Activity budgets in different habitats of a species of conservation concern in Ireland, the Light-bellied Brent Goose *Branta bernicla hrota*

MARÍA PÉREZ TADEO* & MARTIN GAMMELL

Marine and Freshwater Research Centre, Department of Natural Sciences, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland.
*Correspondence author. E-mail: maria.pereztadeo@research.gmit.ie

Abstract

Activity budgets of Light-bellied Brent Geese *Branta bernicla hrota* wintering in Ireland were compared at different sites and associated habitats along the coast of inner Galway Bay. Hourly energy expenditure (HEE) by birds feeding on traditional, natural wetlands was compared to their HEE when on managed grasslands. Their flying and vigilance behaviours, and flock size when on these different habitats, were also assessed. Brent Goose HEE did not vary significantly between general areas or specific habitats, but vigilance behaviour was more frequent when the birds were on managed grassland. Flock size was larger in relatively undisturbed natural wetlands. The effects were limited, however, suggesting that there was little cost to Brent Geese from feeding in grassland *versus* wetland habitats.

Key words: behaviour, conservation, energy expenditure, habitat shift, wetlands.

The Brent Goose *Branta bernicla* is the most maritime of goose species, subsisting on a herbivorous diet mostly in intertidal coastal areas (Ganter 2000; Inger *et al.* 2010; Clausen *et al.* 2012). The population suffered an abrupt decline in numbers during the 1930s, attributed to the "wasting disease" which severely affected eelgrass *Zostera* sp. meadows along Atlantic coastlines (Rasmussen 1977; Ganter 2000; Fox & Madsen 2017). Eelgrass constitutes up to 85% of the birds' diet at stopover sites (Ganter 2000), where the geese not only have to meet their nutritional needs but accumulate fat reserves to fuel their migration to the breeding grounds (Inger *et al.* 2008). Anthropogenic eutrophication has continued to reduce the extent and quality of eelgrass meadows since the 1970s (Clausen *et al.* 2012). These effects have been exacerbated in Ireland because of more rapid depletion caused by increases in Brent Goose numbers (Inger *et al.* 2006a,b). Following low numbers of the 1930s, Brent Geese have recovered, partially as a result of the ability to change feeding habitats from eelgrass meadows to green algae such as *Enteromorpha* sp. and *Ulva* sp. when necessary, and subsequently by moving on to farmland landscapes where managed grasslands offer a less limited and highly nutritional alternative food source (Inger *et al.* 2006a,b) which can comprise > 80% of their diet towards the end of the winter (Inger *et al.* 2006b). This gradual change in feeding patterns has been attributed to the depletion of eelgrass stocks as winter progresses (Inger *et al.* 2006a,b,c; Inger *et al.* 2010).

In the last two decades, the East Canadian High Arctic population of Light-bellied Brent Geese *Branta bernicla hrota* has maintained favourable conservation status, currently consisting of *c.* 40,000 individuals, with population size showing an overall increasing trend (8.3% since 1995; Fox *et al.* 2010). However, there remain potential threats to maintaining current abundance and distribution, as well as maintaining the extent of current eelgrass biomass, the loss of which can have a detrimental effect on Brent Goose body condition (Inger *et al.* 2006a, 2008, 2010; Tinkler *et al.* 2009) and potentially on successful migration to their summer breeding grounds (Stillman *et al.* 2015). Goose habitat selection is believed to reflect food quantity and quality (Tinkler *et al.* 2009), food digestibility and the amount of energy acquired from the food (Inger *et al.* 2006b; Clausen *et al.* 2012; Chudzińska *et al.* 2013) but other factors, such as the level of disturbance within the habitat, also influence habitat selection (Bélanger & Bédard 1990; Tinkler *et al.* 2009; Chudzińska *et al.* 2016). Chudzińska *et al.* (2013) found a greater proportion of geese feeding under undisturbed rather than disturbed environments. Anthropogenic disturbance can reduce geese feeding time (Bélanger & Bédard 1990; Riddington *et al.* 1996; Stillman *et al.* 2015) and elevate energetic expenditure (Bélanger & Bédard 1990; Riddington *et al.* 1996), ultimately affecting fitness by hampering migration to arctic breeding grounds and, following migration, by reducing the likelihood of successful breeding (Chudzińska *et al.* 2013).

Estimating goose energy expenditure in different habitats can facilitate a comparison of anthropogenic impacts on species abundance and distribution (Clausen *et al.* 2012; Christiansen *et al.* 2013), and allow an assessment of the potential fitness consequences of being displaced from one habitat to another (Tinkler *et al.* 2009), which could potentially lead to more sympathetic management of their habitats. This study compiled activity budgets for East Canadian High Arctic Light-bellied Brent Geese at different sites and in different habitats on their wintering grounds in Galway Bay, Ireland, in order to assess whether there are significant differences in flock size, behaviour and energetic expenditure between relatively undisturbed natural wetland habitats and managed grasslands subjected to greater levels of anthropogenic activity. Hourly Energy Expenditure (HEE), flock size, flying and vigilance behaviour of Brent Geese were compared between different sites and their associated habitats. More frequent occurrences of flying and vigilance behaviour, a higher energetic expenditure and a smaller flock size was expected in managed grasslands compared to natural wetlands.

Methods

Study population

The East Canadian High Arctic population of Light-bellied Brent Geese has one of the longest migration routes of all European goose species (Robinson *et al.* 2004). The birds breed on islands in the eastern arctic Canada and migrate in late August to stage on west and east coasts of Greenland and the west coast Iceland (Boertmann *et al.* 1997), before arriving at their wintering grounds along the coasts of Northern Ireland and the Republic of Ireland (Inger *et al.* 2006b,c; Inger *et al.* 2010) by the end of October. Departure on spring migration occurs in April, with the geese spending about 1.5 months in Iceland (Inger *et al.* 2008) and with a briefer staging period in Greenland before reaching the breeding grounds (Gudmundsson *et al.* 1995) during the first two weeks of June (Robinson & Colhoun 2006; Harrison *et al.* 2010).

Study area

Strangford Lough in Northern Ireland is the most important site for the geese in their wintering range (Mathers *et al.* 1998; Robinson *et al.* 2004, Inger *et al.* 2006a,b,c), harbouring up to 75% of the population during late autumn each year. As winter progresses, the population disperses away to coastal areas elsewhere throughout Ireland (Inger *et al.* 2006a), which provide feeding grounds for Brent Geese until they depart in April (Robinson *et al.* 2004). The present study took place in different locations along the coast of inner Galway Bay, a marine-dominated estuary located on the west coast of Ireland (Fig. 1). It was designated as a Special Protection Area (SPA) under the European Union's Birds Directive (2009/147/EC), because it contains valuable wetland ecosystems hosting a wide variety of migratory bird species during winter, including an internationally important part of the Brent Goose population (1,100–1,500 individuals in 2010; NPWS 2013).

After preliminary observations, three sites along the coast of Galway City were selected as suitable for the study on the basis that: 1) good numbers of geese occurred in the areas, 2) different levels of anthropogenic disturbances and different amounts of natural habitat occurred at these sites, and 3) different habitat types (water, fields and intertidal areas) were available for the geese in these areas. The first, classed as Tawin Island (53.219°N, 9.016°W; 204 ha), supported relatively natural Brent Goose habitat, including small islands, wetland ecosystems and the sea, and also contained some rough grazing pasture. Few humans inhabit the island, minimising disturbance at all study sites, which were mainly caused by other bird species. The second site, here referred to as Field, consisted of football pitches (53.264°N, 9.054°W; 9.9 ha) and a golf course (53.257°N, 9.095°W; 14.2 ha), located close to each other along the coast in Galway, with artificial, intensively managed grassland subject to high levels of anthropogenic disturbance due to the presence of people and dogs. Thirdly, the Beach site, which included Grattan beach (53.263°N, 9.068°W; 13 ha) and Salthill beach (53.256°N, 9.096°W; 2 ha) on the coast of Galway City, where geese were either in the sea or the intertidal area, were subject to similarly high levels

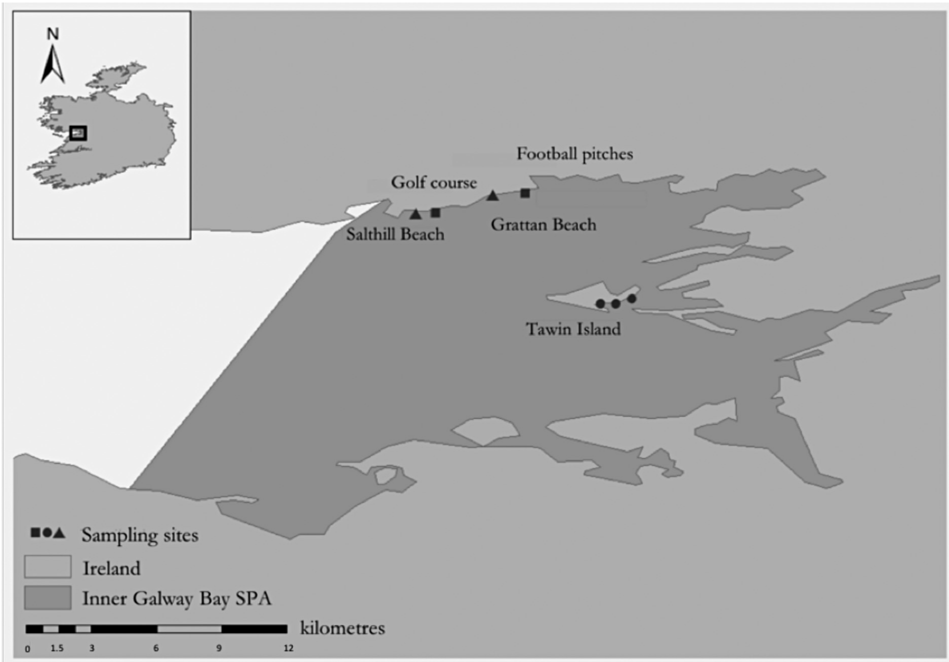

Figure 1. Map showing the different sampling locations in Galway City: Beach (triangle) and Field (square) and in Tawin Island (circle) around the Inner Galway Bay SPA, Ireland.

of anthropogenic disturbance from road traffic noise and the presence of people and dogs.

Within these three sites, habitats occupied by the geese during the observation periods were classified as: 1) Water, when geese were in the water (sea or freshwater pools) feeding on green algae and wetland vegetation; 2) Grass, when geese were feeding on land on lawns, amenity grasslands and other pastures such as the football pitches, golf course or rough pasture on Tawin; 3) Intertidal areas, in Grattan and Salthill beaches and small islands in Tawin, where in all cases geese were feeding on green algae, and 4) Water/Grass, on Tawin Island, when the geese frequently moved between the rough pasture, small islands and the sea during the observation period to feed on green algae and pastures, and consequently could not be allocated to any of the other habitats.

Field observations

A pilot survey was carried out during 14–15 January 2017 to develop an ethogram of Brent Goose behaviour for use in the study (Table 1). Observations were then made of the birds' behaviour at the selected sites (Fig. 1) for two months, from 24 January to 24 March 2017, at all sites on each of the survey days, usually 3 or 4 days per week, when environmental conditions were suitable. The order in which observations took place was randomised and balanced.

Table 1. Ethogram containing different behavioural patterns for Brent Geese and estimated activity-specific energetic costs (X_i) expressed as BMR multipliers for all the behaviours recorded during the present study, adopted from Clausen *et al.* (2012).

Behaviour (Xi)	Subtype	Description
Feeding (1.7)	Foraging	Goose walking on grass or in intertidal areas/islands, searching for food. With its head down, towards the ground.
	Water (digging)	Goose in water or in intertidal areas, putting its head into the water or pushing its beak into the water to feed or trying to reach the food. Foot-paddling can be observed.
	Feeding on grass	Goose in a field, bending its neck towards the ground and pecking at the grass.
	Feeding at the surface of the rocks intertidal	Feeding on algae at the surface of rocks on islands or in intertidal areas.
Swimming (2.2)		Actively moving across the surface of the water.
Drinking (1.5)		Goose bends its head and dips its beak into the water, then raises its head extending its neck and swallows the water.
Walking (1.9)		Goose using its legs to change its location on the ground, with its head held up.
Flying (13.4)		Goose in flight.
Resting (1.6)	Inactive	Sitting on the grass with eyes open.
	Drifting	Inactive on the surface of the water.
Preening (1.8)		Self-maintenance, including using the beak to fix/clean feathers, bathing in water and wing flapping.
Aggressive behaviour (1.9)		Direct attack by pecking or threat position with the neck extended, leading to the displacement of another goose.
Vigilance (1.7)		Goose with its head held in an upright position, looking around and alert.

The general approach was that, in any two-day block of observations, the first location selected for observation on day one (*i.e.* Tawin Island or Galway City: Beach/Field) was chosen randomly, and the following day the order was reversed, thus avoiding the effect of environmental patterns on the result, as well as ensuring an even spread of observations at different locations and times of the day across the study period to cover a range of tide heights and weather conditions. After arriving at the study site, flocks were spotted, GPS position was obtained and the telescope was set up, making sure that no disturbances were caused and waiting some minutes for the Brent Geese to settle at a distance far enough to avoid disturbance but adequate to observe their activities.

Brent Goose behaviour was described by scan sampling (Altman 1974), using a telescope (Opticron, HDF zoom 16–60× on a Manfrotto 128 RC tripod) to scan the flock from one end to the other, with the activity of each successive individual noted as it came into the field of view, and recorded by speaking to a dictaphone (Sony ICD-BX140). Scans were taken at 5 min intervals over one full hour, focusing on a single flock on each occasion, and behaviours recorded were as defined in the ethogram (Table 1). This methodology has been used extensively for behavioural studies, particularly research into geese (*e.g.* Riddington *et al.* 1996; Fox *et al.* 2008; Ladin *et al.* 2011; Clausen *et al.* 2012; Chudzińska *et al.* 2013). Flocks of geese sometimes left the area before the 1 h recording period had been completed, but as preliminary analyses showed that there were no significant differences in HEE values (see below) between flocks that had been under observation for a maximum of 15, 30, 45 or 60 min (Kruskal-Wallis test: $\chi^2_3 = 5.27$, $P = 0.15$, n.s.), all observations of at least 15 min duration were included in the analyses. For each of the 5 min sampling points, the proportion of individuals recorded for each behaviour category was determined and then averaged for the entire 1 h observation period; these data were then used in subsequent analyses. Data were collected from a particular flock just once a day at each of the study sites. Although independence between observations was assumed, it should be noted that some individuals might have been observed and recorded a number of times, as the geese were mostly unringed and highly mobile.

The level of disturbance experienced by the flock during each 1 h observation period was described at the time on a scale ranging from 0 (lowest level of disturbance) to 5 (highest level of disturbance; Table 2), with disturbance levels subsequently grouped into low, medium and high categories to facilitate statistical analysis. Accurate environmental conditions such as precipitation, wind speed and temperature were obtained for each observation from the Irish Meteorological Service (http://www.met.ie/); these data were collected from the Athenry Automatic Weather Station (53.289°N, 8.786°W, at 40 m above mean sea level), *c.* 20 km from the study sites. Tide height data for Galway Bay was collected from the tide and current prediction software WXTide32 (Hopper 2000).

Table 2. Categories for the disturbance levels assigned to different goose sites and circumstances. L = low, M = medium and H = high disturbance levels.

Disturbance level	Tawin Island	Beach	Golf course/ football pitches
0 (L)	No disturbance	No disturbance	No disturbance
1 (L)	Many geese moving or overflying the flock	Many geese moving or overflying the flock	Many geese moving or overflying the flock
2 (M)	Other birds; people or road traffic far from the flock	Other birds	Other birds
3 (M)	Dogs barking; road traffic	People on the promenade and/or road traffic relatively close to the flock	Bikes/people on the promenade
4 (H)	–	People and/or dogs at the beach but far from the flock	People playing golf/ football and/or dogs barking
5 (H)	–	People/dogs running close or chasing the geese	Maintenance work; people and/or dogs approaching or chasing the geese

Activity budgets and hourly energy expenditure (HEE)

Different activities were classified into one of the nine behaviours defined in the ethogram (Table 1). The proportion of individuals involved in each activity during flock scans made for each observation period was calculated and corrected for the duration of that observation period to indicate the proportion of time that the geese spent on each activity in an hour. These activity budgets were transformed into energetic terms by calculating hourly energy expenditure (HEE) for each observation period, following Clausen *et al.* (2012) and expressed in kJ per hour as the sum of active metabolic rates (AMR), including energetic expenditure due to thermoregulation whenever temperature was below 6°C. The equation for calculating HEE is:

$$HEE_{[kJ/h]} = \Sigma(BMR\ X_i\, p_i) + C_t$$

where BMR is the basal metabolic rate in kJ/h which, for Brent Geese with an average weight of 1.168 kg and during winter conditions, is 16.2824 kJ/h (Lasiewski & Dawson 1967). X_i is the energy expenditure of a particular behaviour (i) expressed as a multiplier of the BMR for Brent Geese (Table 1), p_i is the proportion of time involved in every activity (i) for each observation period, and C_t is the thermoregulation cost in kJ/h, calculated as follows:

$$C_t = 1.272 \times N \times \Delta_t$$

where N is the time in hours during which temperature dropped below 6°C. This is the lower critical temperature (LCT) for a similar subspecies, the Pacific Brent Goose *Branta bernicla nigricans* triggering regulatory heat production (Irving *et al.* 1955), that requires an extra energetic cost of 1.272 kJ/h/°C estimated for the Lesser Canada Goose *Branta canadensis parvipes* (Lefebvre & Raveling 1967). Δ_t is the average number of degrees below that temperature during that time.

Statistical analysis

Data were analysed using the statistical R package, version 3.3.1 and RStudio 3.4.0 (R Core Team 2016), following two main approaches.

Firstly, as the residuals were not normally distributed in most cases (Shapiro-Wilk tests: HEE ~ site: $W = 0.830$, $P < 0.001$; HEE ~ habitat: $W = 0.850$, $P < 0.001$; flying ~ site: $W = 0.814$, $P < 0.001$; flying ~ habitat: $W = 0.840$, $P < 0.001$; flying ~ disturbance level: $W = 0.810$, $P < 0.001$; vigilance ~ habitat: $W = 0.961$, $P < 0.05$; vigilance ~ disturbance level: $W = 0.954$, $P < 0.05$; flock size ~ site: $W = 0.950$, $P < 0.01$; flock size ~ habitat: $W = 0.950$, $P < 0.01$; flock size ~ disturbance level: $W = 0.934$, $P < 0.01$), and assumptions for ANOVA therefore were not fulfilled, non-parametric Kruskal-Wallis tests were carried out in order to detect potential differences in HEE between sites and habitats, to evaluate differences in behaviour assumed to indicate high levels of disturbance (*i.e.* flying and vigilance behaviours), and to investigate variation in flock size in relation to site, habitat and disturbance levels. Only the relation between vigilance and site was evaluated with an ANOVA test, as the residuals were normally distributed (vigilance ~ site: $W = 0.970$, $P > 0.05$, n.s.). When an ANOVA or a Kruskal-Wallis test gave a significant result, a *post hoc* parametric or non-parametric pair-wise test (Tukey's or Dunn's test of multiple comparisons, respectively) were carried out in order to determine which groups differed significantly from each other. Flying behaviour was evaluated because it is the most relevant activity in term of energy expenditure, as Brent Geese spend as much as 13.4 units expressed as basal metabolic rate (BMR) multipliers (Clausen *et al.* 2012) (Table 1), and small differences in this behaviour are likely to be relevant in terms of HEE. Furthermore, together with vigilance behaviour, it is expected to be higher under disturbance conditions (Bélanger & Bédard 1990; Clausen *et al.* 2002). Kendall rank correlations were used to test for relationships between group size and vigilance behaviour, as this factor was expected to decrease vigilance behaviour through shared alertness between the geese in the flock (Lazarus 1978).

For the second analytical approach, generalized linear mixed models (GLMM) using a Laplace approximation with a gamma error distribution (in the case of HEE, flock size and vigilance behaviours) and a Gaussian distribution with a logarithmic link function (in the case of flying behaviour) were generated in order to explore which variables were most likely to have an effect on HEE, flock size, vigilance and flying behaviours. The variables included in the initial general models as fixed effects were site, habitat, level of disturbance, tide height, wind speed, time of the day and flock size (except when flock size was the response variable), since these variables were expected to have an impact on HEE, flock size, vigilance and flying behaviours. The time over the study period expressed as week of study was included as a random effect. In all the four different cases (*i.e.* when assessing HEE, flock size, vigilance and flying behaviours), after fitting a global GLMM, the variables were standardised for better interpretation of the parameter estimates (Gelman 2008) and a model set was generated using the top models with ΔAICc = 4 as a cut-off, where AICc is the Akaike Information Criteria (AIC) corrected for small sample size (Grueber *et al.* 2011; Symonds & Moussalli 2011). Finally, a model averaging approach was carried out using multi-model inference as no model was found to be strongly supported and this approach is recommended when the weight of the best models is < 0.9 (Grueber *et al.* 2011). Model goodness-of-fit was assessed by visual evaluation of residual plots in all cases. Multicollinearity among explanatory variables was also assessed visually by using scatterplot matrices.

Results

Observations were conducted on 66 different flocks during the two-month study, totalling 56.91 h of recordings. Thirty-six, 12 and 18 (n = 66) observations were carried out at the Tawin Island, Beach and Field study sites respectively, and 11, 12, 19 and 24 (n = 66) were carried out in the different types of habitat in the following order: water, water/grass, intertidal area and grass. Flock sizes ranged from 7–128 geese, with mean (± s.d.) flock sizes of 46.42 (± 24.48), 41.22 (± 24.26) and 26.67 (± 11.93) in the Tawin, Field and Beach sites respectively, and with mean flock sizes of 55.36 (± 29.83) for geese seen on water, 42.67 (± 22.70) for birds on the water/grass habitat category, 34.74 (± 17.88) at intertidal areas and 39.67 (± 23.46) when on grass.

Brent Geese were most commonly recorded feeding (mean ± s.d. = 59.37 ± 17.61% of the time), then swimming (10.64 ± 15.97%), being vigilant (8.61 ± 7.40%), flying (7.19 ± 9.15%), walking (6.28 ± 4.92%), preening (5.17 ± 6.58%) and resting (2.31 ± 3.98%). The least frequent activities were aggressive (0.30 ± 0.41%) and drinking (0.13 ± 0.34%) behaviours.

Effects of site and habitat type on hourly energy expenditure (HEE)

Average HEE (± s.d.) was slightly higher at the Beach (46.43 ± 13.83 kJ/h) and Field (43.12 ± 22.41 kJ/h) sites than at Tawin Island (42.67 ± 15.74 kJ/h) but the difference between sites in the birds' HEE

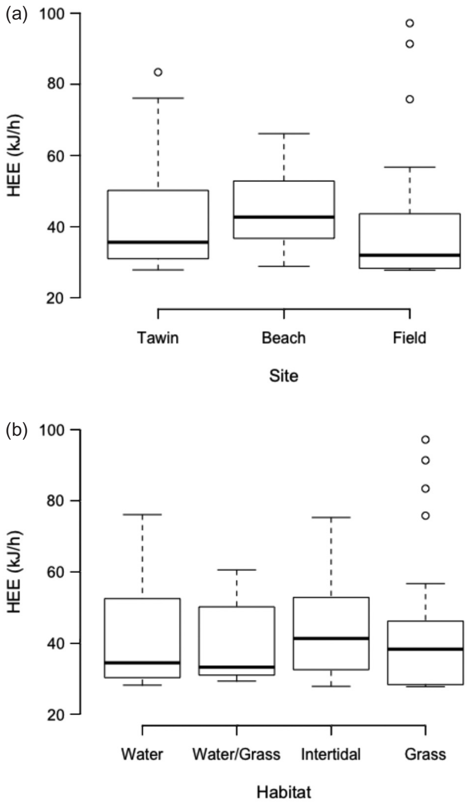

Figure 2. Box plots showing Brent Goose hourly energy expenditure (HHE) (kJ/h) in: (a) each of the different sites of study (Tawin Island, Beach and Field), and (b) in different habitat types (Water, Water/Grass, Intertidal and Grass).

was not significant (Kruskal-Wallis test: $\chi^2_2 = 2.90$, n.s., Fig. 2a).

On considering HEE for geese on different habitat types, the mean (± s.d.) values were higher when the birds were on intertidal areas (45.53 ± 15.09 kJ/h) and grass (44.13 ± 21.3 kJ/h) than when on water (42.74 ± 17.39 kJ/h) and the water/grass (39.56 ± 12.08 kJ/h) habitat categories, but the difference in HEE between habitats also was not significant (Kruskal-Wallis test: $\chi^2_3 = 1.47$, n.s., Fig. 2b).

Effects of site, habitat type and level of disturbance on flock size, vigilance and flying behaviours

Kruskal-Wallis and ANOVA tests carried out to determine whether there were any differences between sites, habitats and disturbance levels in the birds' flock size, flying activity and vigilance activity (Table 3) showed that most of the relationships were not significant. There was however significant variation in flock sizes between study sites ($P < 0.05$; Fig. 3), and vigilance behaviour also varied significantly between sites ($P < 0.001$), habitat types ($P < 0.01$) and levels of disturbance ($P < 0.001$; Table 3).

On average, a greater proportion of the geese were recorded as vigilant at the Field site (mean ± s.d. = 15.49 ± 7.65%), followed by Beach (10.38 ± 7.86%), with relatively low vigilance levels recorded on Tawin Island (4.58 ± 3.44%) (Fig. 4a). For habitat type, vigilance was more frequent on grasslands (12.43 ± 8.70%) and intertidal areas (8.37 ± 7.11%) than on water (3.55 ± 2.56%) and "water/grass" (5.96 ± 3.47 kJ/h). (Fig. 4b). There was no evidence for an association between flock size and vigilance behaviour during the present study (Kendall's rank correlation: tau = –0.005, $n = 66$, $P = 0.95$, n.s.).

Post hoc pair-wise tests (Tukey and Dunn's test of multiple comparisons) revealed significant differences in the proportion of vigilance behaviour between the sites Tawin–Field (difference between the means = –5.80, 95% CI = –10.41 to –1.19, $P < 0.001$) and Tawin–Beach (difference = –10.91,

Table 3. Results of Kruskal-Wallis (χ^2) and ANOVA (F) tests to determine whether flock size, proportion of flight activity and proportion of vigilant activity recorded for Brent Geese varied with site, habitat and disturbance levels. [a] = F value; * = statistically significant.

Variables	χ^2 or F value	d.f.	P
Flock size by site	6.61	2	0.03*
Flock size by habitat	4.49	3	0.21
Flock size by level of disturbance	1.56	2	0.46
Flying behaviour by site	0.97	2	0.62
Flying behaviour by habitat	1.41	3	0.70
Flying behaviour by level of disturbance	0.67	2	0.72
Vigilance behaviour by site	22.25[a]	2	<0.001*
Vigilance behaviour by habitat	11.30	3	0.010*
Vigilance behaviour by disturbance	16.96	2	<0.001*

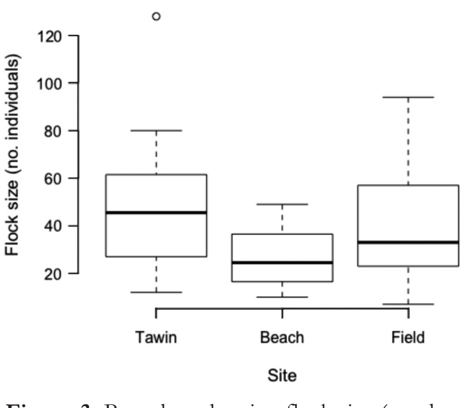

Figure 3. Box plots showing flock size (number of individuals) in the different study sites (Tawin Island, Beach and Field).

95% CI = –14.90 to –6.92, P = 0.01), between the habitats Water–Grass (z = 3.194, P < 0.001), Water/Grass–Grass (z = 2.013, P = 0.02) and Water–Intertidal (z = 1.868, P = 0.03), and between disturbance levels classed as Low–Medium (z = –3.63, P < 0.001) and Low–High (z = 3.283, P < 0.001). The other groups did not differ from each other (Field–Beach: z = –1.596, P = 0.06; Intertidal–Grass: z = 1.539, P = 0.06; Water/Grass–Water: z =1.21, P = 0.11; Medium–High disturbance level: z = 0.472, P = 0.32; n.s. in each case). Significant differences were also found in flock size between the sites Tawin–Beach (z = –2.564, P = 0.005) but not between Field–Beach (z = –1.587, P = 0.06, n.s.) nor Tawin–Field (z = –0.913, P = 0.18, n.s.) (Fig. 3).

Relative importance of explanatory variables on HEE, flock size, vigilance and flying behaviour

GLMM analysis of the effects of explanatory variables (including tide, time, site, wind flock size and disturbance) on HEE found seven models that provided

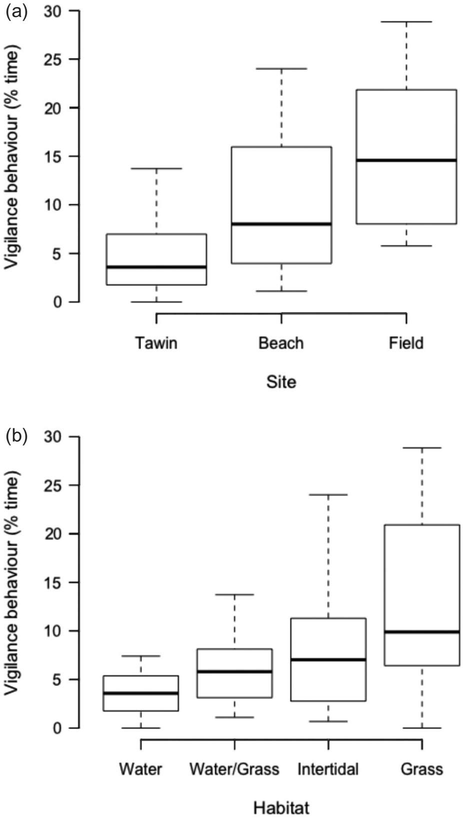

Figure 4. Box plots showing Brent Geese vigilance behaviour (% of time) in: (a) the different sites of study (Tawin Island, Beach and Field), and (b) in different habitats (Water, Water/Grass, Intertidal and Grass).

best fit to the data with ΔAIC < 4, and these were selected for model averaging. Overall, only tide height had a significant influence on HEE (*P* < 0.001), with a relative importance of 100%. Site did not show a significant effect; habitat type was not included in the model averaging because it was not present in the best fit models with ΔAIC < 4 identified by the GLMM (Table 4).

Three models of the effects of explanatory variables on flock size with ΔAIC < 4 were selected for model averaging. Only Site was found to have a significant influence on flock size (Field *vs.* Beach: *P* < 0.05; Tawin *vs.* Beach: *P* < 0.01), with a relative importance of 100% (Table 5). The rest of the variables were not considered as useful predictors of flock size, since they were not present in the averaged models (*i.e.* the models presenting the lowest AICc) (Table 5).

The GLMM for the effect of explanatory variables on vigilance behaviour found that eight best fit models had ΔAIC < 4, and these were selected for model averaging. Variables identified as having a significant influence on vigilance behaviour were Site (Tawin *vs.* Beach: *P* < 0.001) with a relative variable importance of 100%, and time of the day (*P* < 0.05) with a relative importance of 94% (Table 6).

Model averaging was undertaken for nine models with ΔAIC < 4 to determine the effects of explanatory variables on flying behaviour. Only tide height proved statistically significant (*P* < 0.01; Table 7), with a relative variable importance of 100%. Even though all the potential explanatory variables were present in the averaged models, they did not show a significant effect on flying frequency by the geese.

Discussion

Our findings show that Brent Goose behaviour, particularly vigilance, was affected by specific features of a site, such as the level of disturbance. Geese were more vigilant at the coast in Galway City, where they were subject to the most intense anthropogenic disturbances, in comparison

Table 4. Effects of each predictor variable on HEE after model averaging. Only tide height was found to be significant.

Predictor variable		Estimate[a]	s.e.	*z*	*P*	Relative importance (%)
Tide		–7.584e-03	1.84e-03	4.122	<0.001	100
Time		–1.263e-03	1.797e-03	0.689	0.49	20
Site	Field[b]	4.539e-03	2.759e-03	1.612	0.11	18
	Tawin	3.061e-03	2.356e-03	1.273	0.20	
Wind		6.338e-04	1.829e-03	0.34	0.73	13
Flock size		–3.769e-04	1.813e-03	0.204	0.84	12
Disturbance	Low[b]	–7.822e-04	2.443e-03	0.314	0.75	5
	Medium	2.053e-03	2.408e-03	0.835	0.40	

[a]Effect sizes have been standardized following Gelman (2008).
[b]Beach was the reference category for Site and High was the reference category for Disturbance level.

Table 5. Effects of each predictor variable on flock size after model averaging. Only Site was found to be significant.

Predictor variable		Estimate[a]	s.e.	*z*	*P*	Relative importance (%)
Site	Field[b]	–1.356e-02	6.174e-03	2.152	0.03	100
	Tawin	–1.664e-02	5.751e-03	2.836	0.005	
Time		–2.766e-03	3.425e-03	0.791	0.43	26
Disturbance	Low[b]	4.022e-03	6.582e-03	0.599	0.55	9
	Medium	4.653e-05	5.308e-03	0.009	0.99	

[a]Effect sizes have been standardized following Gelman (2008).
[b]Beach was the reference category for Site and High was the reference category for Disturbance level.

Table 6. Effects of each predictor variable on vigilance behaviour after model averaging. Only Site and Time were found to be significant.

Predictor variable		Estimate[a]	s.e.	*z*	*P*	Relative importance (%)
Site	Field[b]	–0.037	0.02	1.850	0.06	100
	Tawin	0.088	0.024	3.555	<0.001	
Time		0.038	0.017	2.194	0.03	94
Flock size		–0.022	0.015	1.428	0.15	38
Tide		–0.000	0.013	0.052	0.96	17
Disturbance	Low[b]	0.023	0.033	0.682	0.50	5
	Medium	–0.006	0.014	0.439	0.66	
Habitat	Intertidal[b]	0.012	0.041	0.289	0.77	
	Water	0.035	0.049	0.698	0.49	5
	Water/Grass	–0.046	0.041	1.100	0.27	

[a]Effect sizes have been standardized following Gelman (2008)
[b]Beach was the reference category for Site, High was the reference category for Disturbance level and Grass was the reference category for Habitat.

with Tawin Island where the geese were largely undisturbed. Habitat type also played an important role, as geese were more vigilant when feeding on managed grasslands than when feeding on natural marine habitats, and the GLMM results showed that study site had a significant effect on vigilance behaviour. Overall, these results confirm the findings of Clausen *et al.* (2012), who found that Brent Geese were more vigilant away from their natural marine habitat. This might have fitness consequences, since anthropogenic disturbance not only reduces feeding time, but increases energy expenditure invested in vigilance or escape activities (Bélanger & Bédard 1990; Riddington *et al.* 1996; Inger *et al.* 2006a).

Flock size differed between sites, being significantly larger at the more undisturbed and natural wetland habitat of Tawin Island, where geese were subject to less anthropogenic pressure (disturbances were infrequent and more remote than elsewhere). The GLMM analyses also confirmed a significant association between site and flock size. Although we predicted an inverse relationship between vigilance behaviour and flock size (Lazarus 1978), the number of geese in the flock had no effect on vigilance behaviour in our study, which supports the results of Chudzińska *et al.* (2013).

Table 7. Effects of each predictor variable on flying behaviour after model averaging. Only tide height was found to be significant.

Predictor variable		**Estimate**[a]	**s.e.**	***z***	***P***	**Relative importance (%)**
Tide		1.137	0.295	3.778	<0.001	100
Time		0.282	0.212	1.303	0.19	43
Wind		0.036	0.205	0.304	0.76	16
Habitat	Intertidal[b]	0.272	0.319	0.841	0.40	
	Water	0.212	0.331	0.628	0.53	16
	Water/Grass	–0.514	0.468	1.187	0.24	
Flock size		0.065	0.275	0.281	0.23	15
Site	Field[b]	–0.514	0.33	1.523	0.06	4
	Tawin	–0.420	0.302	1.363	0.17	

[a]Effect sizes have been standardised following Gelman (2008)
[b]Beach was the reference category for Field and Grass was the reference category for Habitat.

Despite significant differences in vigilance behaviour between study sites, habitats and disturbance levels, there was no significant difference in flying behaviour between sites, habitats, levels of disturbances, or flock size, contrasting with the findings reported by Riddington *et al.* (1996). Similarly, we found no significant differences in Hourly Energy Expenditure (HEE) linked to the use of different sites, habitats or under different levels of disturbance. These results were unexpected because several authors (Riddington *et al.* 1996; Clausen *et al.* 2012; Clausen *et al.* 2013) have reported a higher energy expenditure by geese feeding on managed grasslands.

Our results suggest that Brent Geese still prefer traditional natural habitats, since larger flocks occurred on Tawin Island, where wetland habitats are present. One of the reasons for that preference might be that grasslands present higher fibre content and hence a lower digestibility compared to marine resources (Inger *et al.* 2006b) and some studies have found that Brent Geese feeding on intertidal areas have a better body condition than those feeding on terrestrial grounds (Inger *et al.* 2006a), which has a positive influence on reproductive success (Inger *et al.* 2008).

Other authors have reported gradual changes in the use of food sources and habitats by Brent Geese during winter (Inger *et al.* 2006b; Tinkler *et al.* 2009). Immediately after arrival in autumn, they feed on the eelgrass *Zostera* sp., *i.e.* their traditional food source. However, as winter progresses, other food sources become more important, initially other marine resources such as the green algae *Ulva* sp. and *Entheromorpha* sp., with the geese finally feeding almost exclusively on terrestrial grasslands before returning to their arctic breeding grounds (Inger *et al.* 2006a,b; Clausen *et al.* 2012; Fox & Abraham 2017). Previous studies (Inger *et al.* 2006a,b,c; Inger *et al.* 2010) revealed that the trigger for the search for alternative food sources is the depletion of eelgrass stocks. The anthropogenic pressure exerted on coastal areas and subsequent habitat degradation, marine pollution and eutrophication (Clausen *et al.* 2012), together with the increase in the Brent Goose population over the last two decades (Fox *et al.* 2010), are believed to be the main causes of the decline in eelgrass abundance (Inger *et al.* 2006a,b). Similar changes in habitat use have been observed in other goose species, such as the Dark-bellied Brent Goose *Branta bernicla bernicla,* the Barnacle Goose *Branta leucopsis* and the Pink-footed Goose *Anser brachyrhynchus* (Clausen *et al.* 2012; Fox & Abraham 2017; Fox & Madsen 2017).

Brent Geese could compensate for higher levels of vigilance behaviour and displacement from maritime "natural" optimal foraging habitats by resorting to high quality and abundant terrestrial food resources (Bos *et al.* 2005; Tinkler *et al.* 2009; Ladin *et al.* 2011; Clausen & Clausen 2013; Fox & Abraham 2017). The greater protein and fat content of the diet would increase their energy intake rates, with potential fitness consequences (Tinkler *et al.* 2009; Fox & Abraham 2017). Managed grasslands, such as reseeded leys and recreational lawns offer a dense and concentrated food source, allowing Brent Geese to increase their feeding rate and efficiency and thereby potentially reducing their required feeding time (Ladin *et al.* 2011; Clausen & Clausen 2013). In contrast, the marine environment presents a patchier food source, therefore increasing time spent selecting best quality food patches and thereby foraging time (Fox & Abraham 2017).

According to our results, Brent Geese did not seem to be adversely affected, in terms of hourly energy expenditure (HEE), by shifting from marine to artificial grassland habitats, which has been forced upon them gradually since the 1970s (Robinson *et al.* 2004). The results of the present study suggest a certain resilience and an adaptability to the use of managed grasslands when necessary. Some authors (Fox *el al.* 2010; Fox & Abraham 2017), suggested that this adaptability when shifting to managed grasslands could explain the overall increase in the population size observed from the 1960s. This is also supported by Robinson *et al.* (2004), who state that terrestrial feeding by Brent Geese was recorded in Ireland and Iceland for the first time throughout the 1970s, a period which coincided with increases in population abundance.

This study focused on an important part of the East Canadian High Arctic Light-bellied Brent Goose population (*i.e.* those wintering on the Inner Galway Bay, *c.* 1,100–1,500 individuals in 2010; NPWS 2013) during an important time of the year, *i.e.* from January–March, the period when Brent Geese need to acquire fat stores in preparation for their long spring migration to arctic breeding areas. However, this study had some limitations. Brent Geese are winter site faithful (Lambeck 1990; Harrison *et al*. 2010), so behaviour may simply differ between sites. Sampling other wintering flocks would confirm how representative these results are for the population as a whole. Our study took no account of seasonal variation, as data was collected during two months, whereas Brent Geese stay in Ireland from late autumn until April. In order to draw stronger conclusions about the relationships between Brent Goose energy expenditure, behaviour, sites and habitats, an expansion of temporal and geographical scales is recommended in future studies (Tinkler *et al*. 2009; Ladin *et al*. 2011).

Ireland is one of the main wintering areas for Light-bellied Brent Geese, hosting during winter a high proportion of the population that migrates to the Canadian arctic (Robinson *et al*. 2004), and studies of Brent Goose activity budgets in Ireland could provide reliable information to improve habitat management plans for this subspecies. Whilst the results of our study suggest that there was little cost to Brent Geese from feeding in managed grassland compared to natural wetland habitats, larger numbers of geese were found feeding in relatively undisturbed conditions in the more natural wetland habitats at Tawin Island. Therefore, managing agricultural and coastal fishing activities in this area to further minimise anthropogenic disturbance and to provide more feeding areas for Brent Geese, could increase the carrying capacity of Tawin Island and thereby delay displacement of geese to more managed grassland and pastures. This management approach, if applied more widely, could reduce conflict with agriculture and minimise the associated socioeconomic costs (Fox & Madsen 2017; Madsen *et al*. 2017; Stroud *et al*. 2017).

Acknowledgements

We would like to thank the students from the international MSc in Marine Biodiversity and Conservation (EMBC+, 2015–2017) and other students at Galway-Mayo Institute of Technology who helped with fieldwork throughout this study. We would also like to thank the referees and editors for their useful comments on earlier versions of the manuscript.

References

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227–266.

Bélanger, L. & Bédard, J. 1990. Energetic cost of man-induced disturbance to staging snow geese. *The Journal of Wildlife Management* 54: 36–41.

Boertmann, D., Mosbech, A. & Frimer, O. 1997. Autumn migration of Light-bellied Brent Geese *Branta bernicla hrota* through north-west Greenland. *Wildfowl* 48: 98–107.

Bos, D., Drent, R.H., Rubinigg, M. & Stahl, J. 2005. The relative importance of food biomass and quality for patch and habitat choice in Brent Geese *Branta bernicla*. *Ardea* 93: 5–16.

Christiansen, F., Rasmussen, M.H. & Lusseau, D. 2013. Inferring activity budgets in wild animals to estimate the consequences of disturbances. *Behavioral Ecology* 24: 1415–1425.

Chudzinska, M., Madsen, J. & Nabe-Nielsen, J. 2013. Diurnal variation in the behaviour of the Pink-footed Goose (*Anser brachyrhynchus*) during the spring stopover in Trøndelag, Norway. *Journal of Ornithology* 154: 645–654.

Chudzińska, M.E., Nabe-Nielsen, J., Nolet, B.A. & Madsen, J. 2016. Foraging behaviour and fuel accumulation of capital breeders during spring migration as derived from a combination of satellite- and ground-based observations. *Journal of Avian Biology* 47: 563–574.

Clausen, K.K. & Clausen, P. 2013. Earlier Arctic springs cause phenological mismatch in long-distance migrants. *Oecologia* 173: 1101–1112.

Clausen, K.K., Clausen, P., Fælled, C.C. & Mouritsen, K.N. 2012. Energetic consequences of a major change in habitat use: endangered Brent Geese *Branta bernicla hrota* losing their main food resource. *Ibis* 154: 803–814.

Clausen, K.K., Clausen, P., Fox, A.D., Fælled, C.C. & Madsen, J. 2013. Varying energetic costs of Brent Geese along a continuum from aquatic to agricultural habitats: the importance of habitat-specific energy expenditure. *Journal of Ornithology* 154: 155–162.

Directive, E.E.C. 2009. Directive 2009/147/EC of the European parliament and of the Council of 30 November 2009 on the conservation of wild birds (codified version). *Official Journal L* 20: 7–25.

Fox, A.D. & Abraham, K.F. 2017. Why geese benefit from the transition from natural vegetation to agriculture. *Ambio* 46: 188–197.

Fox, A.D. & Madsen, J. 2017. Threatened species to super-abundance: The unexpected international implications of successful goose conservation. *Ambio* 46: 179–187.

Fox, A.D., Hearn, R.D., Cao, L., Cong, P.H., Wang, X., Zhang, Y. & Rees, E.C. 2008. Preliminary observations of diurnal feeding patterns of Swan Geese *Anser cygnoides* using two different habitats at Shengjin Lake, Anhui Province, China. *Wildfowl* 58: 20–30.

Fox, A.D., Ebbinge, B.S., Mitchell, C., Heinicke, T., Aarvak, T., Colhoun, K. & Kruckenberg, H. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and assessment of trends. *Ornis Svecica* 20: 115–127.

Ganter, B. 2000. Seagrass (*Zostera spp*.) as food for brent geese (*Branta bernicla*): an overview. *Helgoland Marine Research* 54: 63–70.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* 27: 2865–2873.

Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. 2011. Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24: 699–711.

Gudmundsson, G.A., Benvenuti, S., Alerstam, T., Papi, F., Lilliendahl, K. & Åkesson, S. 1995. Examining the limits of flight and orientation performance: satellite tracking of brent geese migrating across the Greenland ice-cap. *Proceedings of the Royal Society of London. Series B* 261: 73–79.

Harrison, X.A., Tregenza, T.O.M., Inger, R., Colhoun, K., Dawson, D.A., Gudmundsson, G.A. & Bearhop, S. 2010. Cultural inheritance drives site fidelity and migratory connectivity in a long-distance migrant. *Molecular Ecology* 19: 5484–5496.

Hopper, M. 2000. *WXTide32, Version 2.6*. Available at http://www.wxtide32.com/ (last accessed 9 September 2018).

Inger, R., Bearhop, S., Robinson, J.A. & Ruxton, G. 2006a. Prey choice affects the trade-off balance between predation and starvation in an avian herbivore. *Animal Behaviour* 71: 1335–1341.

Inger, R., Ruxton, G.D., Newton, J., Colhoun, K., Robinson, J.A., Jackson, A.L. & Bearhop, S. 2006b. Temporal and intrapopulation variation in prey choice of wintering geese determined by stable isotope analysis. *Journal of Animal Ecology* 75: 1190–1200.

Inger, R., Ruxton, G.D., Newton, J., Colhoun, K., Mackie, K., Robinson, J.A. & Bearhop, S.

2006c. Using daily ration models and stable isotope analysis to predict biomass depletion by herbivores. *Journal of Applied Ecology* 43: 1022–1030.

Inger, R., Gudmundsson, G.A., Ruxton, G.D., Newton, J., Colhoun, K., Auhage, S. & Bearhop, S. 2008. Habitat utilisation during staging affects body condition in a long distance migrant, *Branta bernicla hrota*: potential impacts on fitness? *Journal of Avian Biology* 39: 704–708.

Inger, R., Harrison, X.A., Ruxton, G.D., Newton, J., Colhoun, K., Gudmundsson, G.A., McElwaine, G., Pickford, M., Hodgson, D. & Bearhop, S. 2010. Carry-over effects reveal reproductive costs in a long-distance migrant. *Journal of Animal Ecology* 79: 974–982.

Irving, L., Krog, H. & Monson, M. 1955. The metabolism of some Alaskan animals in winter and summer. *Physiological Zoology* 28: 173–185.

Ladin, Z.S., Castelli, P.M., McWilliams, S.R. & Williams, C.K. 2011. Time energy budgets and food use of Atlantic brant across their wintering range. *The Journal of Wildlife Management* 75: 273–282.

Lambeck, R.H.D. 1990. Differences in migratory pattern and habitat choice between social classes of the brent goose *Branta b. bernicla*. *Ardea* 78: 426–440.

Lasiewski, R.C. & Dawson, W.R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *The Condor* 69: 13–23.

Lazarus, J. 1978. Vigilance, flock size and domain of danger size in the white-fronted goose. *Wildfowl* 29: 135–145.

Lefebvre, E.A. & Raveling, D.G. 1967. Distribution of Canada Geese in winter as related to heat loss at varying environmental temperatures. *The Journal of Wildlife Management* 31: 538–546.

Madsen, J., Williams, J.H., Johnson, F.A., Tombre, I.M., Dereliev, S. & Kuijken, E. 2017. Implementation of the first adaptive management plan for a European migratory waterbird population: The case of the Svalbard pink-footed goose *Anser brachyrhynchus*. *Ambio* 46: 275–289.

Mathers, R.G., Portig, A.A. & Montgomery, W.I. 1998. Distribution and abundance of pale-bellied brent geese and wigeon on Strangford Lough, Northern Ireland. *Bird Study* 45: 18–34.

National Parks & Wildlife Service (NPWS) 2013. *Conservation Objectives Supporting Document. Inner Galway Bay Special Protection Area (Site Code 4031). Version 1*. National Parks & Wildlife Service, Dublin, Ireland.

R Core Team. 2016. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Accessible at https://www.R-project.org/ (last accessed 9 September 2018).

Rasmussen, E. 1977. The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. *In* C.P McRoy & C. Helfferich (eds.), *Seagrass Ecosystems*, pp. 1–51. Marcel Dekker, New York, USA.

Riddington, R., Hassall, M., Lane, S.J., Turner, P.A. & Walters, R. 1996. The impact of disturbance on the behaviour and energy budgets of Brent Geese *Branta b. bernicla*. *Bird study* 43: 269–279.

Robinson, J.A. & Colhoun, K. 2006. International Single Species Action Plan for the Conservation of the Light-bellied Brent Goose (East Canadian High Arctic population) *Branta bernicla hrota*. AEWA Technical Series No. 11. African-Eurasian Migratory Waterbird Agreement, Bonn, Germany.

Robinson, J.A., Colhoun, K., Gudmundsson, G.A., Boertmann, D., Merne, O.J., O'Brian, M. & Boyd, H. 2004. Light-bellied Brent

Goose *Branta bernicla hrota* (East Canadian High Arctic population) in Canada, Ireland, Iceland, France, Greenland, Scotland, Wales, England, the Channel Islands and Spain: 1960/61–1999/2000. *Waterbird Review Series*. The Wildfowl & Wetlands Trust/ Joint Nature Conservation Committee, Slimbridge.

Stillman, R.A., Wood, K.A., Gilkerson, W., Elkinton, E., Black, J.M., Ward, D.H. & Petrie, M. 2015. Predicting effects of environmental change on a migratory herbivore. *Ecosphere* 6: 114.

Stroud, D.A., Madsen, J. & Fox, A.D. 2017. Key actions towards the sustainable management of European geese. *Ambio* 46: 328–338.

Symonds, M.R. & Moussalli, A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* 65: 13–21.

Tinkler, E., Montgomery, W.I. & Elwood, R.W. 2009. Foraging ecology, fluctuating food availability and energetics of wintering brent geese. *Journal of Zoology* 278: 313–323.

Photograph: Brent Geese wintering at Galway Bay, Ireland, by María Pérez Tadeo.