Foraging range, habitat use and minimum flight distances of East Atlantic Light-bellied Brent Geese *Branta bernicla hrota* in their spring staging areas

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Abstract

Global Positioning System (GPS) satellite telemetry was used to determine the foraging range, habitat use and minimum flight distances for individual East Atlantic Light-bellied Brent Geese *Branta bernicla hrota* at two spring staging areas in Denmark. Foraging ranges (mean ± s.d. = 53.0 ± 23.4 km^2) were comparatively large, greater than reported elsewhere for this species, and habitat use revealed a high exploitation of salt marshes (64.4%), which now replace traditional fjord habitats as the most important for spring-fattening. At one site (Agerø), geese had started to exploit agricultural fields (winter-sown cereals; 11.8% of the total GPS location data), and in all areas fjords were still frequently used for roosting at night. Minimum flight distances for foraging excursions at the staging sites varied considerably between individual geese (ranging from 4.64–10.14 km/day), and these were related to differences in habitat use. Geese using a high proportion of agricultural areas flew greater distances than those avoiding this habitat. Compared to historical data on the same population, these findings indicate a significant enlargement of foraging ranges and increased use of terrestrial habitats. This might reflect changes in habitat availability, and is probably related to significant declines in Common Eelgrass *Zostera marina* in both these areas. From a historically rather sedentary lifestyle, which centred around foraging on *Zostera* beds in fjord habitats, this population now feeds on scattered areas of salt marsh, and increasingly on inland winter-sown cereals, in a progressively cultivated landscape. As fjord habitats remain the preferred roosting areas (probably as a consequence of differences in perceived habitat-specific predation risk), this "terrestrialisation" of Brent Goose habitat use is associated with increased energetic costs in the form of higher minimum flight distances.

Key words: Climate change, GPS, salt marsh, winter-sown cereal, *Zostera*.

Establishing range use, habitat exploitation and movement patterns of individual birds are essential for underpinning effective management of waterfowl populations (Legagneux *et al.* 2009; Herring & Collazo 2005). In order to foresee potential impacts of environmental change, and to act in time when mitigation measures are needed, basic autecological information is necessary to guide management decisions. Currently, environmental change is occurring at an unprecedented rate, as climate change and its associated impacts are affecting coastal ecosystems and waterfowl populations to a great extent (Parmesan & Yohe 2003; Meinshausen *et al.* 2009; Watkinson *et al.* 2004). More than ever, we need to understand how coastal areas are exploited by its avian inhabitants, and how the changing availability of different habitats might affect behavioural patterns in individual species. For small populations such investigations are even more urgent, as minor lags in adapting to environmental change might be critical to the future persistence of these populations.

In this study we investigate how the small population of East Atlantic Light-bellied Brent Geese *Branta bernicla hrota* exploit coastal areas during spring-fattening in their Danish staging areas, and compare the current situation with both historical descriptions from the same area and the exploitation of intertidal habitats in Lindisfarne, UK during early autumn. This population, presently numbering 6,800 birds (P. Clausen, unpubl. data), is among the smallest goose populations in the world (Clausen *et al.* 1999). The population breeds and moults in the high Arctic (Svalbard and North Greenland) and winters around the North Sea, especially in northern Denmark and increasingly at a single site, Lindisfarne, in northeast England (Denny *et al.* 2004). Traditionally, this population exploited marine and intertidal *Zostera* beds (Fog 1972; Clausen & Percival 1998). While these habitats are still available in some areas (*e.g.* at Lindisfarne), many of the historical staging sites have experienced on-going declines in the area and abundance of *Zostera*, which has forced birds to become increasingly terrestrial in their search for high-nutrient food, relying especially on the fresh growth of salt marsh vegetation in late spring (Clausen & Percival 1998). However, in the modern Danish landscape, salt marshes consist of small and highly scattered patches in a mosaic of agricultural land, and the patchy distribution of available salt marsh may have resulted in a major change in the foraging range and flight distances for the birds on their switching to salt marsh habitat. Little is known about the area and precise habitats currently exploited by individual geese, and movement patterns associated with foraging in a fragmented coastal landscape have not been studied to date. The development of lightweight and highly accurate GPS satellite transmitters allows for objective and accurate investigation of these issues, and is the perfect tool for enhancing knowledge of the spatial patterns of foraging Brent Geese, for the increasingly scattered population that exploits Danish coastal areas. Here GPS technology is used to: 1) describe the foraging range of individual geese, 2) determine habitat use in the spring staging areas, 3) assess individual flight distances, in relation to differences in foraging range and/or habitat use, and 4) compare potential behavioural differences between foraging in a scattered coastal landscape (Denmark) and foraging on larger continuous intertidal flats (Lindisfarne, UK).

Methods

The tracked geese were initially caught with cannon nets at two sites in Denmark, at: 1) Agerø (56°47'N, 8°33'E and 56°42'N, 8°31'E; on 27 April and 3 May 2011), and at 2) Nibe Bredning (56°59'N, 9°34'E; on 3 and 7 May 2012). Seventeen satellite transmitters (30 g solar GPS PTTs from Microwave Telemetry) were glued to the back of well-conditioned male geese (the largest and heaviest individuals) and fastened with an elastic harness which crossed-over on the belly (Glahder *et al.* 1998). In both years, the birds' diurnal positions were determined through five (27 April–14 May) or 11 (14 May until spring migration departure) GPS fixes recorded daily.

Prior to any analysis, positions from flying birds (speed > 10 km/h) were excluded from the dataset. Furthermore, only birds with > 20 days of location data were used in the analyses; one bird whose transmitter was functional for only half the study period was omitted from the data. Foraging ranges were defined by "Minimum Convex Polygons" (MCPs; Mohr 1947), which covered all GPS positions where the birds were either foraging or roosting in Denmark, throughout the spring fattening period (late April/early May until departure). Visual comparison of MCPs using 75%, 90% and 100% of the fixes strongly favoured using all (100%) of the data to describe the birds' foraging ranges, rather than considering smaller "core" areas, as using subsets of the data tended to exclude geographically distant sites even when these were heavily used. Including all positions in the analysis therefore was important for describing individual variation in foraging ranges, and the high precision of individual fixes (80% at ≤ 10 m of actual position; http://www.microwavetelemetry.com/Horizontal%20combined%20GPS.pdf) generally supports this procedure. Furthermore, the spatial distribution of the GPS positions favoured MCPs above kernel analysis, as spatial clustering of fixes in often widely separated areas tends to produce disjointed kernel ranges, and the focus on relatively small core areas in kernel analysis does not capture the importance of distances between exploited sites. Kernel analysis therefore would have been misleading for determining the factors influencing flight distances of individual birds. Upon arrival at the post-breeding areas at Lindisfarne, data from two transmitters still satisfied the criteria outlined above. Because foraging ranges in this area might be more representative of traditional intertidal habitat exploitation, these were calculated in the same manner (from mid-September to mid-October) and used for comparison with the present situation in Denmark. The geographic extent of individual foraging ranges were analysed in ArcMAP 10.0, and general linear modelling (GLM) was used to analyse the effects of staging site (Agerø, Nibe Bredning) and number of GPS positions on foraging range area.

Spring habitat use of individual geese was quantified by overlaying the GPS positions with a digitised habitat map holding data on the distribution of three Danish habitat types: 1) fjord habitats, 2) salt marshes and 3) agricultural areas, with the addition of intertidal mudflats to describe habitat use at Lindisfarne. Geographic delineation of Danish habitat types were based on data from the Danish Natural Environmental Portal, and fjord habitats classified on the basis of the combined categories of mudflat, gravel shore and sandbanks surrounded by seawater (often used as the roost at night). Delineation of Lindisfarne habitats were based on ground-truthed orthophotographs. Potential differences between day and night were investigated by defining "night" as the period from 1.5 h after sunset to 1.5 h before sunrise, and individual habitat use was expressed as the proportion of fixes in any given habitat. Differences in habitat use between sites were tested with Mann-Whitney U tests on these proportional data.

Minimum flight distances recorded for individual geese at the spring staging sites were calculated by summing orthodromic distances (Imboden & Imboden 1972) between consecutive GPS positions, and expressed as an average flight distance in km/day. Potential effects of habitat use, the number of GPS positions and foraging range on minimum flight distances were investigated by GLM. Minimum flight distances of individual birds were used as response variable, and covariates included area of foraging ranges, number of GPS locations, and proportional use of agricultural habitat of individual birds. Due to non-independence of data on habitat use (*i.e.* the proportional use of agriculture, salt marsh and fjord sums to one), agricultural exploitation was used as a proxy of general habitat use. Agricultural habitat use showed the largest individual variation of the three habitat types, and was negatively correlated with the exploitation of both salt marsh (Pearson's r_{15} = –0.78, $P < 0.001$) and fjord habitats (Pearson's r_{15} = –0.49, P = 0.04), meaning that this proxy could represent a measure of terrestrialisation among geese. Proportional data were arcsine square root transformed prior to analysis to satisfy the assumption of normally distributed error terms.

Results

Foraging ranges in the Danish spring staging areas averaged at 53.0 km^2 (s.d. = 23.4), and varied considerably among individual birds (range = 21.4–94.9 km^2; Table 1, Fig. 1). There were no significant differences in foraging range between the two Danish sites ($F_{1,15}$ = 0.40, n.s.), and the geographic extent was unaffected by the number of data points available from individual birds ($F_{1,15}$ = 0.01, n.s.), thereby excluding small transmitter-related differences in the amount of data as an explanatory factor. The two post-breeding intertidal foraging ranges at Lindisfarne averaged 15.0 km^2 (s.d. = 2.5), which was lower than any of the Danish foraging ranges, and (even with only two data points from Lindisfarne) significantly different from these (Mann Whitney U = 0, n_1 = 2, n_2 = 16, P = 0.03). That the Lindisfarne foraging ranges really were small was supported by location data from two additional birds whose

Table 1. GPS-based foraging ranges (Minimum Convex Polygons) and minimum flight distances (summed orthodromic distances) recorded for 16 Light-bellied Brent Geese at their Danish spring staging areas – Agerø and Nibe Bredning – during May 2011 and May 2012 respectively. The ranges and flight distances for two geese whose transmitters were still functioning upon arrival at Lindisfarne, UK, post-breeding (bottom rows) are included for comparison.

Bird name	Transmitter #	Site	Foraging range (km^2)	Minimum flight distances (km/day)
Abel	41179	Nibe Bredning	94.9	8.56
Arner	41181	Nibe Bredning	84.6	5.17
C. McNeile	54599	Nibe Bredning	57.1	4.64
Caretaker	54604	Agerø	61.4	10.14
Ebbe	54603	Agerø	38.0	6.20
Finn	54611[a]	Nibe Bredning	68.8	9.73
Fridtjof	54607	Agerø	30.3	5.45
Herman	54602	Nibe Bredning	21.6	5.87
Jan Ove	54597	Agerø	54.9	9.68
Loff	54611	Agerø	73.3	5.93
Ludvig	54597[a]	Nibe Bredning	47.7	5.59
Magnar	54606	Agerø	60.9	5.45
Niels	54612	Agerø	21.4	8.56
Otto	41177	Nibe Bredning	83.0	5.49
Robert	41180	Nibe Bredning	23.8	4.83
Steve	54610	Agerø	26.3	9.76
Loff[b]	54611	Lindisfarne	16.8	5.42
Steve[b]	54610	Lindisfarne	13.2	5.51
Average[c]			**53.0**	**6.94**

[a]Transmitter from 2011 reused in 2012.
[b]Data from two transmitters still functional after arrival at Lindisfarne post-breeding.
[c]Lindisfarne data excluded.

transmitters did not provide a sufficient number of days with complete data for inclusion in the analysis.

There was a significant difference in goose use of agricultural (Mann Whitney $U = 0$, $n_1 = n_2 = 8$, $P = 0.001$) and fjord

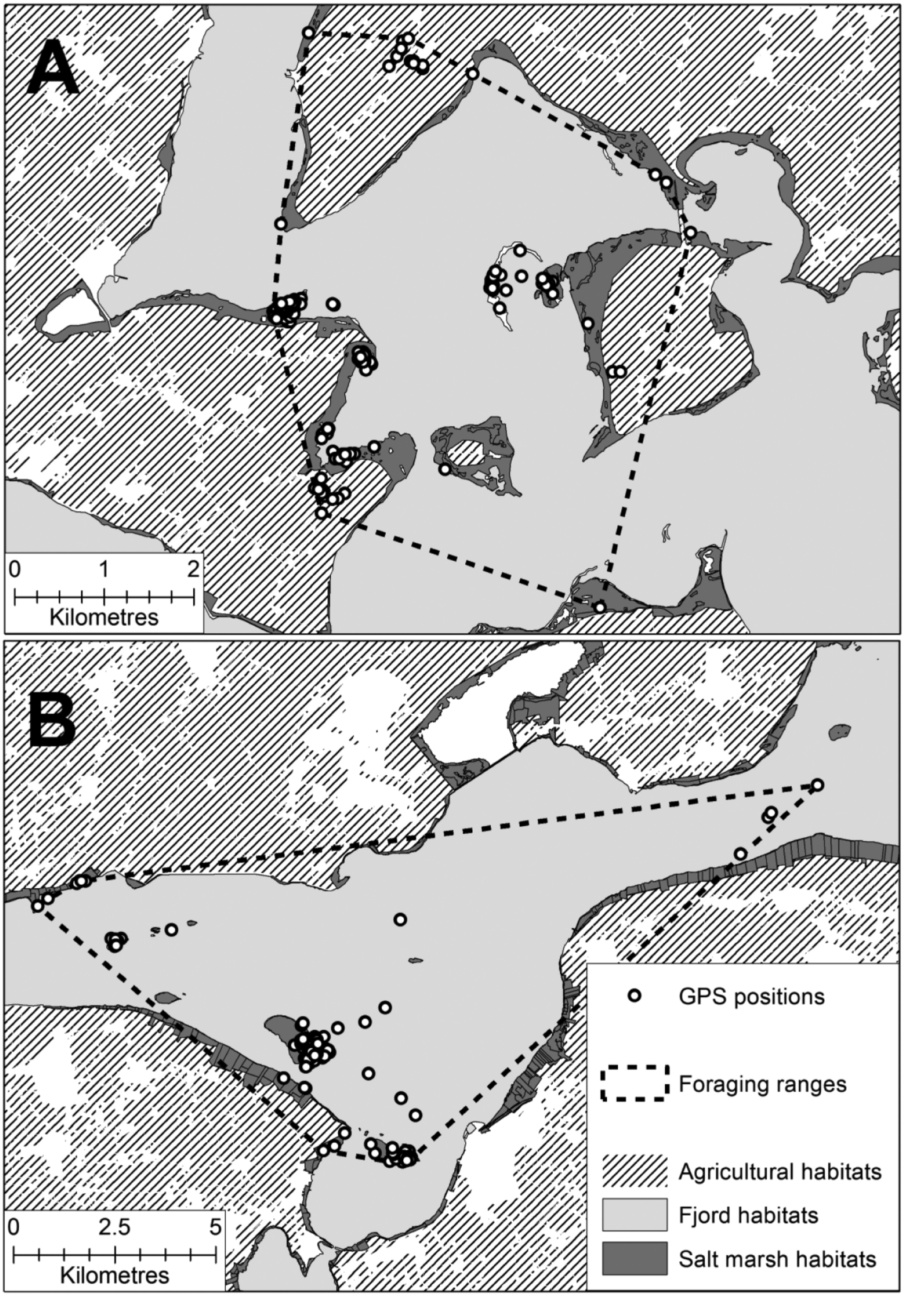

Figure 1. GPS positions and foraging ranges recorded for two Light-bellied Brent Geese: A = "Niels" tracked at Agerø in May 2011; B = "Arner" tracked at Nibe Bredning in May 2012.

(Mann Whitney $U = 9$, $n_1 = n_2 = 8$, $P = 0.02$) habitats at the two sites in Denmark, with use of agricultural habitat being proportionally higher at Agerø, whereas fjord habitats were visited more frequently in Nibe Bredning. The use of salt marsh habitats did not differ significantly between sites (Mann Whitney $U = 24$, $n_1 = n_2 = 8$, n.s.). In both areas, overall habitat use clearly revealed salt marsh as the most important spring habitat (Figs. 2a,b). On Agerø, agricultural fields accounted for 11.8% of the total number of fixes (to our knowledge, all of them on winter-sown cereal), whereas this habitat was not used in Nibe Bredning (Fig. 2). Habitat use also varied considerably between day and night, as the use of fjord areas increased during night when birds returned to roost in this habitat (Fig. 3). Individual variation in overall habitat use, measured as the percentage of GPS fixes recorded on each habitat type for each bird, was substantial for all three habitat categories, ranging from 0–40% (mean ± s.d. = 7.8% ± 11.2, n = 16) for agricultural habitats, 35.8–81.8% (63.2% ± 12.8, n = 16) for salt marshes and 13.1–42.3% (28.9% ± 8.1, n = 16) for fjord habitats. Our limited data from Lindisfarne (Fig. 2c) indicated that post-breeding birds in this area exploited almost exclusively intertidal habitats.

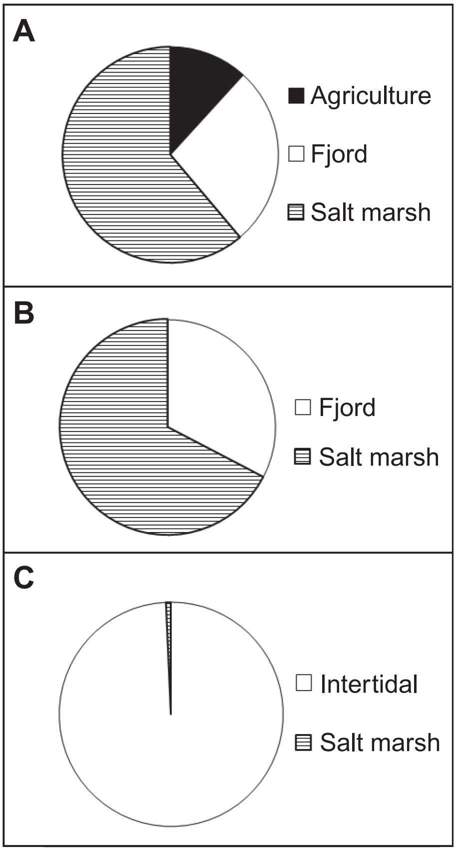

Figure 2. Overall habitat use (proportion of locations recorded) by East Atlantic Light-bellied Brent Geese at: (A) Agerø, Denmark in May 2011, (B) Nibe Bredning, Denmark in May 2012, and (C) Lindisfarne, UK during September–October 2011.

The average of the minimum flight distances recorded for the 16 geese tracked during spring staging in Denmark was 6.94 km/day (s.d. = 2.1; Table 1), and varied considerably between individual birds (range = 4.64–10.14 km/day). Differences in minimum flight distances over the spring staging period were best explained by individual variation in habitat use, so that birds with a higher proportional use of agricultural fields flew significantly further distances (GLM: $F_{1,15} = 10.38$, $P < 0.007$; Fig. 4). The size of the foraging ranges (GLM: $F_{1,15} = 0.14$, n.s.) and number of GPS fixes (GLM: $F_{1,15} = 0.05$, n.s.) did not have a significant effect on the distances

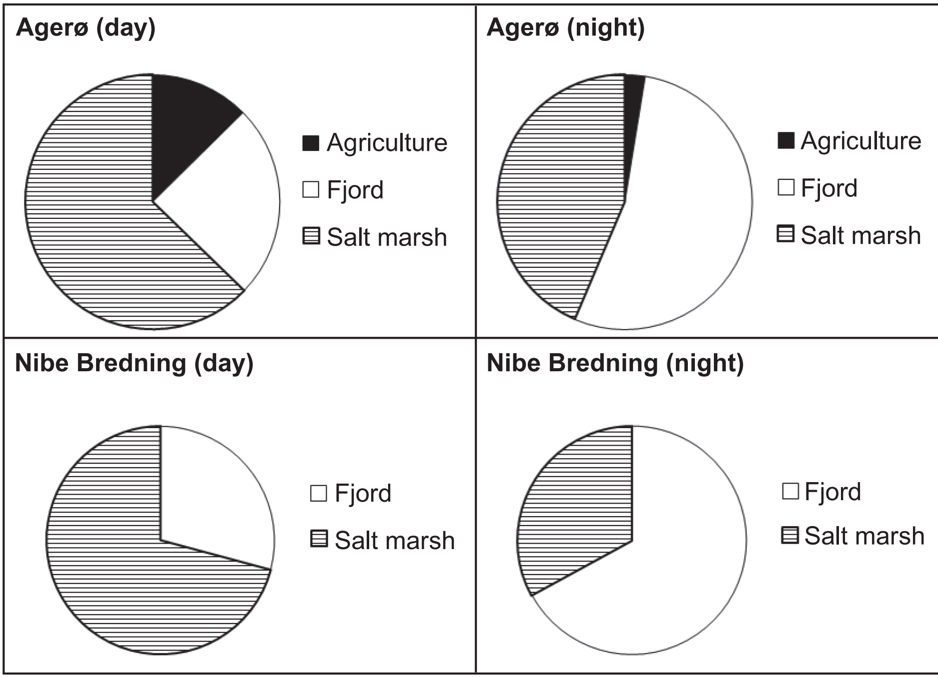

Figure 3. Daily and nightly habitat use of East Atlantic Light-bellied Brent Geese in the Danish spring staging areas Agerø and Nibe Bredning during May 2011 and 2012 respectively.

flown by individual birds, indicating that variation in flight distances was attributable to different habitat exploitation patterns (*e.g.* the frequency of movement between feeding areas and frequency of disturbance) rather than the overall size of the foraging range or amount of data. At Lindisfarne, where geese resided almost exclusively in intertidal habitats, the minimum flight distances were generally very low (mean = 5.47 ± 0.07; Table 1).

Discussion

This study highlights that coastal exploitation patterns varied greatly among individual Brent Geese in their Danish spring staging areas. The average foraging range of 53 km^2 over a four week period was considerably larger than that found for two of the same birds at Lindisfarne (15 km^2) post-breeding. The most obvious explanation for this dissimilarity is the differences in habitat use and movement patterns between the two sites. At Lindisfarne, birds are entirely committed to use of one intertidal area, foraging intensively on intertidal *Zostera* at low tide and roosting near the coast at high tide throughout early autumn (Percival & Evans 1997). This is very well reflected in the low flight distances characteristic of our two Lindisfarne birds, tracked post-breeding in autumn 2011. Visual inspection of their GPS positions found that of 288 individual

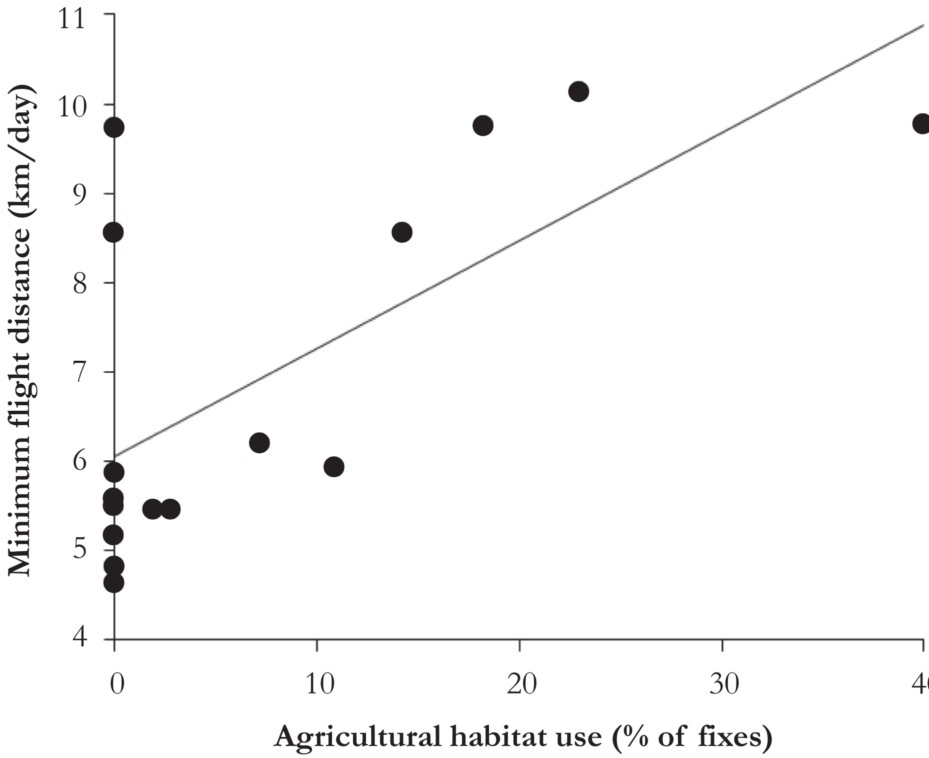

Figure 4. Minimum flight distances recorded for individual Brent Geese at spring staging areas in Denmark, as a function of agricultural habitat use during May 2011 and 2012. Linear regression: $F_{1,15} = 14.77$, $R^2 = 0.46$, $P < 0.002$.

fixes, only two (0.7%) fell outside the intertidal mudflats (on a nearby salt marsh). In Denmark on the other hand, birds were consistently moving between small and scattered salt marsh patches and occasionally agricultural fields adjacent to the coast, foraging on *Zostera* beds only when water levels were very low. This difference in spatial distribution of available habitat seems to be a major driving force behind differences in the geographical extent of Brent Goose foraging ranges. In further support of this view, Black *et al.* (2010) showed that Black Brant *Branta bernicla nigricans* foraging exclusively on dense intertidal *Zostera* in Humboldt Bay, California, had an average foraging range (75% kernel) of only 2.3 km^2. The equivalent area (using the same 75% kernel analysis) in our study site was 16 times larger (37.1 km^2). The relatively large spring foraging ranges in Denmark might therefore be explained by the combined effects of a more terrestrial lifestyle during spring (Clausen 1998) and the distribution of salt marsh habitat in the Danish landscape, undoubtedly further exacerbated by the recent local declines in subtidal *Zostera*

(Clausen *et al.* 2009). When arriving at the *Zostera* beds in Lindisfarne post-breeding, the two geese with functioning transmitters had a 75% kernel area of 8.3 km^2. However, the difference between Humboldt and Lindisfarne might at least partly be explained by stopover duration (length of study period) of individual birds (average of 11 and 33 days, respectively) and the number of locations recorded (average of 18 and 144 fixes, respectively).

Habitat use at both Agerø and Nibe Bredning showed that salt marshes were frequently exploited (Fig. 2), and around Agerø agricultural fields had also become a significant foraging habitat (12.7% of daytime GPS fixes; Fig. 3). Fjords were used mainly at night, when most birds returned to these areas to roost. Visual interpretation of daytime fixes in the fjord (where orthophotos were available) indicated that the birds often used fjord habitats as a temporary roost between terrestrial feeding bouts on salt marsh and/or agricultural fields. Such roosting behaviour was identified by fixes in aquatic areas with sandy bottoms and no vegetation, meaning that aquatic foraging was unlikely. A relatively large proportion of fjord fixes therefore were representative of roosting behaviour, whereas terrestrial fixes were typically indicative of actual foraging. These habitat-specific differences in behaviour is supported by time-budget observations made in the same areas (Clausen *et al.* 2013a), and may relate to differences in perceived predation risk across habitats.

The oldest historical reference on spring habitat use of Light-bellied Brent Geese in Denmark stems from observations made at Nissum Fjord in the 1960s (Jepsen 1967), which reported that: "Brent Goose foraging in spring is concentrated around *Zostera* beds, in the same areas where geese roost during the night… Only in exceptional cases have geese been observed foraging on land, and then only in the outermost (*Salicornia* zone) part of salt marshes". Furthermore, geese are described as "stationary, with no observations of foraging trips away from the fjord", indicating foraging ranges considerably smaller than those documented in the current study. The severe decline of *Zostera* in Nissum Fjord in recent decades resulted in a gradual abandoning of this area, and since 1987 Agerø has become the most important spring staging site (Clausen *et al.* 1998). Clausen and Percival (1998) described spring habitat use on Agerø in the early 1990s, by which time birds had already shifted to a more terrestrial lifestyle, increasingly exploiting salt marshes. This study confirms that the upward trend in usage of terrestrial habitats by Brent Geese continues to the present. Not only have salt marshes become even more important, but around Agerø, agricultural fields are now of growing importance to this population. This pattern of change in habitat use seem to mirror a similar development in other populations of Brent Geese, and increasingly terrestrial habitat use has been reported both for Dark-bellied Brent Geese *Branta b. bernicla* (Ebbinge *et al.* 1999; Ward 2004) and for the East Canadian High Arctic Light-bellied Brent Geese (Merne *et al.* 1999).

Minimum flight distances calculated in this study (by summing orthodromic distances between consecutive GPS positions) is greatly underestimating actual flight costs, as birds are obviously moving around between single fixes. As absolute values, these figures are therefore of little interest. However, as the basis for a relative comparison between individual birds, this measurement is informative for describing the behaviour and movement patterns of different geese, and for investigating how habitat use might affect general flight distance patterns. Our results indicate a very clear relationship between flight distances and use of agricultural habitats, because geese foraging there generally incurred flight costs 2–3 times higher than birds avoiding this habitat (Table 1, Fig. 4). The most plausible explanation for these findings is that agricultural habitats are used only for foraging, whereas fjord habitats (and to some extent salt marshes) are used for both foraging and roosting (Clausen *et al.* 2013a). The higher flight distances associated with agricultural habitat use therefore seem to be the result of frequent commuting between foraging (agricultural) and roosting (fjord) areas. The fact that flight distances were unaffected by the size of individual foraging ranges emphasised that these differences were first and foremost behavioural.

The current high affiliation to salt marshes renders Brent Geese susceptible to changing availability of this habitat. Recent changes in land use and animal husbandry have already reduced significantly the distribution of salt marshes in the modern Danish landscape (Buttenschøn 2007; Clausen *et al.* 2013b), and current projections for future rises in sea levels threaten a further reduction in the availability of these spring-fattening areas, which have assumed greater importance for the geese in recent years (Hughes 2004; Clausen *et al.* 2013b). Given that this goose population is one of the smallest in the world, and the only Svalbard-breeding goose population not to show substantial increases over the last couple of decades (Fox *et al.* 2010), this development might be of conservation concern. The addition of agricultural fields to the palette of exploited habitats might be seen as a behavioural response to reduced salt marsh availability, to some extent compensating for the loss of coastal habitats. Elsewhere however, it has been shown that foraging on agricultural land involves significant behavioural changes that potentially translate into higher energy expenditure for individual geese (Clausen *et al.* 2013a; Clausen *et al.* 2012). This conclusion is supported by the current study, where birds with a high proportional use of agricultural habitats also had significantly higher minimum flight distances. To this end, it should be emphasised that in our study "agricultural areas" relate to the exploitation of winter-sown cereal fields. Pasture foraging has been found to be a good alternative to salt marshes among spring-fattening geese (Spaans & Postma 2001), but the addition of cereals to the diet (often cultivated on inland fields) might carry with it an additional cost. The current habitat-specific differences in behaviour may partly explain the findings of Inger *et al.* (2008), who found that geese foraging on marine resources had higher body mass than those foraging mainly on terrestrial habitats. The possible carry-over effects highlighted in that study, and associated impacts on individual productivity, are a growing cause for concern in view of the on-going changes in habitat utilisation among East Atlantic Light-bellied Brent Geese.

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Photograph: Light-bellied Brent Geese at Agerø, Denmark, by Kevin Clausen.

