Population-scale drivers of individual arrival times in migratory birds

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Summary

1. In migratory species, early arrival on the breeding grounds can often enhance breeding success. Timing of spring migration is therefore a key process that is likely to be influenced both by factors specific to individuals, such as the quality of winter and breeding locations and the distance between them, and by annual variation in weather conditions before and during migration.

2. The Icelandic black-tailed godwit *Limosa limosa islandica* population is currently increasing and, throughout Iceland, is expanding into poorer quality breeding areas. Using a unique data set of arrival times in Iceland in different years for individuals of known breeding and wintering locations, we show that individuals breeding in lower quality, recently occupied and colder areas arrive later than those from traditionally occupied areas. The population is also expanding into new wintering areas, and males from traditionally occupied winter sites also arrive earlier than those occupying novel sites.

3. Annual variation in timing of migration of individuals is influenced by large-scale weather systems (the North Atlantic Oscillation), but between-individual variation is a stronger predictor of arrival time than the NAO. Distance between winter and breeding sites does not influence arrival times.

4. Annual variation in timing of migration is therefore influenced by climatic factors, but the pattern of individual arrival is primarily related to breeding and winter habitat quality. These habitat effects on arrival patterns are likely to operate through variation in individual condition and local-scale density-dependent processes. Timing of migration thus appears to be a key component of the intricate relationship between wintering and breeding grounds in this migratory system.

Key-words: habitat quality, migration, seasonal matching, shorebirds, waders.

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Introduction

For migratory birds, the timing of arrival on the breeding grounds is critical. Arriving too early, to risk facing unfavourable weather, can be costly (especially at northerly latitudes) while late arrival incurs fitness costs associated with poor breeding success (e.g.

McNamara, Welham & Houston 1998; Kokko 1999). A range of factors influence timing of spring migration (Alerstam & Hedenström 1998; Alerstam, Hedenström & Åkesson 2003), including phenotypic (e.g. Piersma & Jukema 1993; Møller *et al*. 2003), density-dependent (Hasselquist 1998; Currie, Thompson & Burke 2000) and abiotic factors (e.g. Forchhammer, Post & Stenseth 2002). However, most studies tend to be restricted to relatively local scales and limited parts of populations. The importance of the processes will depend on the extent to which they operate throughout a population. Patterns of arrival of individuals across an entire population are likely to be complicated by the variation in local processes, such as within-site density-dependent competition for breeding territories.

Although genetic factors are likely to provide initial cues as to when to migrate (Gwinner 1986; Pulido *et al*. 2001), individual animals will experience different conditions on wintering grounds or staging sites, which can affect their feeding opportunities and body condition on migration (Bearhop *et al*. 2004). This can result in individual variation in timing of migration (Marra, Hobson & Holmes 1998; Gill *et al*. 2001; Drent *et al*. 2003). Similarly, different breeding grounds will vary in their quality, optimal timing of breeding and local levels of density dependence (e.g. Brooke 1979; Svensson and Nilsson 1995; Newton, Rothery & Dale 1998) and so the benefit from arriving early will differ (Kokko 1999). Although studies have shown relationships between local territory quality and/or density dependence and timing of migration (Hasselquist 1998; Currie *et al*. 2000; Mahoney & Schaefer 2002), none have yet addressed how population-scale variation in habitat quality influences the range of arrival times of individuals across the population.

Abiotic factors may also affect individual timing of migration. For example, migration distance could influence arrival times, particularly if individuals depart from different sites at a similar time. To investigate this, data on both the wintering location, destination and timing of migration of individuals are needed. Recent advances in satellite transmitter technology have allowed small numbers of individuals to be tracked in detail (e.g. Nowak, Berthold & Querner 1990; Pennycuick *et al*. 1996; Tourenq *et al*. 2004), and migration distance has been related to timing of spring arrival in colour-marked populations that winter in few distinct areas (e.g. Hötker 2002), but these data are rarely available for large numbers of individuals across entire populations.

Weather conditions in spring can also affect the process of migration directly by interfering with schedules of individuals already underway (e.g. Pennycuick *et al*. 1996) or by affecting conditions prior to departure. This has been shown in a number of recent studies (e.g. Forchhammer *et al*. 2002; Hubalek 2003; Hüppop & Hüppop 2003; Vähätalo *et al*. 2004) that relate average timing of migration to large-scale climatic phenomena such as the North Atlantic Oscillation (NAO) (Hurrell

1995; Hurrell, Kushnir & Visbeck 2001; Visbeck *et al*. 2001). The effects of these on individuals have never been investigated, presumably as the necessary multiple-years data on timing of migration of the same individuals are rarely available (Bêty, Giroux & Gauthier 2004).

The Icelandic black-tailed godwit *Limosa limosa islandica* is a migratory shorebird that breeds almost exclusively in Iceland and winters in western Europe. About 1–2% of the population is individually marked with colour rings and the wintering and breeding grounds of many of these have been located through an extensive network of volunteer observers and by systematic searches (Gill *et al*. 2001; Gunnarsson *et al*. 2004). The population has recently been rapidly increasing (Gunnarsson *et al*. 2005a,b), during which time birds have been occupying new, poorer quality areas, at both ends of the range (Gill *et al*. 2001; Gunnarsson *et al*. 2005b,c). Godwits arrive in Iceland from mid-April and the majority of the population use the small number of staging sites that are mainly located on the few estuaries around the coastline before moving inland to the breeding sites. Timing of spring arrival of marked birds in Iceland has been monitored extensively on these passage sites since 1999 (Gill *et al*. 2001; Gunnarsson *et al*. 2005a).

In this paper we explore a range of potential large-scale drivers of spring arrival patterns of individual black-tailed godwits. Using a unique data set (e.g. Gunnarsson *et al*. 2004) of year-round movements of individual Icelandic black-tailed godwits, we assess whether (1) climatic conditions during migration influence annual variation in the timing of individual migration; (2) individual timing of arrival is consistent between years; and (3) the arrival times of individuals are influenced by breeding habitat quality, winter habitat quality, sex or migration distance. We also explore components of habitat quality that may influence patterns of arrival.

Methods

WINTER AND BREEDING LOCATIONS OF MARKED BIRDS

Between 1992 and 2003, individual black-tailed godwits were caught on the wintering grounds, on spring staging sites in Iceland and on the breeding grounds, and fitted with individual combinations of colour rings. Through an extensive network of volunteer observers throughout the range, winter (November to mid-February) locations have been obtained for more than 50% of all birds ringed as adults (Gunnarsson *et al*. 2004). Adult godwits are highly philopatric in winter (Gill, Hatton & Potts 2002). Similarly, breeding locations were known for all birds ringed on their breeding territories, and the locations of many other marked breeding birds around Iceland were also reported by volunteers. Birds were sexed using a discriminant function analysis of biometric data after calibration

based on molecular analyses (Gunnarsson *et al.* in press).

TIMING OF SPRING MIGRATION

To obtain spring arrival dates for individual birds in Iceland, we monitored the major staging sites of godwits around Iceland on a daily basis during spring migration from mid-April to early May, from 1999 to 2004 (Gill *et al.* 2001; Gunnarsson *et al.* 2005a). The main staging areas are in south-west and south-east Iceland (see locations in Gunnarsson *et al.* 2005a). In the south-west, godwits arrive from mid-April onwards but in the south-east, the peak passage period spans the end of April (Gunnarsson *et al.* 2001) and the first few days of May (Tiedemann 1990). At all sites, any marked birds that were present when our monitoring began were excluded from the analyses as the date of arrival was unknown. Although flocks of godwits occasionally exceeded 3000 individuals, marked birds were usually seen on all intervening days between the first and last sighting, suggesting that very few birds were overlooked. Arrival date was considered to be the first day a bird was seen at any location in Iceland. In total we obtained spring arrival dates for 113 marked birds for which breeding location, winter location or arrival date in more than one year were known. Arrival dates in 2 years were known for 30 individuals, in 3 years for 12 individuals, in 4 years for three individuals and in 5 years for one individual. The remaining 67 individuals were seen only in one year.

CHARACTERISTICS OF WINTERING AND BREEDING AREAS

The Icelandic black-tailed godwit population has increased rapidly (Pollitt *et al.* 2003), and previous studies have shown that the godwits are following a buffer effect on the wintering grounds (Gill *et al.* 2001). The black-tailed godwits that winter in England are expanding into poorer quality sites in which prey intake rates and adult survival are reduced (Gill *et al.* 2001). Although the quality and timing of colonization of winter sites elsewhere in the range is not known, Prater (1974) identified sites that were occupied prior to *c*.1970, and these 'old' sites can be distinguished from sites occupied since then (Gunnarsson *et al.* 2005c). Winter sightings (mid-November to mid-February) of individually marked birds were therefore classified into those occupying old sites (occupied since before 1970), new sites (occupied since 1970) or mixed sites (birds recorded using old and new sites in different winters). If, as Gunnarsson *et al.* (2005c) suggest, the buffer effect pattern described in Gill *et al.* (2001) extends throughout the winter range, then 'new' sites will be relatively poorer quality than 'old' sites throughout the range.

Recent studies have shown that a buffer effect is also operating on the breeding grounds with birds progressively expanding into areas of Iceland with an increasing proportion of the poorer quality type of breeding habitat. The year of colonization of breeding areas around Iceland can thus be used as an index of the relative availability of good quality breeding habitat (Gunnarsson *et al.* 2005b).

The relative quality of different breeding habitats and areas may also be influenced by the timing of breeding habitat availability in spring, which is likely to be related to local temperatures. We therefore extracted the mean May (the month when breeding starts) temperature (available at: http://www.vedur.is) in eight separate breeding areas. Mean temperatures were calculated from the long-term average (1961–2004), and averaged over two to three stations in each area. The mean number of birds from each area for which we had timing of migration was $6{\cdot}3 \pm 1{\cdot}4$ SE.

MIGRATION DISTANCE

Mapping software (Navtreck) was used to calculate migration distance as the straight line (great circle; orthodrome) in km between the mid-winter location and nearest part of the coastline of Iceland.

DATA ANALYSIS

A two-stage process was used to determine the relative importance of annual variation in weather conditions (NAO) and the individual-based variables (sex, breeding and winter area characteristics and migration distance) on arrival dates of individual godwits on spring staging areas in Iceland. First, annual variation in arrival dates was explored with a General Linear Model constructed with the GENMOD procedure in SAS (SAS Institute 2001), using the date that birds were first seen in Iceland in each year as the response variable, for all birds that were seen in more than one year ($n = 46$ individuals). The NAO index and a factor representing the individual were used as the predictor variables. NAO variables were available on a monthly basis and to determine which month had the most significant effect, separate models were constructed for the average NAO values for January to May each year. NAO data were obtained from http://www.cru.uea.ac.uk/cru/data/nao.htm.

To understand the factors influencing the between-individual variation in arrival in the previous model, a repeated-measures GLM was then constructed in GENMOD with individual specified as the variable on which repeated measures are made. The March value of NAO was kept in the model (see Results), but the individual factor was replaced with the variables in Table 1, to determine which aspects of individual life history (breeding and winter area characteristics, sex and migration distance) contributed to individual arrival dates. A step-backward procedure was used to determine the Minimum Adequate Model (Crawley 1993), with all variables initially included in the model,

Table 1. Variables included in the analysis of between-individual variation in timing of arrival in Iceland in spring. See text for details

Variable	Type	Values
NAO	Continuous	March index values
Breeding area characteristics	Continuous	Year of colonization or mean May temperature
Winter area characteristics	Three-level factor	Old (occupied pre-1970), new (post-1970) or mixed
Migration distance	Continuous	km from mid-winter location to Iceland
Sex	Two-level factor	Male or female

and the least and nonsignificant ($P > 0.05$) variables sequentially removed until only significant variables remained.

LOCAL BREEDING DENSITIES AND PATTERNS OF ARRIVAL WITHIN BREEDING AREAS

To assess the relationship between timing of arrival on breeding sites and local breeding density, we carried out studies on 12 sites in south Iceland in 2002. The vast majority of godwits arrive in Iceland in the last 10 days of April and the first 10 days of May (Gunnarsson *et al.* 2005c). Systematic counts were carried out on each of the sites one to two times a week, from mid-April until all birds had left (*c.* late July). Breeding densities (birds km^{-2}) were calculated from the average of the three maximum counts on each site during the nesting period. To estimate arrival patterns on those sites we measured the proportion of birds (of the maximum density) at each of 12 sites that arrived during the first half of the arrival period (last 10 days in April).

Results

The 113 individual godwits for which we measured arrival dates in Iceland originated from winter sites throughout the range (Portugal, Spain, France and the British Isles), and from locations throughout the breeding range in Iceland. Records of arrival dates in more than one spring were available for 46 of these birds. A comparison of the effect of the NAO values for the different months on annual variation in godwit arrival times resulted in a significant fit for February and March (Table 2). March NAO values were the strongest predictor of timing of arrival in Iceland and were used in subsequent analyses. Arrival dates for these 46 individuals were significantly related to the March NAO value but the individual factor had much stronger effects on timing of spring arrival (Table 2), indicating that individual timing of arrival was consistent between years. NAO and the individual factor together explained 73% of the variance in annual arrival dates (regression of predicted values on observed: $y = 0.72x + 7.43$, $R^2 = 0.73$, $P < 0.001$). Analysis of repeatability (Lessells & Boag 1987) confirmed that the arrival dates of individuals were repeatable between years ($r = 0.18$, $F_{5,107} = 14.4$, $P < 0.001$).

In the second part of the analysis, the individual parameter was replaced with variables relating to the

Table 2. Results from four different GLMs predicting the date that 46 individual Icelandic black-tailed godwits were first seen on spring passage in Iceland, based on the NAO value for different months (January to April) and a factor variable representing each individual. The parameter values and the significance of both the NAO parameter and the individual factor in each model are shown

Month	Parameter estimate	NAO		Individuals	
		χ^2_1	P	χ^2_{45}	P
January	0.54	3.73	0.0535	108.15	< 0.0001
Feb	0.55	10.97	0.0009	105.13	< 0.0001
March	−2.52	40.69	< 0.0001	122.34	< 0.0001
April	0.17	1.24	0.2662	105.3	< 0.0001

breeding and winter location, distance between the two and sex of each bird. The year of colonization of breeding areas is strongly related to the mean May temperature in those areas ($r = -0.85$, $P = 0.01$, $n = 8$), thus the effects of colonization year and mean May temperature were both explored separately within these analyses. In the final model, the NAO and two of the four individual variables (Table 1) were retained in the minimum adequate model (sex: female parameter = 2.25 ± 0.8 SE days later than males, $\chi^2_1 = 5.92$, $P = 0.0149$; mean May temperature: parameter = -1.65 ± 0.47, $\chi^2_1 = 7.47$, $P = 0.0063$ and NAO: parameter = -2.71 ± 0.56, $\chi^2_1 = 10.31$, $P = 0.0013$). May temperatures were used as the indicator of breeding area characteristics in this model, as they gave a better fit than the colonization pattern. Across the eight breeding areas for which we had both information about individual timing of migration and temperature, godwits breeding on sites with a higher average May temperature arrived significantly earlier in Iceland (Fig. 1). When the nonsignificant variables (age of winter site and migration distance, Fig. 2) were removed from the model, the sample size increased from 31 to 47, as the remaining parameters were known for a larger sample of individuals. This larger sample produced results consistent with the previous ($n = 31$) model, so only results based on the larger sample size are presented (Table 3). Interaction terms were also tested but were not significant. This model explained 44% of the variation in arrival dates (regression of predicted values on observed: $y = 0.44x + 15.29$, $R^2 = 0.44$, $P < 0.001$).

The effects of breeding site characteristics and sex on patterns of arrival in Iceland are shown in Fig. 3. The
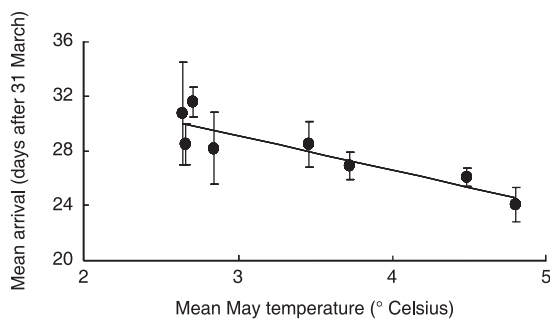
Fig. 1. The relationship between mean May temperature and mean (± SE) timing of arrival in Iceland of black-tailed godwits breeding in eight separate areas around Iceland ($y = -2 \cdot 50x + 36 \cdot 65$, $R^2 = 0 \cdot 79$, $P = 0 \cdot 003$, $n = 8$).
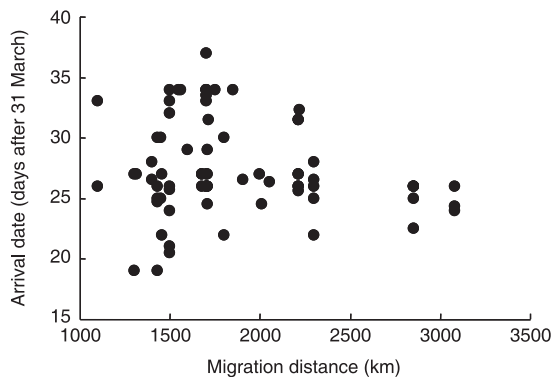

Fig. 2. The relationship between mean individual timing of arrival of black-tailed godwits in Iceland in spring and the distance between Iceland and the wintering grounds of those individuals.

Table 3. Results of the minimum adequate repeated measures GLM model, which explored the effects of sex, breeding habitat quality (measured as mean May temperature) and the NAO on individual arrival dates of black-tailed godwits in Iceland

Variable	χ^2_1	P
Sex	5·92	0·0149
Mean May temperature	7·47	0·0063
NAO	10·31	0·0013

first godwits to arrive in spring are males that are going to breed in the most traditionally occupied breeding areas, closely followed by the females that will also breed in these areas. Males that are going to breed in areas occupied between 1920 and 1940 arrive, on average, 1 day later, but the females from these sites arrive 2–3 days later. Males and females from the most recently occupied sites in the east of Iceland both arrive about a week after the first godwits. Although the age of occupation of winter sites was not retained within the model, this is likely to largely be because of collinearity between breeding and winter site characteristics, as individuals from traditionally occupied breeding sites also tend to use 'old' winter sites (Gunnarsson *et al.*
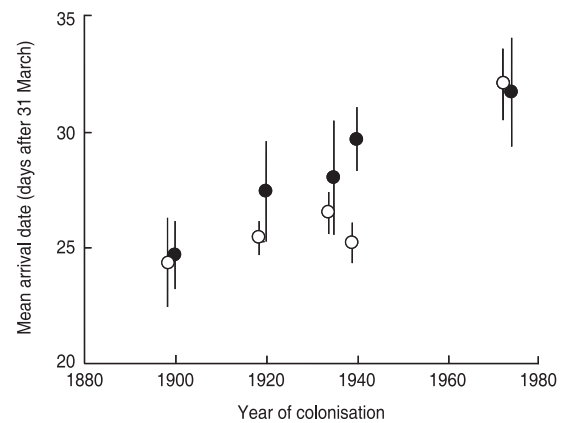

Fig. 3. Variation in the mean (± SE) timing of arrival of male (open circles) and female (filled circles) black-tailed godwits from breeding areas colonized for different periods of time.
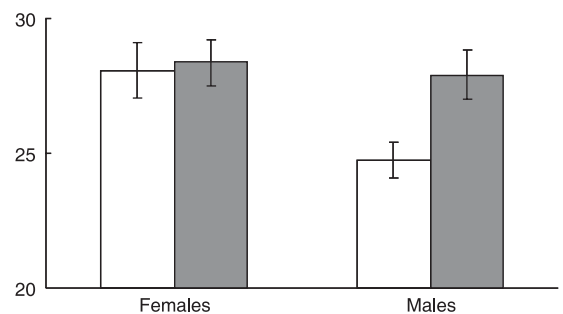

Fig. 4. Differences in the mean (± SE) timing of arrival of male and female black-tailed godwits from traditionally occupied (open bars; pre-1970) or recently occupied (filled bars; post-1970) winter sites.

2005c). Thus, early arriving godwits are likely to also be from traditionally occupied winter sites. Figure 4 shows that the earliest males are from winter sites occupied prior to 1970 (males: $t_{36} = -2 \cdot 56$, $P = 0 \cdot 014$; females: $t_{30} = 1 \cdot 69$, $P = 0 \cdot 83$).

Although the proportion of good and poor quality habitat within breeding areas around Iceland is known, the actual habitat type occupied by individuals is not known for most birds. However, detailed studies of godwit breeding ecology in eight good quality (marshes) and four poor quality (dwarf-birch bogs) breeding habitats in the southern lowlands of Iceland (see Gunnarsson *et al.* 2005c) show a clear relationship between breeding density and the pattern of arrival on these sites (Fig. 5). The proportion of birds arriving on the breeding site early (before the end of April) increases with breeding density, and good quality sites generally have higher breeding densities than poor quality sites.

Discussion

Individual godwits from traditionally used breeding areas, where average habitat quality and spring temperatures are higher, arrive in Iceland earlier than those
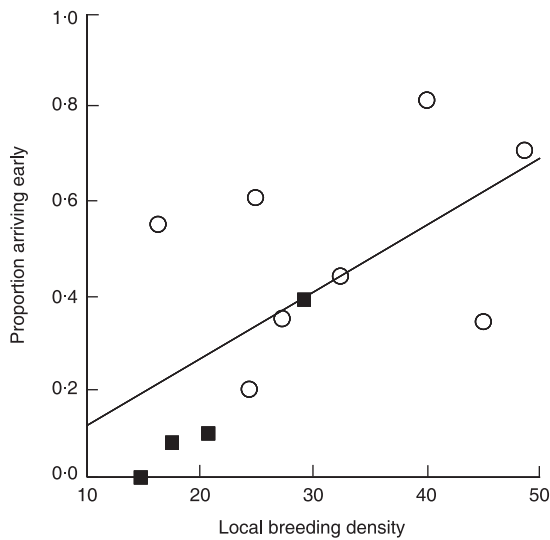
Fig. 5. The relationship between local breeding density (birds km^{-2}) and arrival patterns (proportion of maximum number that arrives in the first half of the arrival period) in spring ($y = 0.014x - 0.031$, $R^2 = 0.39$, $P = 0.029$) across 12 breeding sites in southern Iceland in 2002. Filled squares indicate poorer quality habitat (dwarf-birch bog) and open circles indicate higher quality habitat (marsh).

from recently occupied areas, where average habitat quality and spring temperatures are lower. This pattern could result from one, or a combination, of the following mechanisms: (1) the strength of density-dependent pressure to arrive early is higher in more traditionally used areas if these have higher densities and local competition (e.g. Kokko 1999); (2) variation in habitat quality may result in different trade-offs between the risks of early arrival and the potential reproductive gain, such that the benefits of early arrival are higher in better areas; (3) earlier arrival in traditionally used areas could be a carry-over effect from the wintering grounds if birds using traditional breeding areas are more likely to winter on higher quality sites and to be in better condition for early migration; (4) individuals could be on different schedules, with the earliest arrivers occupying slightly milder climates and breeding earlier, independent of other aspects of habitat quality.

At present it is not possible to distinguish between the above mechanisms, as the pattern of expansion into new breeding areas with lower availability of good quality habitat is so closely correlated to spring temperatures. However, the increase in the proportion of early arrivals with local breeding density in sites in the southern lowlands (Fig. 5), is indicative of the importance of local density-dependent processes in driving patterns of arrival. Although breeding densities tend to be higher on the better quality marsh habitats, this is not exclusively the case (Fig. 5). Thus, it seems likely that arrival dates are directly related to the quality of the breeding habitats, which is influenced both by the level of competition for resources and potentially also the optimal timing of breeding in relation to temperature.

In addition to this, the earlier arrival of males from traditional wintering sites (Fig. 4) suggests that carry-over effects are also important drivers of individual arrival times. The godwit population has recently expanded into novel wintering areas throughout western Europe. Previous studies from winter sites within England have shown that prey intake rates and adult survival are lower on novel winter sites, and that birds from these areas arrive in Iceland later than those from the traditionally occupied sites (Gill *et al.* 2001). Direct estimates of the quality of winter sites throughout the rest of the winter range are not yet available, but if expansion into poorer quality winter areas is occurring throughout the range, then both breeding and winter site characteristics will explain a considerable part of the variation in individual timing of migration. As this population shows strong seasonal matching of habitat quality, with the same individuals using higher quality sites at both ends of the range (Gunnarsson *et al.* 2005c), we cannot currently determine in which season the effects are stronger.

Throughout the population, the NAO affects arrival times. Many recent studies have described the important effect of the NAO on the mean timing of migration across populations (e.g. Forchhammer *et al.* 2002; Hubalek 2003; Hüppop & Hüppop 2003; Vähätalo *et al.* 2004). The NAO does explain some of the annual variation in timing of spring arrival of godwits but is of relatively minor importance compared with the combined sources of individual variation. The strength of the effect of the NAO increased from January to March but was nonsignificant during the main migration period in April (Table 2). This suggests that the effects of the NAO on timing of migration operate mainly through their influence on feeding conditions prior to migration, and that these effects become more pronounced as migration approaches. During migration, smaller-scale weather patterns are more likely to be important than large-scale climatic phenomena, which may explain the lack of an effect of the NAO in April on timing of arrival (Table 2).

The direction of the effects of the NAO on timing of arrival also varies between months (Table 2). This may reflect changes in the spatial distribution of godwits in late winter. In mid-winter, the population is distributed from the British Isles to northern Morocco, with more than half of the population in France and Iberia (Gunnarsson *et al.* 2005a). Movements of marked individuals show that the spatial arrangement of the population changes rapidly in late winter (February– March), as many southern wintering birds move north (44% of 124 birds known to winter in France or further south have been seen during spring staging in Britain, Ireland or the Netherlands). In the Netherlands alone, one-quarter of the population aggregates in late March (Gerritsen & Tijsen 2003). As the effects of the NAO differ in southern and northern Europe (Hurrell *et al.* 2003), the direction of the correlation between the NAO and arrival dates might be expected to change as

the population moves northwards. The relationship between the NAO and arrival dates is positive in January and February but negative in March, by which time most of the birds have gathered in the north of the range prior to departure (Table 2). This pattern supports the suggestion that migration schedules become tighter the closer birds are to the breeding grounds (Battley *et al*. 2004).

The range of distances travelled by individual birds from their mid-winter location to Iceland (*c*. 1000–3000 km) did not significantly influence timing of arrival. This suggests that godwits from the south of the winter range (southern Iberia) can fully compensate in time for the increased travel costs over these spatial scales, and (given a relatively constant travel speed across individuals) that godwits depart their mid-winter locations at different times in order to time their arrival at the breeding site in relation to others. Very few studies have addressed this issue. Hötker (2002) showed that avocets *Recurvirostra avosetta*, with the shortest distance to travel arrived earlier in spring than those wintering further away. A similar pattern has been shown for cormorants *Phalacrocorax carbo*, breeding in Denmark (Bregnballe, Frederiksen & Gregersen in press) where birds wintering close (≤ 300 km) to the colonies arrive 2–3 weeks earlier than those wintering further away. The discrepancy between studies might be because, in both avocets and cormorants, a proportion of the population winters very close to the breeding sites, and may thus be able to assess conditions for breeding very accurately. Icelandic black-tailed godwits winter at least 1000 km away from the breeding grounds, and conditions within Iceland during spring may thus be difficult to gauge. Birds wintering in southerly sites may be trading-off travel costs with higher site quality, which could provide them with the fuel necessary for rapid spring migration, but may require them to begin spring migration earlier than those in the north. Interestingly, cormorants wintering at a similar distance from their breeding sites as godwits (600–2500 km) also show no relationship between distance and timing of arrival (Bregnballe *et al*. in press), thus there is a scale issue that has to be considered when comparing different systems.

Males arrive in Iceland on average 2·3 days earlier than females. Earlier arrival of males is a typical pattern for species where males defend territories (e.g. Currie *et al*. 2000; Hötker 2002). Male territorial defence is predominant in most species of waders (Cramp & Simmons 1983), and this has typically been used to explain why males of migratory birds tend to arrive earlier than females. However, this overlooks the fact that, early in the season, males with a territory are likely to be a rare commodity and females should also be selected for early arrival to secure a territory with a male. Indeed, recent theoretical advances suggest that selection for earlier arrival of males in migratory birds might require processes that enhance male–male competition, such as biased sex ratios or high levels of extra-pair copulations, to provide the pressure to arrive early (Kokko *et al*. in press). The very small differences in arrival between male and female godwits (Fig. 3) suggests that there is also strong selection acting on female arrival times.

Migratory systems are best described as a sequential process, where the effects of events operating in one season can carry over to the next. The seasonal matching in the godwit system, in which individuals tend to use either high or low quality habitat in both seasons, is an example of these carry-over effects. The analyses presented here show that, while climatic conditions influence annual variation in the timing of spring migration, the order in which individuals arrive is strongly influenced by the conditions that they experience on their breeding and wintering sites. Timing of migration is thus likely to be a key aspect of seasonal matching, with individuals from good quality sites both able to arrive earlier and under greater pressure to arrive earlier, either because good quality sites are available earlier in the season or because of stronger density-dependent competition for good quality territories.

Acknowledgements

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