

Research



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Evolutionary biology

Generational shift in spring staging site use by a long-distance migratory bird

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In response to environmental change, species have been observed altering their migratory behaviours. Few studies, however, have been able to determine whether these alterations resulted from inherited, plastic or flexible changes. Here, we present a unique observation of a rapid population-level shift in migratory routes—over 300 km from Spain to Portugal—by continental black-tailed godwits *Limosa limosa limosa*. This shift did not result from adult godwits changing staging sites, as adult site use was highly consistent. Rather, the shift resulted from young godwits predominantly using Portugal over Spain. We found no differences in reproductive success or survival among individuals using either staging site, indicating that the shift resulted from developmental plasticity rather than natural selection. Our results therefore suggest that new migratory routes can develop within a generation and that young individuals may be the agents of such rapid changes.

1. Introduction

The migratory behaviour of species is frequently altered in response to changes in their environment [1], including shifts in phenology [2] and habitat redistribution [3]. Although the ultimate causes leading to changes in migratory behaviour are fairly well understood, few studies have been able to document the processes that contribute to such changes [1,4,5].

In general, three processes could lead to these changes in migratory behaviour: (i) phenotypic flexibility, whereby adults adjust their migratory behaviour in response to changes in conditions within their lifetime [1]; (ii) changes in inherited genetic or epigenetic pathways that influence migratory behaviour [4]; or (iii) developmental plasticity, which is an inter-generational change in migratory behaviour resulting from changes in environmental conditions during ontogeny [5,6]. Because different species appear to respond to similar environmental changes in different ways [1,4], the frequency with which these three processes account for changes in migratory behaviour remains a topic of intense debate [7].

Continental black-tailed godwits (*Limosa limosa limosa*, hereafter 'godwits') use two major stopover sites during northward migration—Extremadura, Spain, and the Tejo and Sado river estuaries in Portugal [8]—where they arrive from either West Africa or southern Spain [9]. From 2005 to 2007, the number of godwits using Extremadura peaked at $24\,214 \pm 3327$ individuals [10], while counts in Portugal peaked, simultaneously, at $44\,185 \pm 2768$ individuals (2006–2009; [11]). However, from 2013 to 2017, peak counts in Extremadura decreased to $10\,400 \pm 5238$ individuals, but increased in Portugal to $51\,400 \pm 15\,551$ (T. Piersma *et al.* 2013–2017, unpublished data).



Figure 1. Map of the study area. Birds from Tejo and Sado estuaries were pooled. (Online version in colour.)

To investigate whether this apparent shift resulted from inherited, flexible or plastic changes in migratory behaviour, we use data from godwits marked in The Netherlands to analyse the staging site use of godwits marked either as chicks or adults. This enables us to infer whether the observed shift from Spain to Portugal was driven by individuals switching between sites, or by the increased use of Portugal by young birds. To the best of our knowledge, this is one of the first studies to take an individual-based approach to examining shifts in a population's migratory behaviour across generations.

2. Material and methods

(a) Resightings

In The Netherlands, we marked godwits with unique colour codes [12]. During northward migration (2013–2017), we resighted colour-marked birds daily at two staging sites: Extremadura, Spain (39.0167° N, 5.9666° W) and the Sado (38.4772° N, 8.6926° W) and Tejo (38.9084° N, 8.9519° W) river estuaries, Portugal (figure 1). To ensure similar resighting efforts at both locations, we analysed only those periods with observers in both regions (electronic supplementary material, table S1 and figure S1). To minimize the effects of ring-reading mistakes, we only included individuals observed on two or more occasions in a single year in our analyses.

(b) Staging site use

To pinpoint if and when a shift in staging site use took place, we determined the consistency of staging site use among individuals observed in consecutive years, as well of those seen in multiple, but not necessarily consecutive, years.

We then used generalized linear models, with the total number of marked individuals recorded at each staging site (Spain or Portugal) as the response variable, to quantify whether there was a difference in the proportional use of the two sites and whether the proportion of birds using either site changed over time. Next, we calculated the staging site use of individuals born from 2012 to 2016. To quantify whether the proportional use of the two sites differed between these birds and those marked as adults, we used a generalized linear model with staging site as the response variable and age at marking (juvenile/adult) as the independent variable. We used the same type of analysis to infer whether the subsequent probability of resighting an individual after it was observed in Spain or Portugal differed depending on

individual site use. For all analyses, we excluded individuals that used both sites (electronic supplementary material, table S2); for the latter analysis, we assumed that the resighting probability was equal for all individuals.

Finally, we used adult survival rates from Kentie *et al.* [12] to estimate (i) how many individuals observed in 2007—when counts peaked in Extremadura [10]—were alive in 2017 and (ii) whether the proportion of young birds observed at each site corresponds with the number of new birds estimated to have entered the population since 2007.

(c) Reproductive success

It is possible that fitness differences among individuals using the two sites, in combination with heritable migratory route choice, could account for the shift [4]. We therefore analysed the brood success of colour-marked godwits in the Haanmeer Polder, The Netherlands (52.9226° N, 5.4336° E) during the 2013–2017 breeding seasons. Twenty-five days after hatch, we began surveys for alarming colour-marked parents [13]. If either parent was encountered within 3 days, at least one chick from the brood was considered fledged.

We fitted a generalized linear mixed-effect model with brood success as the response variable, staging site as a fixed effect and year and individual as random effects. We did this for males and females separately, as the sexes could contribute unequally to brood success and because pairs can consist of individuals using either staging site; individuals using both sites were excluded. All analyses were carried out in R v. 3.3.1 [14] with the R-package 'lme4' v. 1.1–12 [15].

3. Results

Site use was highly consistent, with only a few individuals moving between sites within or between years (table 1). From 2013 to 2017, Dutch-breeding godwits used Portugal more than Spain ($p < 0.001$, $n = 745$; table 1), but the proportion of birds using each site did not change over time ($\chi^2 = 1.35$, d.f. = 1, $p = 0.25$, $n = 5$; table 1). However, individuals born from 2012 to 2016 used Portugal more than individuals marked as adults ($\chi^2 = 14.98$, d.f. = 1, $p < 0.001$, $n = 160$ and 745; table 2), and therefore Spain less ($p < 0.001$). Furthermore, the proportion of young birds using each site closely corresponded with expectations based on adult survival rates and current population estimates for each site (electronic supplementary material, table S3). Finally, neither the probability that an individual survived at least one season after its initial observation (84.2% Spain versus 82.9% Portugal; $\chi^2 = 0.018$, d.f. = 1, $p > 0.05$, $n = 160$) nor fledging success ($\mu = 0.23 \pm 0.23$; female: $\beta_{\text{Portugal}} = 0.34$, $\chi^2 = 0.27$, d.f. = 1, $p > 0.05$, $n = 105$; male: $\beta_{\text{Portugal}} = -0.31$, $\chi^2 = 0.27$, d.f. = 1, $p > 0.05$, $n = 97$) differed among individuals using the two sites.

4. Discussion

We followed adult godwits of a variety of ages during five northward migrations (a period that is 1 year longer than the average godwit lifespan [12]) and found that these individual godwits were highly consistent in their staging site use. Thus, the shift in numbers from Spain to Portugal did not result from individual flexibility or an age-dependent migration strategy. Instead, the shift resulted from young godwits being more likely to use the Portuguese staging sites in more recent years.

Table 1. The use of staging sites in Portugal and Spain by Dutch-breeding godwits from 2013 to 2017 and the individual consistency of site use during consecutive years (above) and across the entire study period (below).

year	location	individuals	repeated ($t + 1$)	switched ($t + 1$)	% repeated ($t + 1$)
2013	Portugal	222 (73.8%)	128	0	100.0%
	Spain	79 (26.2%)	43	4	91.5%
	both	0			
2014	Portugal	358 (77.3%)	180	6	96.8%
	Spain	104 (22.5%)	63	5	92.6%
	both	1 (0.2%)			
2015	Portugal	386 (75.4%)	94	5	94.9%
	Spain	124 (24.2%)	50	1	98.0%
	both	2 (0.4%)			
2016	Portugal	195 (66.8%)	78	2	97.5%
	Spain	97 (33.2%)	48	10	82.8%
	both	0			
2017	Portugal	334 (73.6%)	—	—	—
	Spain	114 (25.1%)	—	—	—
	both	6 (1.3%)			
year	individuals	one location	both locations	switched between years	switched within year
>1 year	531	494 (93.0%)	37 (7.0%) →	30 (5.7%)	7 (1.3%)

Table 2. The site use of individual godwits observed from 2013 to 2017 and whether they were marked as an adult or chick in The Netherlands.

year marked	observed in Portugal		observed in Spain		observed in both areas	
	as adult	as chick	as adult	as chick	as adult	as chick
2004–2011	215	NA	86	NA	11	NA
2012	81	41	21	8	8	2
2013	127	52	40	4	8	0
2014	72	40	18	7	3	0
2015	37	5	19	0	1	0
2016	25	3	4	0	0	0
all years	557 (71.8%)	141 (87.0%)	188 (24.2%)	19 (11.7%)	31 (4.0%)	2 (1.2%)

What process, then, caused the change in the migratory behaviour of young birds?

The shift could have arisen as a result of selection for migration through Portugal. For instance, adults using Portugal could have had greater reproductive success than those using Spain. However, consistent with previous results [13,16], we found that reproductive success in the Dutch-breeding population did not depend on an individual's staging site usage. Alternatively, young birds genetically inclined to migrate through Portugal could have higher survival prior to their first northward migration than those inclined to migrate through Spain [17]. Although we could not directly address this question, we believe that such a difference is highly unlikely: in this study, we found that the survival of young godwits to the subsequent season did not differ between the two staging sites, while our previous work has shown that at no point during their annual cycle did the survival rates of adults differ between

individuals using Spain or Portugal (N.R. Senner *et al.* 2013–2017, unpublished data). Furthermore, overall rates of juvenile and adult survival did not change during the period when godwits were shifting from Spain to Portugal [12]. Finally, because young godwits did not necessarily use the same staging site as their parents (electronic supplementary material, table S4), migratory route choice is likely not heritable.

Developmental plasticity (*sensu* [6]) is therefore the most likely process by which the recent shift from Spain to Portugal occurred. Such a scenario could arise as a result of a variety of circumstances. For instance, the shift could be a response to changes in wind conditions *en route* [18], making the migration along the Atlantic coast more efficient than flights across the Mediterranean Sea [18]. Alternatively, the creation and proper management of new habitats may have been important. For example, since 2011, the rice fields surrounding the Tejo estuary have been expanded and partially managed for the

benefit of migratory waterbirds (J.A. Alves 2015, personal communication). The existence of extensive high-quality habitat may have induced young godwits to preferentially use Portugal over Spain. In fact, the establishment of new habitats has driven shifts in the migrations of other species as well [1], and godwits themselves have previously exhibited changes to their migratory patterns in response to the cultivation of new rice fields [8].

Continental black-tailed godwits thus resemble Icelandic black-tailed godwits *L. l. islandica*, which show a generational shift in the timing of northward migration and are arriving increasingly early on their breeding grounds [5]. Although we cannot unequivocally rule out that natural selection acting on heritable migratory behaviours played a role, the combination of these studies suggests developmental plasticity to be a common mechanism by which new migratory routines arise. Future work should therefore focus on identifying what makes such rapid, plastic changes possible.

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Ethics. Fieldwork was carried out under license numbers FF/75A/2004/117, FF/75A/2009/064 and FF/75A/2014/060 of the Dutch Enterprise Agency.

Data accessibility. Data from the study has been archived at Dryad: <http://dx.doi.org/10.5061/dryad.pc1b6> [19].

Authors' contributions. M.A.V. and A.H.J.L. designed the study. All authors carried out the fieldwork. M.A.V. and A.H.J.L. performed the analyses. M.A.V., A.H.J.L. and N.R.S. wrote the manuscript. All authors offered comments, agree to be held accountable for the content herein and approve the final version of the manuscript.

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