Articles

Journal of Avian Biology 45: 396–405, 2014
doi: 10.1111/jav.00273

Subject Editor: Thomas Alerstam. Accepted 11 February 2014

Age-dependent dispersal and habitat choice in black-tailed godwits *Limosa limosa limosa* across a mosaic of traditional and modern grassland habitats

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Whether to disperse, and where to, are two of the most prominent decisions in an individual's life, with major consequences for reproductive success. We studied natal and breeding dispersal in the monogamous black-tailed godwit *Limosa limosa limosa* in the Netherlands, where they breed in agricultural grasslands. The majority of these grasslands recently changed from wet herb-rich meadows into well-drained grassland monocultures, on which godwits have a lower reproductive success. Here we examine habitat selection with a multistate mark–recapture analysis. Habitat transition probabilities between meadows and monocultures were estimated on the basis of 1810 marked chicks and 531 adults during seven years in a 8500 ha study area. Young and adult godwits may differ in habitat selection because: 1) adults may have gained experience from previous nest success where to settle, 2) younger individuals may find it harder to compete for the best territories. Both young and adults moved at a higher rate from the predominant monocultures to meadows than the other way around, thus actively selecting the habitat with better quality. However, dispersal distance of adults was not affected by previous nest success. The average dispersal distance from place of birth of godwits breeding for the first time was ten times larger than that of adult godwits. That godwits breeding in their second calendar year arrived and laid at similar dates and were equally able to select territories in areas with high breeding densities, suggests that young birds were not competitively inferior to adults. Although on monocultures reproduction is insufficient to maintain constant populations, birds sometimes moved from meadows to monocultures. This explains why even after 30 years of land-use intensification, godwits still breed in low-quality habitat. The adjustment to changing habitat conditions at the population level appears to be a slow process.

The abundance and distribution of organisms in changing landscapes depend not only on habitat quality, but also on the process of habitat selection and dispersal ability of individuals (Greenwood and Harvey 1982, Pulliam 1996, Bowne and Bowers 2004, Bowler and Benton 2005). A species may be absent from a good habitat because that habitat lacks the right selection cues (Gilroy and Sutherland 2007), or because the area is too isolated for dispersers to reach (Hanski 1998). Habitat selection may have become maladaptive if the cues to assess habitat quality become disconnected from actual habitat quality, which can happen in rapidly human-altered environments (Gilroy et al. 2011). If good quality breeding habitat is available but not chosen, population sizes may still decline (Kokko and Sutherland 2001). A case in point is the agricultural landscape complex where land use changes have happened fast (Müller et al. 2005, Reid et al. 2010, Gilroy et al. 2011).

Dispersal of first-time breeders (natal dispersal) generally differs from dispersal of older individuals (breeding dispersal), because young individuals 1) lack information and experience (Delgado et al. 2009), and/or 2) may be subordinate, so that older individuals force them into lower quality habitats (Bowler and Benton 2005, Sergio et al. 2007). Also, in migratory species young individuals often arrive later than older birds (Smith and Moore 2005, Cooper et al. 2009) and thus may find the high-quality territories already occupied (Greenwood and Harvey 1982, Kokko 1999). Young birds may lack the ability to gather information about habitat quality at the relevant spatial and temporal scales, although, in long-lived species non-breeding subadults prospect during their younger years to assess habitat quality for breeding (Dittmann et al. 2005, Becker and Bradley 2007). After an unsuccessful breeding attempt adults may change nest location (Jackson 1994, Fisher and Wiebe 2006, Ost et al. 2011).

The black-tailed godwit *Limosa limosa limosa*, a ground-breeding shorebird, has shown rapid declines since the 1970s (Gill et al. 2007, Boele et al. 2013). Their breeding habitat, agricultural grassland, has changed from herb-rich meadows into well-drained grassland monocultures which are mowed during the nesting phase (Groen et al. 2012). On these monocultures, breeding density (Groen et al. 2012) and chick survival is lower (Kentie et al. 2013) than on meadows, which represent the remains of the traditional agricultural grassland and are now usually managed especially for meadow-breeding birds. Based on nine years of colour ring mark–resighting efforts, we examined age-dependent dispersal distance and habitat selection on a mosaic of meadows and monocultures. Additionally, we examined whether nest success affects breeding dispersal distance, and whether intraspecific competition affects nesting habitat selection in young individuals.

Material and methods

Study area

The study was carried out between 2004 and 2012 in southwest Friesland, the Netherlands (52°55′N, 5°25′E), first on 415 ha area partially managed for godwits and other meadow breeding birds, and between 2007–2012 on 8480 ha of agricultural land (Fig. 1). The expanded study area was 23 km long and 7 km wide. The measurement units were fields, agricultural land separated by ditches. Fields were on average 3.6 ha (SD = 2.3, range 0.3–17.4 ha) and usually have a uniform grassland and management type. We classified grassland on the basis of herb-richness and the occurrence of foot drains (small drainage channels which are 10–30 cm deep) into two types which accurately summarized the intensity of modern agricultural management (Groen et al. 2012). Herb-rich meadows (20% of the study area) contained diverse grass and herb species and had groundwater tables no more than 30 cm below surface, while grassland monocultures (69% of the study area) had lower water tables, consisted dominantly of reseeded high-productive ryegrasses *Lolium* sp. and had instead of foot drains an underground drainage system. The remainder consisted of arable fields, mostly used for growing corn *Zea mays*. Black-tailed godwits are migratory and present in the study area from early March until mid-July (Lourenço et al. 2011). There were around 900 breeding pairs in our study area, of which 40% were breeding in monocultures (Groen et al. 2012).

Data collection

Godwits are ground breeders. Their nests were located (by members of our field team, by volunteers and by farmers), and nest positions determined by GPS. To prevent abandonment of the nest and because the birds are easier to trap when the eggs were nearly hatching, adults were trapped at the end of their incubation stage. They were caught in a walk-in-trap, a mist net which was held vertically over the nest, or occasionally picked up by hand from the nest. Adults were uniquely marked with four plastic colour rings and one flag, and a numbered metal ring. The sex was determined by genetic sexing, for which we obtained 30-μl blood samples, bleeding the brachial vein in adults and the leg vein in chicks. Blood was stored in individual 1.5-ml Eppendorf tubes containing 97% alcohol buffer and frozen at −80°C as soon as possible (usually within days or weeks). The genetic sexing techniques used here are described in full by Trimbos et al. (2013).

Godwit chicks leave the nest within hours of hatching; we therefore used egg flotation (Liebezeit et al. 2007) to predict hatching date so that we could ring newly hatched chicks while still in the nest. Laying date was determined by subtracting 25 d of the day when the first egg hatched. A nest was considered successful if at least one egg hatched. From 2008 onwards, chicks were marked with a plastic flag engraved with a unique code of three characters, as well as a metal ring. Chicks older than ten days that were captured in the field were given the same markings as the adults, as from this age onwards the legs of the chicks were large enough to fit a full colour ring combination. In recaptured chicks the engraved leg flags were replaced, because colour ring combinations were easier to read from a distance. In total we marked 531 adults and 1810 young.

In 2007–2010 and 2012 from early March until the end of April we counted all godwits in the entire study area at weekly intervals, using binoculars and telescopes. We distinguished non-territorial foraging groups from territorial birds by their behaviour. From late April we would have missed the birds that had started to incubate. When encountering a marked bird, we noted its behaviour (foraging, resting, fighting, nest making, alarming, displaying, copulating, chick guiding), whether it was paired, and if so, with which bird. We continued searching for marked birds until the end of June, when they start to migrate towards their wintering areas. In 2011, with fewer observers, we only monitored for marked birds. During the entire study period, the areas surrounding the study area were visited in less regular intervals. With direct observations, recaptures and based on evidence from small video cameras placed for an hour next to the nest, we tried to allocate as many nests as possible to marked godwits. A marked bird was considered territorial if it was seen with a nest, or was seen at least twice with territorial behaviour.

Data analyses

In species with long-lasting pair bonds, dispersal cannot be analysed purely on an individual basis because this results in pseudo-replication (Schmutz et al. 1995). Thus, we first analysed if divorces were common. Two birds were considered a pair if they have been seen incubating on the same nest, or if birds were seen together at least two times in a breeding season. We used the total study period of nine years, during which pairs were on average 3.4 yr under observation. Two individuals that were marked in the first year were known to be together as a pair for the whole study period of nine years. Of the 64 females for which we knew which partner she had for multiple years, two changed partner but in both cases the old partner was never resighted and probably deceased. Of the 60 males for which we knew the partner for more than one year, three changed mate under similar conditions. In the analyses we corrected for this high partner fidelity by using only one pair member of known pairs, or by using territories instead of individual godwits.

We calculated breeding dispersal distances between the midpoints of the fields where pairs were seen with nests or territorial behaviour in consecutive years (from meadows: n = 564, from monocultures: n = 152). For natal dispersal we used the midpoints between the field where chicks

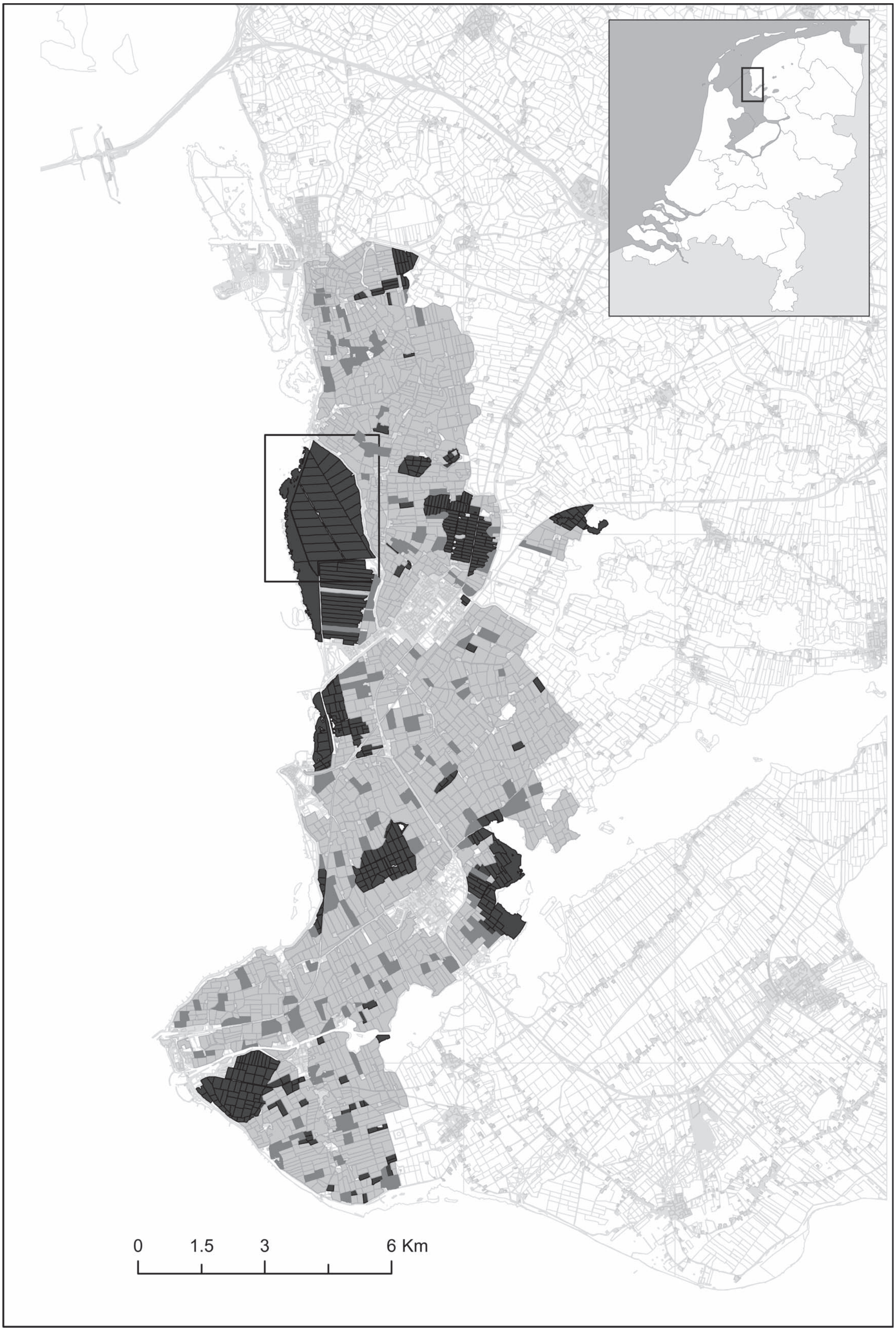

Figure 1. Research area with monocultures (light grey), arable fields (grey) and meadows (dark grey). The boxed area is the Workumerwaard, where we recorded arrival times more accurately.

hatched and the field where we located their first territory (from meadows: $n = 44$, from monocultures: $n = 9$). To prevent zero-truncation of the data, we calculated distances from midpoint to the nearest side of the field for birds that stayed on the same field, assuming the field was square: $\sqrt{\text{area}}/2$. We analysed if natal and breeding dispersal distance differed, and if grassland type (wet herb-rich meadows or grassland monocultures) influenced dispersal distance in the following year. We examined the effect of sex on dispersal distance for chicks hatched on meadows (16 males and 18 females, not all chicks were sexed). The sample size for chicks hatched on monocultures was too low to include in the analysis (2 males and 7 females). We analysed the effect of hatching success on breeding dispersal distances only for pairs of which we knew their territory in the succeeding year (232 pairs with a hatched nest and 34 pairs with an unsuccessful nest). Note that unsuccessful breeding is highly underestimated, because we concentrated our observation and catching of adults at the later stage of the incubation period. We used a linear mixed effect model, where we added pair identity and region as random effects as we knew the breeding location of some pairs in multiple years, and to account for possible area effects, e.g. breeding density and geographical position. As chicks leave their nest within a day after hatching and are difficult to observe, from then onward due to their cryptic behaviour, we were unable to analyse if fledging success was correlated with dispersal distance.

We analysed differences in arrival and egg laying dates for known-age birds that were marked as chicks, which we divided into three age classes: 2 cy (calendar year), 3 cy, and older than 3 cy. For arrival dates we only used data collected on the Workumerwaard, a herb-rich meadow area within our larger research area, which had with daily surveillance the highest resighting effort (resighting probability of 0.24 ± 0.02 d^{-1}, van den Brink et al. 2008, Lourenço et al. 2011). Birds sighted later than 17 May were omitted, as the latest known egg laying date of the known-aged birds was 18 May. Egg laying dates were only used for meadow-areas, as the sample size on monocultures was too low for comparison. To analyse variation in arrival dates we used a linear mixed effect model with individual as random effect, as 15 of the 70 known aged birds were seen more than one year. For egg laying dates we used a linear model, as of only one of the 29 birds we knew laying date in more than one year.

Breeding densities were calculated per field as individuals per ha. We used the maximum counted individuals within the whole period. For 2011 we used the average of 2010 and 2012, which is justified because breeding densities per field are correlated between years ($r > 0.61$ between consecutive years). Because of the left-skewed character of the data, we divided densities into three classes: low density (fewer than 1 ind. ha^{-1}), medium density (between 1 and 2 ind. ha^{-1}) and high density (> 2 ind. ha^{-1}). Based on an average field size of 3.6 ha, low densities represents pairs breeding alone or with one other pair on the field, medium density represents pairs that share the field with 1–3 other pairs and high densities share their field with 3 or more pairs.We tested whether godwits seen breeding for the first time in their second calendar year settled on a field with a different breeding density than godwits which were seen breeding for the first time at an older age. Because of low sample sizes of the 2 cy age class (7, 5, 6 for low, medium and high respectively), we used a Fisher's exact test.

We used R 2.14 to carry out the statistical analyses. Distance was log-transformed, but the predictions based on the models were back-transformed. Linear models were tested with the lm() function, linear mixed models with the lmer() function from the lme4 package and we used the fisher.test() for the Fisher's exact test. The function pvals.fnc() from the language package was used to calculate p values and confidence intervals for the fixed effects of the linear mixed models, using MCMC estimation.

To analyse the probability of changing habitat type, we used a multistate mark–recapture model (Nichols and Kendall 1995) in the program MARK (White and Burnham 1999). The states in our model were: 'breeding on monocultures', 'breeding on meadows' and 'dead'. In this way it was possible to account for the possibility that on monocultures the detection rates of territorial birds were lower given that nests faced higher predation rates (unpubl.). Multistate models consist of resighting probabilities, apparent survival probabilities and transition probabilities. Resighting probabilities were assumed to differ between second calendar year and older birds, as some of the 2 cy birds will not have attempted to breed or returned to the breeding area yet (Groen and Hemerik 2002). Moreover, resighting probabilities were modelled to be able to differ between habitat type and/or per year both as factors and as additive effects. Noting that engraved leg flags were more difficult to read, we accounted for different resighting probabilities for birds ringed with a colour ring combination and an engraved leg flag.

Apparent survival was modelled with an age structure, as young have a lower survival rate (Kentie et al. 2013). Because the chicks ringed with an engraved leg flag were younger than the chicks ringed with a colour ring combination, survival rate was assumed to differ between these two categories as well. Earlier we showed (Kentie et al. 2013) that chicks growing up on monocultures have lower survival probabilities in their first year than chicks from meadows, so grassland type differences were modelled to affect chicks with engraved leg flags. Apparent survival of older chicks and adults could vary or could be constant between grassland types. We also tested if survival differed per year between age classes. Transition probabilities between grassland types may differ between birds in their first year and older birds, and the direction of movement (from meadows to monocultures or the other way around) may differ as well. As we did not have enough data to add extra age classes in the transition probability matrix, the age differences in transition probabilities will be the difference between birds observed from hatch to their second calendar year and the category of older birds. To prevent over-parameterization, we did not add year differences in the transition models.

To reduce the number of models we used a step-down approach (Doherty et al. 2012); we tested whether the data could be more parsimoniously modelled by first testing reduced parameterizations for the resighting probabilities, then for survival probabilities and finally for transition probabilities. Model selection was based on Akaike's information criterion adjusted for small sample size (AICc) (Burnham and Anderson 2002). When multiple models were supported at step 1 and step 2 (ΔAICc < 2), we tested the robustness of the results by applying subsequent steps using all of these models.

To prevent pseudo-replication caused by the long-term pair bonds, we randomly selected one individual from pairs of which both partners were known. Goodness-of-fit was tested in U-CARE (Choquet et al. 2009), and the data were not over-dispersed ($\chi^2 = 78.8$, DF = 66, p = 0.13).

Results

Dispersal distances

The maximum recorded distance for breeding dispersal was 15 km, but 75% of the adults were breeding within 500 m during a subsequent breeding attempt. For natal dispersal, the maximum recorded distance was 18 km, and 74% of the young godwits were breeding further than 1000 m from the nest of birth (Fig. 2). Average natal dispersal distance from chicks born on meadows was 915 m (95% CI: 550–1515 m) and from chicks born on monocultures 1700 m (95% CI: 1190–2430 m), which was ~ 7 times greater than adult breeding dispersal (from meadows: 125 m, 95% CI 85–195 m, from monocultures: 235 m, 95% CI 185–295 m, Table 1, Fig. 3). There was no interaction between age and grassland type of origin ($p > 0.6$). There was no difference in natal dispersal distance between males and females ($p > 0.9$, Table 1). We found no difference in dispersal distance between pairs with a hatched nest and pairs with an unsuccessful nest ($p > 0.7$, Table 1, Fig. 4). There was no interaction between the effects of nest success and grassland type ($p > 0.3$).

Probability of changing grassland type

Model selection of the multistate models describing resighting, survival and transition probabilities, of which the details are shown in Supplementary material Appendix 1, resulted in two models within 2 ΔAICc. Both models included an age and grassland type dependent transition probability. The difference between the two models is that the best supported model showed a year-dependent survival for chicks ringed in the nest, whether the second best model did not. Because of boundary effects in the survival of chicks ringed with an engraved leg flag in some years, estimates that are close or equal to one cause the standard errors not to be estimated correctly; hence, model averaging was not possible. However, the two models showed similar transition estimates: young birds in their first year moved with a higher rate from monocultures to meadows (0.58 ± 0.12 SE) than the other way around (0.16 ± 0.06 SE). Also, a higher rate of adults moved from monocultures to meadows (0.24 ± 0.03 SE) than the other way around (0.04 ± 0.01 SE) (parameter estimates in Supplementary material Appendix 2, Table A2). Note that the

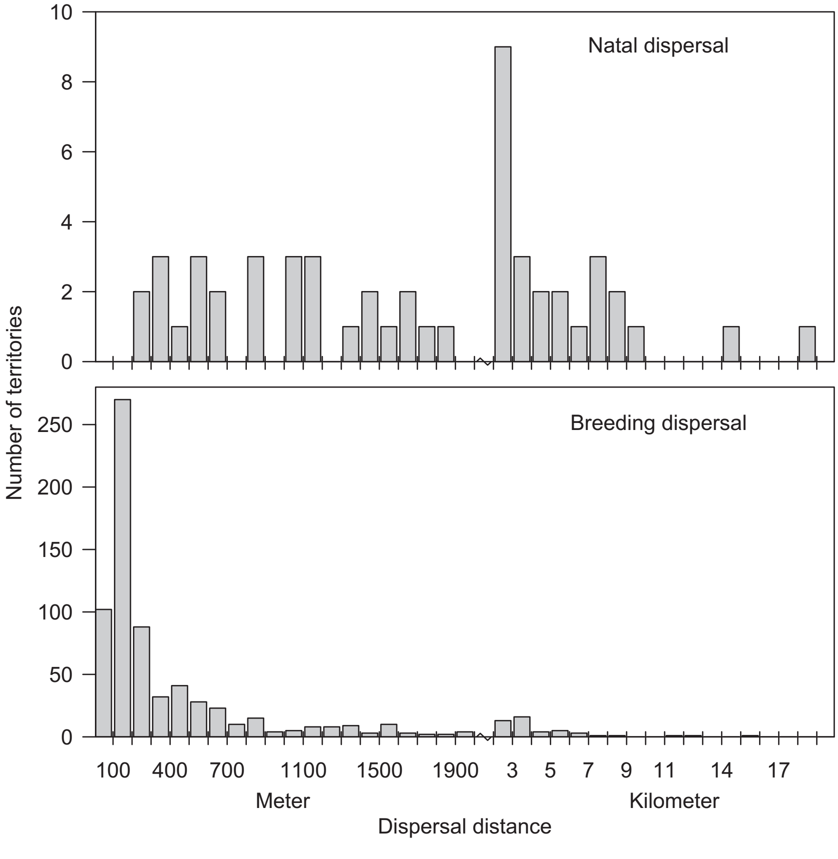

Figure 2. Frequency distribution of natal and breeding dispersal distances for black-tailed godwits between subsequent years. Distances between territories known for pairs for multiple years are not accounted for.

Table 1. Results of a linear mixed model explaining dispersal distance (log-transformed) of black-tailed godwits. ^{1}Reference age is young, ^{2}reference type is monoculture, ^{3}reference is female, ^{4}reference is unsuccessful.

Parameter	Estimate	95% CI	p
Age and habitat effect on dispersal distance (n = 769)			
Intercept	8.05	7.65–8.41	< 0.001
Age^1	−1.98	−2.24– −1.65	< 0.001
Habitat type^2	−0.62	−0.87– −0.35	< 0.001
Random effects	SD		
Bird	0.63	0.00–0.13	
Region	0.30	0.13–0.49	
Residual	0.84	0.98–1.08	
Sex effect on natal dispersal distance (n = 34)			
Intercept	7.92	6.60–8.95	< 0.001
Sex^3	−0.02	−0.66–0.64	0.95
Random effects	SD		
Region	0.63	0.00–0.82	
Residual	0.95	0.78–1.27	
Nest success and habitat effect on breeding dispersal distance (n = 266)			
Intercept	6.64	5.78–7.47	< 0.001
Habitat type^2	−0.52	−0.98– −0.09	0.02
Nest success^4	−0.17	−0.45–0.35	0.77
Random effects	SD		
Bird	0.61	0.00–0.22	
Region	0.30	0.14–0.62	
Residual	0.84	0.99–1.18	

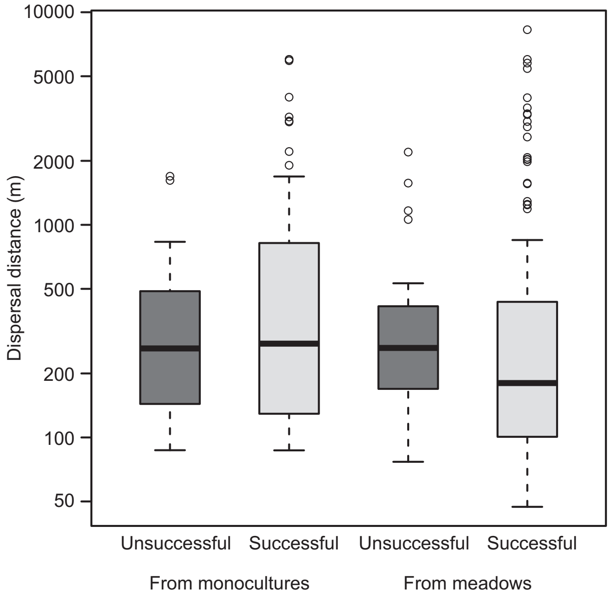

Figure 4. Dispersal distance after a successful and unsuccessful nest, for black-tailed godwit pairs coming from monocultures and meadows. Box-and-whisker plots give the median (horizontal line inside the box), interquartile range (box), range (bars) and outliers (open dots).

apparent survival estimates in the appendix are estimates of birds found with a nest or with territorial behaviour only.

Arrival and laying date and settlement densities of known-age birds

The arrival dates of second and third calendar year birds in the Workumerwaard did not deviate from that of older birds (2nd cy: $\beta = -3.35$, 95% CI $-12.19-4.94$, $p > 0.4$, 3rd cy: $\beta = -1.08$, 95% CI $-9.55-7.10$, $p > 0.7$, SD of random effects: individual = 0.00, residual = 16.67; Fig. 5a). Five birds with known-ages were found breeding on meadows in their second year, nine in their third and 16 were older than three. Laying dates did not differ between the age classes (2nd cy: $\beta = 1.53$, 95% CI $–8.82-11.87$, $p > 0.7$, 3rd cy: $\beta = 0.46$, 95% CI $–7.96-8.88$, $p > 0.9$; Fig. 5b).

Godwits that we found occupying territories in their second calendar year had similar probabilities of settling in high, medium or low densities than godwits that were discovered on territories for the first time in their 3rd calendar year or when older (Fisher's exact test: $p > 0.5$, Fig. 6).

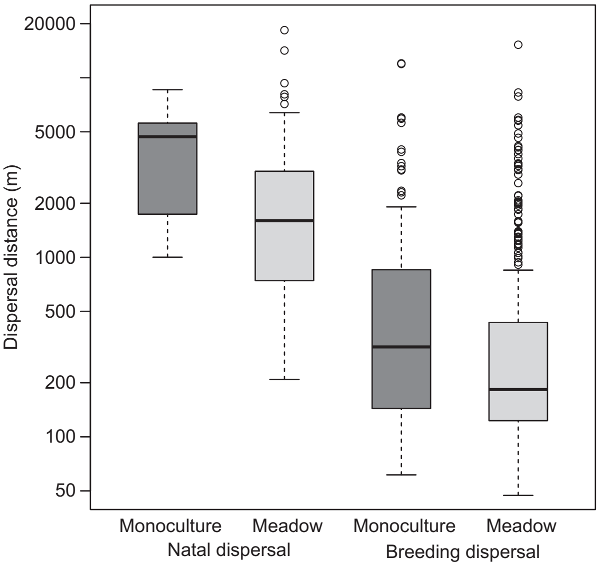

Figure 3. Natal and breeding dispersal distance for black-tailed godwits coming from monocultures and meadows. Box-and-whisker plots give the median (horizontal line inside the box), interquartile range (box), range (bars) and outliers (open dots).

Discussion

In our large scale study we found that both young and adult black-tailed godwits were more likely to disperse from poor to high quality habitat than in the opposite direction. We were unable to show that dispersal distance of adults correlated with nest success. In addition, adult godwits were more site-faithful to their previous breeding location than first-time breeders to their natal site. In view of the similar experienced densities at settlement, the lower site-faithfulness of young first-time breeding godwits compared to older birds does not seem to be caused by intraspecific competition.

Natal and breeding dispersal distance

Within our study area, 47% of adult black-tailed godwits bred within 100 m of their previous nest site. This is a slightly lower percentage than in previous studies on nest site fidelity of adult black-tailed godwits, which was 60% within

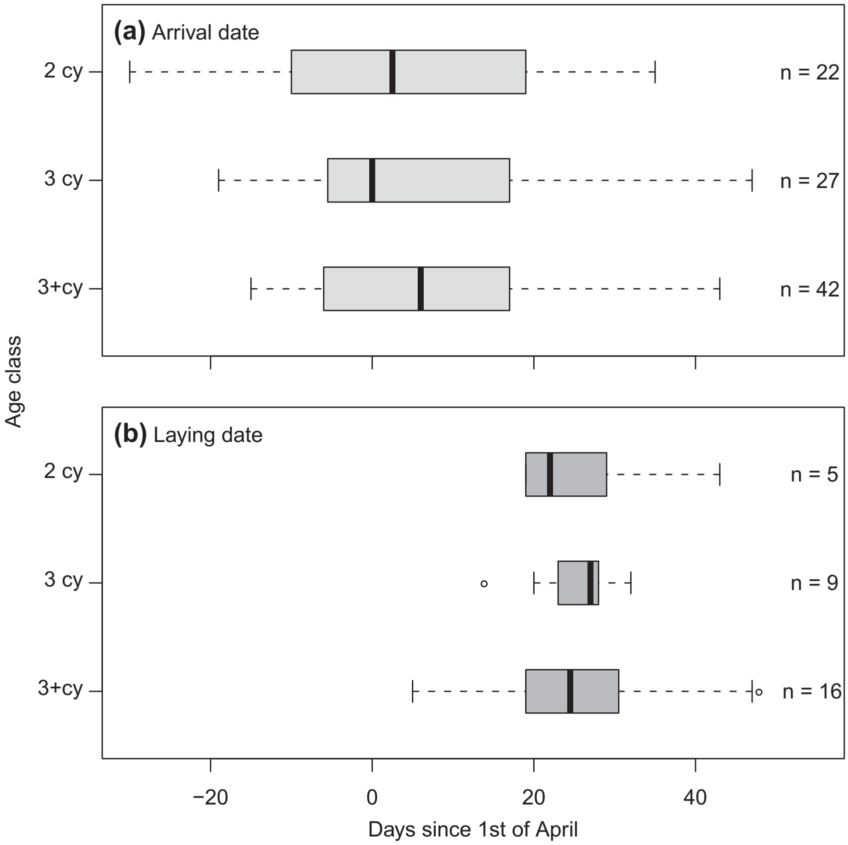

Figure 5. Arrival (a) and laying (b) date of black-tailed godwits, counted from 1 April, per age class of godwits with known ages. Arrival date is for godwits on the Workumerwaard only, and laying date is for godwits on meadows throughout the study area. Box-and-whisker plots give the median (horizontal line inside the box), interquartile range (box) and range (bars). Sample sizes are shown at the right side of the plot.

100 m in two herb-rich meadow areas between 2002–2004 (Roodbergen et al. 2008), and 50% within 50 m in a herb-rich meadow site between 1984–1988 (Groen 1993).

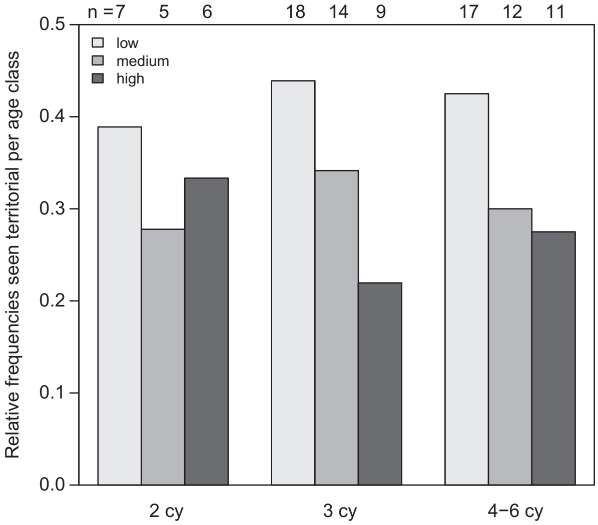

Figure 6. Relative frequencies of known-aged black-tailed godwits which settled on low (<1 ind. ha^{-1}), medium (>1 and <2 ind. ha^{-1}) and high (>2 ind. ha^{-1}) breeding densities measured on field level.

These small differences may either have a methodological or a biological basis. With respect to the first possibility, our study area is larger and we were therefore better able to record individuals showing long-range dispersal. With respect to the second, in comparison with the previous studies our study area contained less high-quality meadow habitat, areas that were positioned as islands in the predominant low-quality monocultures habitat (Fig. 1, Groen et al. 2012). This may have induced greater dispersal.

Young godwits are less site-faithful to their natal site than adults, as 58% started breeding further than 2 km away from where they hatched. This suggests that more chicks than adults moved out of the study area (van Noordwijk 1995, Winkler et al. 2005). Consequently, the difference between natal and breeding dispersal distances would be underestimated. A study on the Icelandic black-tailed godwits *Limosa limosa islandica*, a subspecies distinct from the godwits studied here, revealed a difference in natal dispersal distance between males and females (Gunnarsson et al. 2012). We were not able to find such a sex difference.

In most bird species, young disperse further than adults (Greenwood and Harvey 1982, Thompson et al. 1994, Blums et al. 2003a). A common functional explanation of this difference of natal and breeding dispersal distance is the avoidance of inbreeding (Greenwood and Harvey 1982, Bowler and Benton 2005). The difference between natal and breeding dispersal distance might also be induced because familiarity of the territory is higher for older birds than for young, making it more beneficial for adults to return to the same breeding area (Piper 2011). The large natal dispersal distance is consistent with the finding that the Dutch black-tailed godwit population is genetically panmictic (Trimbos et al. 2010). We found no evidence for another, mechanistic, explanation, namely that young godwits may suffer more from intraspecific competition than older godwits. A higher breeding density is found in good-quality meadows (Groen et al. 2012), and second calendar year birds are as able to settle in high-density territories as older birds. In eastern kingbirds *Tyrannus tyrannus*, young individuals arrive later and are therefore less able to access good-quality territories (Cooper et al. 2009). Godwits in their second calendar year arrived and laid their nest at the same date as older ones. This suggests either that young godwits are not competitively inferior, or that enough territories were vacant because of on-going population declines.

As not all godwits started to breed when one year old, it is possible that birds starting to breed at a later age prospected the year(s) before, as is usual in long lived seabirds (Becker and Bradley 2007). Of the birds we ringed as chicks, we observed a higher percentage of individuals in their second year only in the post-breeding gatherings in June and July (28%, $n = 149$), than birds known to be older than two years (14%, $n = 198$, $\chi^2 = 29.56$, $DF = 2$, $p = 0.002$). Although part of these individuals probably went unnoticed during and before breeding because they were breeding outside the study area, the higher percentage suggests that at least some of the two-year old godwits returned to the breeding area as prospectors.

Habitat choice

As the likelihood of movement was four times higher in the direction of herb-rich meadows than to monocultures (24 vs 6%), adult godwits clearly preferred herb-rich meadows over grassland monocultures. Young godwits born on monocultures were also more likely to move to meadows (58%) than young godwits born on meadows were to move to monocultures (16%). As our study area contained mostly grassland monocultures, this higher proportion indicates an active choice of adults and first-year breeders. For adults, this choice may be based on life-time experience. Reproduction on monocultures is lower than on meadows (Kentie et al. 2013), yet we found that nest success was not directly correlated with dispersal distance. An effect of nest failure on dispersal distance is seen in some studies (Jackson 1994, Fisher and Wiebe 2006, Chalfoun and Martin 2010, Ost et al. 2011), but not in all (Jackson 1994, Blums et al. 2003b, Colwell et al. 2007). For individuals of long-lived species such as the black-tailed godwit it may not be beneficial to move to another area as a result of nest failure in one year, and instead cumulative reproductive success may explain movement decisions better (Greenwood and Harvey 1982). Additionally, low reproductive success of close conspecifics, high perceived predation risks (Lima 2009) and disturbance, may all be more likely to be highest on the more intensively managed monocultures, which would affect the decision to move away from there.

If, as in blue-footed boobies *Sula nebouxii*, unsuccessful birds only dispersed if they also switched partners (Kim et al. 2007), the great faithfulness of godwits to their partner may help explain why they stay so close to their previous sites. Indeed in a small-scale study, godwits arrived closer to their previous nest site than the precise nest location that they eventually settled on (van den Brink et al. 2008). As male godwits arrive on average 3 d earlier than females (Gunnarsson et al. 2006, Lourenço et al. 2011), the previous nest site can act as a meeting place for partners. In years with an unusual distribution of arrival, e.g. due to extreme weather conditions en route, divorce and dispersal rates are predicted to be higher.

Chicks which fledged early in the breeding season might be able to gather social information on habitat quality (Doligez et al. 2002), such as presence of other godwit families. However, most growing and flightless chicks would have no access to these social cues due to limitations on movement until three weeks of age. Post-breeding location cues such as the presence of territorial males that triggered habitat choice in Nelsons's sharp-tailed sparrows *Ammodramus nesloni* (Nocera et al. 2006), are unavailable to black-tailed godwits, as parents do not remain territorial after breeding. Moreover, all grassland fields are mown after breeding (Schekkerman and Beintema 2007), and this may reduce the amount of information on breeding habitat quality later in summer. It seems that most second calendar year godwits must choose their first breeding habitat on habitat cues or social information upon arrival in the breeding area the following year. In the settlement phase it might be difficult to tell meadows and monocultures apart, as their most obvious distinction, herb-richness, will be most pronounced in May. First-year breeders arrive and lay their nest at similar times as older breeders, suggesting that they occupy their territory also at a similar date. The question of how young birds decide where to breed remains open and calls for more detailed studies, as numerous potential sources of social information are available (Bijleveld et al. 2010).

Consequences for the population

Although most adults and young godwits choose to breed on meadows of higher breeding quality than monocultures, still, we showed that yearly 6% of the adults and 16% of the young godwits move from meadows to monocultures, and 76% of the adults and 48% of the young stay in this habitat. This explains why even after 30 yr of land-use intensification and the creation of ryegrass monocultures (Gill et al. 2007), godwits still breed in this low-quality habitat where reproduction is likely to be insufficient for a stable population (Groen et al. 2012, Kentie et al. 2013). Because the population in good-quality areas has declined as well, negative effects of density dependence on settlement decisions are probably small. As in other migrants, the adjustment to changing habitat conditions seems to be a slow process (Lok et al. 2013).

Acknowledgements – We thank the fellow members of the respective 'grutto-teams' of the Univ. of Groningen that contributed to this study: Ysbrand Galama, Niko Groen, Petra de Goeij, Pedro Lourenço, Krijn Trimbos, Julia Schroeder, Rinkje van der Zee, Valentijn van den Brink, Job ten Horn, Rienk Jelle Hibma, Haije Valkema, Egbert van der Velde, Niels Bot, Gjerryt Hoekstra, Sjoerd Hobma, Sytse-Jan Wouda, Lucie Schmaltz, Rocio Marquez and many students and volunteers. Nature conservancy organisations (It Fryske Gea and Staatsbosbeheer) and private land owners generously issued permission to access their properties. Volunteers of local bird conservation communities (Fûgelwachten Makkum, Warkum, Koudum-Himmelum, Stavoren-Warns) provided locations of many nests. We thank Marco van der Velde and Krijn Trimbos for molecular sexing, and Jenny Gill and Tomas Gunnarsson for their helpful comments. This study was mainly funded by the 'Kenniskring weidevogels' of the former Ministry of Agriculture, Nature Management and Food Safety, with additional financial support of the Prins Bernhard Cultuurfonds, the Univ. of Groningen, the Province of Fryslân, and BirdLife-Netherlands. This work was done under licence number 4339E following the Dutch Animal Welfare Act Article 9.

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Supplementary material (Appendix JAV-00273 at <www.avianbiology.org/readers/appendix>). Appendix 1–2.