Seasonal matching of habitat quality and fitness in a migratory bird

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When species occupy habitats that vary in quality, choice of habitat can be critical in determining individual fitness. In most migratory species, juveniles migrate independently of their parents and must therefore choose both breeding and winter habitats. Using a unique dataset of marked black-tailed godwits (*Limosa limosa islandica*) tracked throughout their migratory range, combined with analyses of stable carbon isotope ratios, we show that those individuals that occupy higher quality breeding sites also use higher quality winter sites. This seasonal matching can severely inflate inequalities in individual fitness. This population has expanded over the last century into poorer quality breeding and winter habitats and, across the whole population; individual birds tend to occupy either novel or traditional sites in both seasons. Winter and breeding season habitat selection are thus strongly linked throughout this population; these links have profound implications for a wide range of population and evolutionary processes. As adult godwits are highly philopatric, the initial choice of winter habitat by juveniles will be critical in determining future survival, timing of migration and breeding success.

Keywords: migratory birds; seasonal interactions; habitat quality; conservation

1. INTRODUCTION

A key driver of fitness in individual animals is the quality of the habitat they occupy. In migratory species, individuals must select breeding habitat at one end of the range and winter habitat at the other. Summer and winter habitat selection are generally studied in isolation, but a growing number of studies have pointed to the importance of interactions between seasons. For example, geese (*Branta bernicla bernicla*) that have larger fat reserves on departing the winter or staging grounds have higher breeding success (Ebbinge & Spaans 1995; Madsen 1995), and marked individuals and stable isotope technology have been used to show that winter habitat quality is related to timing of migration (Marra *et al.* 1998; Gill *et al.* 2001), body condition during spring migration (Bearhop *et al.* 2004) and even local breeding success (Norris *et al.* 2004). These patterns could arise either through winter conditions determining individual condition for migrating and breeding, or through individuals selecting similar quality habitats in both seasons. Our study system, the Icelandic black-tailed godwit, *Limosa limosa islandica*, provides an opportunity to identify the mechanism linking summer and winter events at a range of scales as: (i) we have detailed information on the locations of individuals throughout the annual cycle (Gunnarsson *et al.* 2004); (ii) the winter habitat of breeding birds can be identified through stable isotope analyses of feathers and; (iii) we have traced the pattern of population expansion in both summer and winter, allowing us to assess individual use of novel and traditional sites.

Icelandic black-tailed godwits are migratory shorebirds that breed almost exclusively in Iceland and winter in Western Europe (Wernham *et al.* 2002). Recent studies of this species demonstrated that individuals on recently occupied wintering sites in eastern England experienced significantly lower prey intake rates in late winter and lower annual survival rates than those wintering in the traditionally occupied south of England (Gill *et al.* 2001). In Iceland, black-tailed godwits breed principally in two habitat types; ‘coastal sites’ typically comprise a flat mosaic of marshes with shallow wetlands and tracts of grassland, whereas ‘inland sites’ are characterized by homogenous marshes dominated by dwarf birch, *Betula nana* and the sedge, *Carex rostrata*.

In this study, we first assess the variation in reproductive success between godwit breeding habitats in Iceland. We then use tracking of marked individuals and stable carbon isotope analyses of feathers to show how individual use of high or low quality habitats in summer and winter are linked. Finally, we use changes in the patterns of use of habitats of varying quality during a period of population expansion to assess the scale at which these links operate, and their potential to influence evolutionary and demographic processes.

2. MATERIAL AND METHODS

(a) *Habitat-specific breeding success*

Three commonly used indicators of breeding habitat quality were measured in each of 14 study sites (eight

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coastal and six inland) in the southern lowlands of Iceland (which is the largest and single most important breeding area of the population): (i) arrival patterns; in migratory species the more productive territories are often occupied first (e.g. Currie *et al.* 2000). The vast majority of godwits arrive in Iceland in the last ten days of April and the first 10 days of May (Gunnarsson *et al.* 2005), thus the proportion of birds at each of 14 sites that arrived during April was calculated from regular surveys (1–2 per week) throughout the breeding season in 2002. (ii) Breeding density; densities may be expected to be higher on better quality sites if increased resource availability results in smaller breeding territories. Breeding densities (birds km⁻²) were calculated from the average of the three maximum counts on each site during the nesting period. (iii) Breeding success; the cryptic nature of godwit nests and chicks makes it extremely difficult to accurately measure the number of chicks fledged on each site, hence the mean proportion of pairs with chicks in the latter part of the fledging period (when chick presence is clearly indicated by the agonistic behaviour of the adults) was used as an index of productivity. Data on marked individuals show that broods stay on the breeding site after hatching, thus movements of broods into and out of sites are unlikely to confound the results. Eight study sites (four coastal and four inland) were surveyed in both 2002 and 2003, whereas six (four coastal and two inland) were only surveyed in 1 year. On the eight sites surveyed in both years, both breeding densities ($r=0.95$, $p<0.001$) and breeding success ($r=0.77$, $p<0.05$) were highly correlated between years, thus all 14 sites were included in the analyses and averages of the two years were used for the eight relevant sites.

Invertebrate densities were also estimated on the breeding sites as a further indicator of breeding habitat quality. Densities were compared by taking 10 non-overlapping strokes with a 40 cm diameter hand-net through vegetation at 5–6 random points on each site in the second week of July. Pitfall traps (12 cm diameter) were also monitored from the onset of godwit incubation into the fledging period. All animals with body lengths exceeding 3 mm were counted.

(b) *Isotopic analysis of winter habitat use*

Black-tailed godwits forage on both saline (estuarine mudflats and saltpans) and freshwater (lowland wet grassland) habitats during winter. Individual use of these habitats can be assessed with analysis of the stable carbon isotopes assimilated into feathers during the period of moult (February–April), since the $\delta^{13}\text{C}$ ratio varies with salinity (Rubenstein & Hobson 2004). For each bird, ca 10 summer plumage body feathers were cut and freeze-ground into a fine powder, from which 0.7 mg was weighed into 0.3×0.5 mm tin capsules. Analysis was carried out by continuous flow isotope ratio mass spectrometry using a Carlo Erba NA1500 elemental analyser connected to a Thermo Finnigan TracerMat. Fourteen gelatine standards of unequal mass run daily give typical standard deviations of 0.16 ‰ ($\delta^{13}\text{C}$). More negative values for $\delta^{13}\text{C}$ indicate that a higher proportion of assimilated food comes from freshwater sources and less negative values indicate more saline food.

(c) *Statistical analysis*

We employed a bootstrapping procedure to assess the statistical significance of the relationship between average isotope ratios and breeding success, which is based on variable numbers of individuals (between 3 and 16) at each site. For each site, we sampled, with replacement, isotope ratios from the distribution of observed ratios, a number of times that corresponded to the number of samples actually available. The resulting mean isotope ratios for each site could then be related to breeding success. We then repeated this entire process 999 times, to generate a distribution of regression coefficients.

3. RESULTS

(a) *Habitat-specific breeding success*

In Iceland, coastal breeding sites appear to be significantly higher quality for black-tailed godwits than inland sites. Godwits arrive significantly earlier on coastal breeding sites, breed at higher densities and breed more successfully (figure 1) than on inland sites. Prey densities were also higher in coastal areas (hand-net samples: coastal 188 ± 22.3 s.e. prey/sample; inland 65 ± 10.76 , $t_{36}=2.2$, $p=0.034$. Pitfall traps: coastal 3.7 ± 0.39 prey/trap/day; inland 2.5 ± 0.31 , $t_{25}=2.37$, $p=0.026$), further indicating the higher quality of coastal breeding sites.

(b) *Seasonal matching of habitat quality*

Extensive individual colour-marking and re-sighting of godwits resulted in 27 individuals for whom both the quality of breeding sites (coastal versus inland) and wintering sites (south coast vs east coast of England) were known. Of 15 godwits from high quality breeding sites, 11 (73%) used high quality winter sites, while of 12 godwits from poor quality breeding sites, 9 (75%) used poor wintering sites ($G=6.15$, $p=0.013$). This seasonal matching indicates that individuals that benefit from breeding in higher quality sites also benefit from wintering in areas where survival is higher.

In common with many migrant birds, juvenile godwits migrate independently of their parents and siblings. Figure 2 shows that no family members have yet been found wintering in the same location, or even the same country, thus winter locations do not seem to be learned from parents. Seasonal matching must therefore be driven directly by some feature of the habitats themselves. Gill *et al.* (2001) suggested that variation in the use of freshwater and saline feeding habitats was a key aspect of winter habitat quality for Icelandic black-tailed godwits. In order to assess whether the use of these habitats in winter was related to subsequent breeding success in Iceland, we used stable isotope analyses to explore patterns of habitat use by individual godwits during late winter and early spring. Black-tailed godwits moult into their breeding plumage from February until April, before they migrate to Iceland. During this time, birds from the high quality sites in southern England use saline habitats more extensively than those from the poor quality eastern England sites (mean $\pm$ s.e. proportional use of saline, rather than freshwater, habitats by marked individual godwits on south coast = 0.61 ± 0.1 and east coast = 0.23 ± 0.03 sites, $t_{235}=-3.6$, $p<0.001$). Thus, use of either saline or freshwater habitats may be related to the differences in survival between these regions (Gill *et al.* 2001).

Figure 1. Differences in breeding habitat quality for black-tailed godwits. On coastal sites, godwits arrive earlier (percentage of breeding birds arriving in the first half of the arrival period, $t_{12} = -3.5$, $p < 0.005$), have higher breeding densities (birds km^{-2} , $t_{12} = -2.8$, $p < 0.015$) and greater breeding success (percentage of breeding birds with chicks just before fledging, $t_{12} = 2.54$, $p < 0.026$) than inland sites.

Figure 2. Winter locations of black-tailed godwit families. Open circles indicate adults and filled squares indicate juveniles. Lines link members of the same family.

We collected body feathers of breeding birds on nine breeding sites (four inland and five coastal) in Iceland and used stable carbon isotope analyses to investigate the extent to which individuals had been feeding on saline or freshwater habitats during moult in late winter. These godwits winter at sites right across Western Europe and

hence, we could assess whether saline and freshwater habitat use across the wintering range was linked to breeding success in Iceland, as suggested by the patterns obtained within England. Across the nine sites in Iceland, mean breeding success increases significantly as isotope ratios become more saline (figure 3). The bootstrapped mean slope and confidence intervals of the resampled relationships were 0.053 (95% CIs = 0.052–0.055), thus the relationship is strongly statistically significant. Individuals from throughout the winter range that feed on more saline habitats in late winter are therefore likely to breed on better sites in Iceland.

(c) Population expansion and seasonal matching

Over the last century, the godwit population has expanded dramatically, and an increasing proportion of the population is now occupying poorer quality wintering sites, where survival rates are lower (Gill *et al.* 2001). In Iceland, godwits traditionally occupied areas where good quality marsh habitats are more abundant, however, the population increase has also resulted in expansion into new breeding areas, where poorer quality dwarf birch bog habitats are more abundant (Gunnarsson *et al.* in press).

On the breeding grounds, the year of colonization is known for many breeding areas (Gunnarsson *et al.* in press). For the wintering grounds, the exact time when new sites were colonized is not known, but Prater (1975) identified the major wintering sites prior to 1975 (here termed 'old'), and sites that have been occupied since then ('new') were identified from published national counts (Gunnarsson *et al.* 2005). Tracking of colour-marked individuals clearly shows that those breeding in sites that have been occupied for longest, winter almost exclusively on old sites, whereas those breeding in more recently occupied sites are significantly more likely to winter on new sites (figure 4a).

To investigate whether differences in saline or freshwater habitat use in winter are also related to the pattern of expansion around Iceland, we sampled feathers from eight breeding populations around Iceland that have been occupied for differing lengths of time. Stable carbon isotope analyses revealed that birds breeding in more traditionally occupied areas are more likely to use saline habitats in late winter (figure 4b).

4. DISCUSSION

(a) Seasonal matching of habitat quality

Selection of either good or poor quality summer and winter habitats by individual black-tailed godwits appears to be strongly linked at a range of scales. These links are likely to significantly influence individual fitness, since those individuals with high breeding success are also likely to be those with high survival. These links may also play a key role in driving population demography since, throughout this population, godwits appear to be expanding into breeding areas dominated by the habitat on which breeding success is lower, and into winter areas where stable carbon isotope ratios indicate the use of habitats in which survival is lower.

How might these links between summer and winter sites of similar quality be initiated? Given that adult godwits are highly philopatric in winter (Wernham *et al.* 2002) and given the independent migration of godwit

Figure 3. The influence of winter habitat type on breeding success. Godwits that breed on more productive sites in Iceland are more likely to have used saline habitats in Europe in late winter. Each datapoint relates the mean carbon isotope ratio (a measure of the extent of saline or freshwater winter habitat use) of birds from each of nine breeding sites to the index of reproductive success (mean proportion of pairs with chicks at an advanced stage) on each site. Linear regression: $R^2=0.82$, $p<0.001$, $y=0.09x+2.06$. See text for confidence calculations.

Figure 4. Links between colonization patterns of breeding and winter sites. Individuals that breed on traditionally occupied sites are more likely to (a), winter on traditionally occupied sites (the percentage of marked individuals on old (occupied since at least 1975) winter sites declines with the year of occupation of their breeding site. Linear regression: $R^2=0.80$, $p<0.04$, $y=-11.4x+102.6$) and (b), have higher (more saline) stable carbon isotope signals (1=sites occupied for longest). Linear regression: $R^2=0.55$, $p<0.034$, $y=-0.35x-16.8$).

parents and offspring (figure 2), there are two likely explanations. Birds in good quality breeding habitats may fledge earlier, which could then provide more time to sample and identify the best winter locations. Alternatively, juveniles may disperse and select winter sites independently of their natal habitat quality, but those that settle on better winter sites may be more likely to arrive earlier in Iceland, and thus have a wider choice of breeding territories. Godwits from the higher quality wintering sites in south England are in fact known to arrive in Iceland earlier than those from the poor quality east England sites (Gill *et al.* 2001), suggesting that juvenile settlement decisions are critical in determining future success.

(b) Implications of seasonal matching

Links between summer and winter habitat selection have numerous evolutionary and population consequences. For example, variance in fitness will be increased by individuals with higher breeding success also experiencing higher survival; such increases in fitness variance can have very important implications for effective population size (N_e). For the godwit population, N_e can be approximated with some basic assumptions and generalizations of the demographic parameters obtained for this system. Lifetime reproductive success (LRS) can be calculated from the estimates of survival in good (south coast of England, 94% annual adult survival) and poor (east coast of England, 87%) winter sites (Gill *et al.* 2001), and from the estimates of breeding output obtained in this study, for good quality (marshes, 53.7% of pairs fledging chicks) and poor quality (dwarf-birch bogs, 29.3%) sites in the southern lowlands of Iceland. Assuming (i) perfect matching (all individuals that breed in good habitat also winter in good habitat), (ii) an average productivity of 1 chick per pair, (iii) all birds breed in the second year (iv) a fixed juvenile survival of 0.5 and (v) estimating average lifespan (at the point where 50% of individuals are dead) using $\ln(0.5)/\ln(\text{survival})$, gives a value of LRS of 4.476 recruits *per capita* for individuals using higher quality habitats and 1.126 for those using poorer quality habitats. This gives a variance in the number of progeny (V_k) of 5.609. Using our calculated adult population size of 37 500 (Gunnarsson *et al.* 2005), we can now calculate N_e for perfect matching according to Falconer (1981)

$$N_e = 4N/V_k + 2.$$

This gives an effective population size of 19 714 individuals. When matching is perfectly negative (where gain in one season is compensated perfectly in the other season), $V_k=0$ and thus $N_e=N$. Assuming a linear relationship between this and perfect positive matching (where $N_e=19\,714$), results in a decline in N_e that follows the equation $N_e = -8893.2m + 28607$, where m is the level of seasonal matching. At $m=0.75$ (the approximate strength of seasonal matching in the godwit system, as measured by the exchange of birds between poorer and higher quality breeding and wintering habitats in the present study), yields an effective population size of approximately 22 000 individuals, or only *ca* 60% of the total estimated population size. These are, of course, only approximate calculations based on restricted data and several key assumptions but the magnitude of the effect

strongly suggests that seasonal matching may be a very important driver of evolutionary processes.

Seasonal matching also has potentially important implications for demographic studies which, to ensure sufficient sample sizes, frequently focus on sites with high breeding densities, and on which breeding success is likely to be higher than average (Bock & Jones 2004). If individuals in these better breeding sites also winter in better locations, this approach will not only overestimate average breeding success, but also average survival. Seasonal matching also mean that breeding success can be determined both by the quality of the breeding habitat and by the influence of winter habitat quality on body condition and arrival dates, although the former is considered far more frequently than the latter. Seasonal matching may prove to be a common and widespread feature of migratory systems, and understanding the population-scale demography of these systems will thus require large-scale, cross-seasonal studies of individual settlement decisions.

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