

Estimating flight ranges to unravel migratory strategies: spring migration of continental Black-tailed Godwits *Limosa limosa limosa*

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Summary

Mapping migratory routes and the distribution of species during migration requires information collected over large scales (e.g. survey data), or the ability to follow specific movements (e.g. using tracking devices), which is often limited to a few individuals. For endangered species, such techniques may be impractical, but developments in flight range modelling allow inferences about migratory routes and potential site occupancy, given a few morphological parameters. We modelled flight range in a rapidly declining population of continental Black-tailed Godwits *Limosa limosa limosa* departing from a staging site in Iberia during spring migration and found that the vast majority of godwits are able to reach the breeding grounds in a single flight. Contrary to the traditional use of staging sites in France (and Morocco), godwits currently staging in Iberia are predicted to fly directly to The Netherlands and be present at breeding locations earlier than previously expected and observed. Despite harbouring approximately 75% of the total population during spring migration, Iberian staging sites currently lack any legal protection. Our example of the Black-tailed Godwit illustrates the potential of this approach to identify migration strategies and locate staging sites for species of conservation concern for which such information may be virtually absent.

Introduction

Migratory species are likely to select their routes and migration strategies in order to reach their destination in the best condition possible and at the optimal time (Alerstam and Lindström 1990), but several factors can constrain their options. Crossing large barriers (e.g. mountain ranges, water-bodies, deserts), as well as the location of suitable habitats, often results in detours from the shortest route (Moreau 1972, Berthold 1993). For species that undertake long-distance non-stop flights, the maximum flight range can also be an important constraint. Flight range depends on wing characteristics, but also on the amount of fuel available, which is mainly stored as fat and, to a lesser extent, protein (Pennycuik 2008). If these parameters are known, flight range can now be predicted accurately (Alves *et al.* 2012). Although morphological parameters, such as wing shape, vary little among individual adults of the same species (Pennycuik 2008), the amount of fuel may show considerable individual variation, as it depends on migration strategy (e.g. long or short flight; Piersma 1987) and on resource availability and quality as well as foraging rates (Atkinson *et al.* 2007).

The distance an individual is able to cover in a single flight from a given starting point will determine whether it is able to arrive at its final migratory destination or needs to use further staging areas. Consequently, the estimation of flight ranges on a known route (i.e. heading) can be used to predict whether non-stop flights to a destination are possible, or whether additional

staging is required and also predict the possible locations of such refuelling sites. Despite the advent of remote tracking technology that allows detailed tracking of individual migratory flights, the estimation of flight range can be a powerful tool to unravel migratory strategies for species that are either too small for such devices and/or that urgently need staging sites to be identified for conservation purposes.

In this study, we estimate the flight range of individuals from a rapidly declining population of Black-tailed Godwit *Limosa limosa limosa* during the final step of their northward migration between West Africa and The Netherlands. The western population of continental Black-tailed Godwits (hereafter, godwit) has declined by c.50% since the 1980s (Birdlife International 2004). Agricultural intensification on the breeding grounds and habitat change at non-breeding sites have recently been identified as the most influential factors in the decline (Gill *et al.* 2007, Zwarts *et al.* 2009). In order to tackle this decline a list of key research gaps was identified, highlighting the need to improve the understanding of the location, timing and duration of use of passage sites in Europe (Iberia) and Africa (Gill *et al.* 2007). After staging in Iberia during spring migration, godwits leave for The Netherlands about two weeks before arriving at the breeding sites (Wymenga and Sikkema 2011). The location of a large portion of these individuals (38–44%; Lourenço *et al.* 2010) during those weeks is currently uncertain (Kuijper *et al.* 2006), which prevents targeted conservation measures during this period of the annual cycle. The migratory flight (c.1,900 km) is estimated to be feasible in less than 30 hours, so the location of many godwits between leaving Iberia and reaching The Netherlands remains an unsolved issue (Lourenço *et al.* 2011). Two possible explanations have been suggested (Kuijper *et al.* 2006): (1) godwits stage in France *en route* to the Netherlands, but in small flocks with high levels of turnover, and/or in sites not covered during counts; (2) godwits move directly to The Netherlands but are missed early in the season. We use flight range models to estimate the proportion of godwits that are predicted to require further staging after departing from Iberia in order to investigate the likelihood of these two possibilities. We aim to investigate the potential use of sites by godwits during spring migration in order to target conservation measures for this population during this stage of the annual cycle.

Methods

Sampling godwits departing from Iberia

The vast majority of continental godwits migrate to core non-breeding areas in West Africa (Zwarts *et al.* 2009) before moving north to Iberia as early as December (Alves *et al.* 2010). In Iberia they make a prolonged stop-over between late December and early March (Lourenço *et al.* 2010), feeding almost entirely on rice-fields (Alves *et al.* 2010). Godwits were mist-netted in the rice-fields of Samora Correia (38°56'N, 8°50'W) in the vicinity of the Tagus estuary, just prior to departure, between 19 February and 4 March 2008–2010. In 2008, most godwits had left the rice-fields by 1 March (with a few staying until 7 March), and in 2009 and 2010 most had left by 27 February (P. Lourenço pers. obs.). All captured birds ($n = 88$) were weighed to the nearest gram and the exposed culmen, wing and tarsus length were measured to the nearest millimetre. For parameterisation of the flight model (see below), the wing spans of 29 individuals were measured to the nearest millimetre and tracings of wing shape were also taken in order to calculate wing area of 16 individuals, following Pennycuik (2008).

Godwits are sexually size dimorphic and females have duller breeding plumage than males (Shroeder *et al.* 2008). During staging in Iberia most individuals have moulted extensively into breeding plumage (P. Lourenço unpubl. data), hence sex was assigned based on plumage (resulting in bill lengths for all males ≤ 98.5 mm and all females ≥ 101 mm). In addition, four individuals (one female and three males) were identified as juveniles based on plumage characteristics and were excluded from subsequent analysis because not all juveniles migrate to the breeding grounds (Zwarts *et al.* 2009).

Estimating flight range of Godwits departing from Iberia

Flight program (Version 1.21; Pennycuik 2008) was used to model individual flight ranges from measurements of wing shape and body mass components. Average wing measurements were inputted separately for each sex given the significant differences in wing span ($U_{28} = 30.5$, $Z = -3.17$, $P < 0.01$) and wing area ($U_{15} = 6.0$, $Z = -2.44$, $P = 0.015$; Table 1). Flight muscle mass has previously been measured for godwits of the Icelandic subspecies *Limosa limosa islandica* in Iberia about to undertake the same migratory flight (from Portugal to The Netherlands; Alves *et al.* 2012) so we used the same values for continental godwits. The estimation of fat fraction (in relation to total body mass) was done following Pennycuik (2008) and, similarly to Alves (*et al.* 2012), by establishing a relationship between body mass and fat fraction using a large sample of body mass measurements for this population: 371 males and 349 females. Several model runs were executed with the heaviest individual in the sample (male = 364 g, female = 404 g) in order to test a range of values for fat fraction, attained from previously published studies (Alves *et al.* 2012). The relationship between body mass and fat fraction was established when the initial fat fraction considered from that range would allow the heaviest individual to terminate a simulated flight (i.e. without a set distance) with the body mass of the lightest individual ever recorded (male = 213 g, female = 234 g). Measurements of body mass were amassed from captures of breeding birds in The Netherlands (details in Shroeder *et al.* 2008) and departing birds captured in Iberia during this study, when both the heaviest male and female were recorded.

All simulations were run in Flight 1.21 (Pennycuik 2008) using default parameters as described by Alves (*et al.* 2012), with flight mode set to continuous flapping, speed control set to standard, departing altitude set at 0 m above sea level and cruising altitude set at 2,000 m.

Distance between the departure location of the Tagus rice-fields and a core breeding location in the Netherlands, the Workumerwaard (52°59'N, 5°25'E), was measured using the distance tool in Google Earth Version 5.1 (earth.google.com), assuming that the flight route follows great circle lines. This breeding site was selected as > 100 godwits colour-ringed there have been recorded staging on the Tagus rice-fields (Lourenço *et al.* 2011). The mapping of flight ranges was executed in ArcGIS 10 (ESRI).

Results

All females and almost every male godwit sampled had sufficient body mass to fly non-stop c.1,900 km or more and therefore to reach the breeding grounds in The Netherlands in one flight (Figure 1). The lightest female was estimated to be able to fly a total distance of 2,161 km, and approximately 90% of the males were also predicted to be able to reach the breeding site in a single flight (Figure 1). Of those lightest five males, only three (c.6%) were estimated to be unable to reach the Netherlands. The remaining two (c.4%) were predicted to cover a total distance of c.1,750 km or more, which would equate to the northern area of the Dutch delta, an alternative breeding location. The lightest male was predicted to cover a total distance of c.1,350 km,

Table 1. Wing, muscle and fat parameters of male and female continental Black-tailed Godwits used in Flight Version 1.21 to estimate flight range. Fat fraction is indicated for the heaviest individual.

	Female			Male		
	Mean	SD	N	Mean	SD	N
Wing span (m)	0.726	0.021	12	0.699	0.013	17
Wing area (m ²)	0.0767	0.0031	5	0.069	0.0046	11
Aspect ratio	6.87	-	-	7.08	-	-
Muscle fraction	0.206	0.005	3	0.214	-	1
Fat fraction	0.306	-	1	0.300	-	1

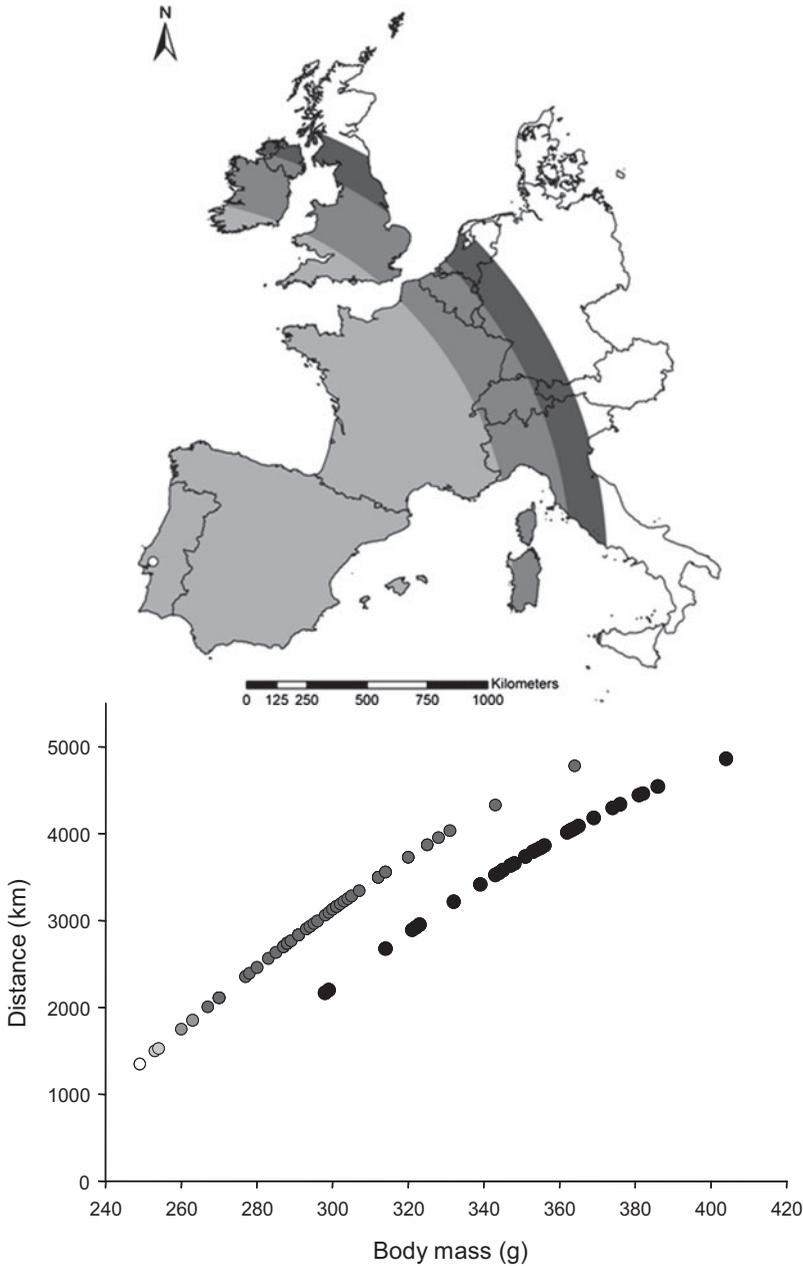


Figure 1. Predicted non-stop flight range for both sexes (graph) and male (map) Continental Black-tailed Godwits departing from a major Iberian stop-over site, the Tagus rice-fields (white circle). All females (black) are predicted to reach the breeding grounds in The Netherlands in one flight and flight ranges are therefore not mapped. The lightest male (open circle - not mapped) is predicted to fly only 1,348 km non-stop, whereas 98% of males (light grey), 94% (grey) and 90% (dark grey) are predicted to reach the limit of shaded areas or beyond.

which is insufficient to reach the core breeding locations in the Netherlands. However, this male was among the very early captures (weighed on 20 February) and possibly could have still been in the process of fattening. Even without additional fattening, this individual, as well as the following two lighter males, were predicted to reach the French coast of the English Channel, an area with suitable habitats for refuelling, and would not therefore have been likely to require a stop-over at traditional sites on the Atlantic coast of France.

Discussion

Of 84 adult godwits caught and weighed just prior to departure on the Tagus rice-fields, all except three males caught early in the departure period were predicted to be capable of reaching the breeding grounds in The Netherlands in a single flight. This evidence suggests that only a very small percentage of godwits require an obligatory second staging event in order to refuel during northward migration. Indeed, from a total of 478 individually colour-ringed godwits recorded in Iberia between 2005 and 2009, only $1.4\% \pm 0.7$ (\pm SE) have on average, been subsequently recorded in France during spring of the same year (P. Lourenço unpubl. data). Although resighting effort on the French Atlantic coast is lower than in Iberia, these sites have been regularly surveyed for marked godwits since 2007. An alternative reason for a second staging event could be unfavourable winds experienced *en route* or conditions at the breeding grounds. However, it should be expected that godwits time their departure under favourable wind conditions and given the relatively short flight time to reach a suitable location in France (c.14 hours), similar wind conditions should be expected as these are correlated with those encountered up to 18 hours further along this same route (Shamoun-Baranes *et al.* 2010). Likewise, weather systems in the French Atlantic coast and the Wadden Sea are typically correlated, particularly in exceptionally cold springs (Hörker 2002). Hence, unfavourable environmental conditions would likely occur simultaneously at both locations.

As most godwits sampled just prior to departure were predicted to reach The Netherlands in one single flight, the apparent approximately two-week gap between departure from Iberia and median arrival in The Netherlands seems unlikely to be due to a second staging event on the Atlantic coast of France. The alternative explanation is that continental godwits may arrive in The Netherlands but avoid detection by surveys at that time of year, either because not all major Dutch arrival locations are covered (Kuijper *et al.* 2006), or because arriving birds are spread over many different locations in small flocks. Given that a considerable number of sightings of colour-ringed individuals on the breeding areas only occur after 20 March (Lourenço *et al.* 2011), this suggests that godwits might not go straight to territories upon arrival in the Netherlands, but rather use arrival locations prior to returning to territories, as do Icelandic godwits (Gunnarsson *et al.* 2006). Despite the individual variation in annual schedules (Lourenço *et al.* 2011), the number of individuals present at arrival sites scattered across the breeding grounds is likely to be a better descriptor of the use of sites by continental godwits during this period.

Since the 1980s, traditional staging sites along the French Atlantic coast and particularly in Morocco have become less important to godwits during northward migration (Kuijper *et al.* 2006, Gill *et al.* 2007) and currently host declining numbers (Zwarts *et al.* 2009). The causes of this reduced use of French staging sites during spring are unknown but might be linked to habitat change, e.g. conversion of wetlands into agricultural crops (Gill *et al.* 2007). Alternatively, this could be due to the reduced use of Moroccan sites and increased use of Iberian sites. Indeed, the Tagus and Sado rice-fields in Portugal and Extremadura and Coto de Doñana in Spain harbour c.75% of the current population (Kuijper *et al.* 2006), although currently lacking legal protection. From a migratory perspective, making a single refuelling stop-over in Iberia rather than two (Morocco and France), is likely to reduce the total time of migration and therefore allow faster migration speed. The use of sites in Iberia appears to be linked to the development of large rice-field areas that form suitable habitat for refuelling godwits

(Sánchez-Guzmán *et al.* 2007). If godwits depart from non-breeding sites (e.g. rice-fields of Rio Mansôa in Guinea-Bissau) in good condition (similar to departure from the Tagus) and fly directly to an Iberian staging site (e.g. Tagus rice-fields) instead of using the major traditional staging site in Morocco (Merja Zerga), only 500 km have to be added on to a total flight of c. 3,200 km, a distance which would be within the range of most individuals (see graph in Figure 1).

The analysis of flight ranges for threatened migratory species can be used as a tool to predict the need and identity of possible locations of staging sites between the breeding and wintering areas. One potential such case is the Spoon-billed Sandpiper *Eurynorhynchus pygmeus* that breeds in north-east Russia and has core wintering locations in Myanmar, but staging sites are virtually unknown (Zöckler *et al.* 2010). Given that in both seasons individuals are caught (by scientists or hunters), the required parameterisation values are possible to obtain, making it feasible to model flight range and therefore map potential staging sites (N. Clark *in litt.* 2013).

Conservation actions and recommendations

Godwits staging in Iberian rice-fields are likely to fly directly to The Netherlands. We therefore believe that they will be present in that region (including Belgium) as early as late February and early March. It is likely that these individuals are scattered in small flocks and use many locations across the region, including some that might not be used for breeding, thus making it difficult to assess the total numbers present. Coordinated surveys and counts during this time of year would solve this issue and also indicate the location of key pre-breeding sites across the region. Some of these sites have already been identified, as large flocks are present in spring, e.g. Landje van Geijsel (52°17'N, 4°55'E). This site regularly holds 1,000–3,000 roosting godwits in early March but in very cold springs, during which fewer sites are suitable, it is known to hold 5,000–9,000 godwits (A. Duijnhouwer *in litt.* 2013). Given that turnover is likely to be high in such sites (but possible to estimate given the extensive marking and tracking programme currently developed for this population), knowing their location and extent of use would aid development of targeted conservation and management actions for these sites, which might serve a high proportion of individuals.

Vast numbers of godwits stage in Iberian rice-fields that currently lack any form of protection. These areas allow godwits to undertake a single stop-over in spring, instead of two (in Morocco and France), which was a likely strategy before the creation of the rice-fields. Given that rice production is subject to market fluctuations and that changes in this crop are known to affect birds (see review in Sutherland *et al.* 2012), the permanence of this habitat, or ecologically similar wetlands, should be secured, because natural wetlands in the region have diminished following agricultural and urban development (Dias 2009) and are currently used by fewer numbers of waders (e.g. Catry *et al.* 2011). The conservation of rice-fields and the restoration of the remaining natural wetlands in Iberia should be a priority as they are critical for a large number of wetland species. Although the creation of legislation for the protection and management of rice-fields has been identified as a high priority in the species action plan (Jensen *et al.* 2008), the Iberian rice-fields remain largely unprotected. Both Portugal and Spain have adopted this action plan and should act upon it, thus promoting the conservation of several other species (Lourenço and Piersma 2009). The inclusion of rice-fields that exist in the vicinity of already established protected areas (e.g. Tagus and Sado Nature Reserves in Portugal and Doñana National Park in Spain) as well as the inclusion of farming practices that make godwit conservation compatible with rice production (see Lourenço and Piersma 2008 for details) under Agri-Environmental Schemes (and CAP) would address the conservation issues faced by this population during spring migration.

Lastly, given that unpredictable weather events can force the use of secondary stop-over sites by waders in some years (Leyrer *et al.* 2009), the restoration of formerly used staging sites in France and Morocco should also be considered, as recommended in the species action

plan (Jensen *et al.* 2008). These actions would secure the conservation of the migratory route of this rapidly declining population, as well as halting habitat loss and degradation for several other species currently using rice-fields (Elphick *et al.* 2010) and natural wetlands in the same areas.

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