449	1.001
p 2 nd calendar year 2014	0.412	0.065	0.290	0.540	1.002
p 2 nd calendar year 2015	0.648	0.179	0.348	0.997	1.005
prop marked birds 2007	0.002	0.000	0.002	0.002	1.001
prop marked birds 2008	0.003	0.000	0.003	0.003	1.001
prop marked birds 2009	0.003	0.000	0.003	0.004	1.001
prop marked birds 2010	0.004	0.001	0.003	0.005	1.001

Table S1. Continued

Parameter*	posterior mean	SD	2.5% CI	97.5% CI	R-hat
prop marked birds 2011	0.004	0.001	0.003	0.005	1.001
prop marked birds 2012	0.005	0.001	0.004	0.007	1.001
prop marked birds 2013	0.009	0.001	0.007	0.010	1.001
prop marked birds 2014	0.011	0.000	0.010	0.012	1.001
prop marked birds 2015	0.016	0.001	0.013	0.018	1.001
prop marked birds 2016	0.013	0.001	0.011	0.016	1.001
prop 2 nd calendar year birds	0.533	0.097	0.361	0.742	1.001
prop Icelandic Godwits	0.065	0.015	0.039	0.096	1.001
prop Dutch Godwits	0.866	0.050	0.753	0.948	1.001
total population 2007	115305	9162	98304	134265	1.001
total population 2008	109806	9467	92480	129539	1.001
total population 2009	118629	9336	101376	138187	1.001
total population 2010	151309	24363	110442	205736	1.001
total population 2011	164010	20735	128479	209253	1.001
total population 2012	141498	15179	114424	174234	1.001
total population 2013	109621	8356	94275	127185	1.001
total population 2014	106690	5167	96944	117249	1.001
total population 2015	81793	8251	66973	99309	1.003
breeding pair Netherlands 2007	46717	4650	37922	56103	1.001
breeding pair Netherlands 2008	44490	4685	35800	54168	1.001
breeding pair Netherlands 2009	48066	4785	39026	57679	1.001
breeding pair Netherlands 2010	61304	10546	43431	84692	1.001
breeding pair Netherlands 2011	66451	9320	50376	86506	1.001
breeding pair Netherlands 2012	57332	7067	44572	72306	1.001
breeding pair Netherlands 2013	44415	4319	36264	53188	1.001
breeding pair Netherlands 2014	43228	3352	36461	49724	1.001
breeding pair Netherlands 2015	33140	3894	26031	41303	1.002
mean <i>p</i> adults	0.821	0.013	0.795	0.847	1.001
mean <i>p</i> 2 nd calendar year	0.296	0.047	0.208	0.392	1.002
mean <i>phi</i> adults	0.854	0.008	0.838	0.869	1.001
mean <i>phi</i> juv	0.388	0.029	0.333	0.448	1.003
random effect <i>phi</i> year adults	2.706	0.659	1.705	4.312	1.001
random effect <i>phi</i> year juv	0.468	0.231	0.089	1.002	1.045
random effect <i>p</i> individual	1.335	0.112	1.122	1.560	1.002
Deviance	9183.043	142.312	8896.685	9449.126	1.003

* *p* is resighting probability, *phi* is apparent survival probability, *prop* is short for proportion, *juv* is short for juvenile.