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Multi-scale habitat selection and spatial analysis reveals a mismatch between the wintering distribution of a threatened population of Taiga Bean Geese *Anser fabalis* and its protected area

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ABSTRACT

Capsule: Our multi-scale habitat selection and spatial analysis of a threatened population of Taiga Bean Geese *Anser fabalis* highlights the importance of monitoring and review programmes to determine whether species conservation measures are being implemented at the correct spatio-temporal scales.

Aims: To undertake a habitat selection and spatial analysis of an internationally important population of Taiga Bean Geese, and quantify the extent to which their foraging range overlaps with a protected area classified to protect their roost sites and foraging areas.

Methods: A five-year field count dataset was used to quantify foraging habitat selection at the population range scale. In addition, global positioning system (GPS)/ultra high frequency loggers were attached to 12 birds and GPS location data were collected to quantify foraging habitat selection at an individual foraging range scale.

Results: Generalized linear models predicted that, at the population foraging range scale, Taiga Bean Geese selected agriculturally improved pasture, and this selection was more pronounced at greater distances from public roads. At an individual foraging range scale, compositional analysis revealed that agriculturally improved pasture was significantly selected over all other habitats. There was a substantial mismatch between their individual foraging ranges and the protected area, with less than 35% (median: 21%; range 9.5–31.9%) of their individual full foraging ranges overlapping with the protected area.

Discussion: Fixed protected areas may fail to fully accommodate the spatio-temporal foraging dynamics of geese, however a more appropriate conservation measure may be the use of flexible management schemes to maintain their foraging areas within and beyond protected area boundaries. This case study highlights the importance of developing dynamic conservation strategies for species liable to undergo range shifts.

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Protected areas are widely recognized as essential components of biodiversity conservation strategies around the world (European Environment Agency 2012). However, there is rarely any post-designation review to determine whether these areas continue to meet the requirements of their focal habitats and species (Geldmann *et al.* 2013). For bird species, this requires a good understanding of habitat use at different spatial and temporal scales, to identify their roosting, foraging, and breeding habitats (Wiens 1989, Fuller 2012). For some highly mobile species, requiring large home ranges, protected areas may be insufficient to meet all their annual life cycle requirements, and wider countryside conservation mechanisms, such as agri-environment schemes, may be required (Guixé & Arroyo 2011).

Since the 1970s, many goose (Anatidae) populations across the world have largely abandoned foraging on traditional, semi-natural wetland habitats, to forage on highly productive nitrogen- or carbohydrate-rich agricultural crops such as cereals, stubbles, root crops, and intensive grassland (Vickery & Gill 1999, Van Eerden *et al.* 2005, Conover 2011, Fox & Abraham 2017). This has contributed to rapid population growth across their global ranges, in the absence of any apparent density-dependent population limitation

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(Van Eerden *et al.* 2005, Fox & Madsen 2017). As a consequence, much recent applied goose research has focused on developing and testing management measures to mitigate conflicts between rising goose populations and agricultural production (Owen 1990, Tombre *et al.* 2013, Bainbridge 2017, Madsen *et al.* 2017, Mason *et al.* 2017, McKenzie & Shaw 2017). This has included the use of sacrificial crops to provide alternative feeding refuges, where geese can forage undisturbed away from important agricultural crops (Owen 1977, Percival 1993, Patterson & Fuchs 2001, Fox *et al.* 2017).

Despite this preference for cropped foraging habitats, the extent of inclusion of these habitats in Special Protection Areas (SPAs) for geese, designated under Article 4 of the European Union Birds Directive (Council Directive 79/449/EEC), varies across European Union member states, with Austria and Denmark including cropped habitats in over 85% of their SPAs, whilst in Sweden (20.3%), Netherlands (13.3%), Ireland (3.5%), and Finland (1.6%), these habitats account for much less of their SPA networks (Baker & Stroud 2007).

In the UK, SPAs designated for their non-breeding goose populations usually only include important roost sites and exclude cropped foraging habitats (Baker & Stroud 2007). This is largely due to the UK government's policy to base the selection of SPAs on existing Sites of Special Scientific Interest (SSSI), designated under UK legislation (Wildlife and Countryside Act 1981) to protect semi-natural habitats, and not highly modified cropped habitats (Bainbridge *et al.* 2013). In addition, UK governments have largely relied on the use of wider land use policies, including goose management schemes, to reconcile conservation and agricultural objectives (Bainbridge 2017, McKenzie & Shaw 2017). However, the exclusion of cropped habitats in the UK SPA network has been criticized as an important omission for geese, as this excludes essential foraging habitat and fails to fully meet their conservation requirements (Rowell & Robinson 2006, Baker & Stroud 2007).

Stroud *et al.* (2016) note that the use of cropped foraging habitats varies between bird species. It is therefore important that there is an understanding of habitat selection for populations of focal species, and of how the use of cropped habitats varies, before determining the optimal conservation strategy.

For many goose species, the use of cropped foraging habitats varies in response to a range of interacting habitat, spatial, and disturbance factors (Chudzinska *et al.* 2015). Several studies have shown that geese can be highly selective in their choice of foraging site, and select more nutritious and palatable vegetation (Owen 1971, Conover 1991, Gauthier & Bedard 1991). However, foraging site selection can also be influenced by spatial factors, such as field size, with selection for larger fields with longer sight lines to reduce predation risk (Gill 1996, Stenhouse 1996, Chudzinska *et al.* 2016, Jensen *et al.* 2017). Several studies have shown that geese select sites further away from roads as a predation or disturbance avoidance strategy (Madsen 1985, Keller 1991, Jensen *et al.* 2017). Finally, geese have been described as central place foragers, that concentrate their foraging activity within proximity of roost sites to reduce energetic costs associated with searching for foraging resources (Johnson *et al.* 2014, Chudzinska *et al.* 2016, Jensen *et al.* 2017).

The Taiga Bean Goose *Anser fabalis* is one of the few declining goose species in the Western Palearctic with international conservation priorities agreed in an international single species action plan under the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) (Marjakangas *et al.* 2015). Although the factors causing its decline are not yet fully understood, it is important that the habitat requirements of this declining species are understood, to ensure that suitable habitat is protected and maintained throughout its international range (Marjakangas *et al.* 2015).

In the UK, the Slamannan Plateau in central Scotland was designated as a SSSI in 2006, and subsequently as a SPA in 2008, for its non-breeding population of Taiga Bean Geese (hereafter Bean Geese) (SNH 2006). One of only two regularly occupied sites in the UK, the Slamannan Plateau now supports over 90% of the UK wintering population of this species. In contrast to the majority of UK SSSI/SPAs designated for non-breeding geese, the Slamannan Plateau SSSI/SPA was designated to include both the principal roost sites, as well as a significant area of agriculturally improved pasture foraging habitat used by the geese at the time of designation. In addition, a Bean Goose management scheme was established in 2006 to support management measures to benefit the Bean Goose population within the Slamannan Plateau SSSI/SPA (SNH 2017).

The objectives of this study were to: (i) undertake a habitat selection analysis at the population foraging range scale, using field count data, to understand how the selection of agriculturally improved pasture foraging habitat varies in relation to habitat, spatial, and disturbance variables, (ii) use global positioning system (GPS) telemetry data to quantify habitat selection at the individual foraging range scale, and (iii) quantify the extent to which the contemporary foraging range of Bean Geese overlaps with the Slamannan Plateau SSSI/SPA.

Because geese respond to spatial variation in forage palatability (Conover 1991, Gauthier & Bedard 1991), and Bean Geese are frequently observed foraging outside the SSSI/SPA, we hypothesized that the SSSI/SPA no longer fully matches their foraging range. Additionally, we hypothesized that the geese employ a foraging strategy to maximize their nutrient intake, and minimize predation or disturbance risk, by selecting agriculturally improved pasture closer to roost sites, in larger fields, and further away from roads (Chudzińska *et al.* 2015).

Methods

Study area and population

The Slamannan Plateau SSSI boundary (centred at 55.94°N 3.88°W, 170 m above mean sea level; Figure 1) was selected by Scottish Natural Heritage (SNH – now NatureScot) in 2006 to include fields containing 99% of all Bean Geese counted between the winters of 2000/2001 and 2004/2005. The final designation included both the principal open water roost sites (approximately 5% by area) and agriculturally improved pasture foraging fields and loafing areas (95% by area) (SNH 2007). The designation of agriculturally improved grassland foraging fields in the SSSI was not consistent with the UK SSSI selection guidelines (Bainbridge *et al.* 2013), which were designed to protect semi-natural habitats and not cropped foraging habitats. However, SNH made the decision to include agricultural grassland foraging habitats in the designation, as it was concluded that any changes in the distribution of the geese would be gradual, and that the birds would largely remain within the SSSI boundary for most of the time (SNH 2005). The SSSI boundary was subsequently used to designate the Slamannan Plateau SPA in 2008, as a site regularly supporting more than 1% of the UK wintering population of Bean Geese. The SPA area covers 5.9 km^2, split across four separate areas (Figure 1). The network of public roads within and around the Slamannan Plateau SSSI/SPA (hereafter protected area), largely consists of quiet, minor roads used by local vehicular traffic. However, a busier B class road runs north from Slamannan village, and along the southern boundary of the study area.

SNH established a Bean Goose management scheme in 2006 to reward land management considered to be beneficial to the geese in the protected area (SNH 2017). This scheme was only eligible to land managers within the protected area and offered standard payments for the reseeding of agriculturally improved grassland, fertilizer application, management of rushes, and grazing management to maintain and enhance grassland foraging areas for the Bean Geese.

The Slamannan Plateau Bean Goose population has been counted annually since the area was colonized in the late 1980s (Minshull *et al.* 2014). An intensive study investigated field selection by the population during the early 1990s, prior to the designation of the Slamannan Plateau Protected Area (Smith *et al.* 1995). During the last 20 years, the population has remained stable, with mean five-year peaks of 221 (±15 se) birds between 2000/2001 and 2004/2005; and 237 (±8 se) birds between 2014/2015 and 2018/2019. The Slamannan Plateau now supports 25% of the 'Western flyway management unit' population, as identified within the AEWA International Single Species Action Plan (Marjakangas *et al.* 2015).

Data collection

In 2013, data were collected on a range of field characteristics from 385 numbered fields and land units within the recorded winter range of Bean Geese, based on goose field counts undertaken since 1993/1994 (Minshull *et al.* 2014). This included fields not recorded as having been used by Bean Geese. All field boundaries were identified using 1:10,000 base maps. Field habitat type was classified following the Phase 1 habitat survey (Joint Nature Conservation Committee 2010) as old agriculturally improved pasture (OIP), where no ploughing or reseeding had occurred during the previous five years, and recently agriculturally improved pasture (RIP), where ploughing and reseeding had occurred within those five years. Rough grassland (RG) had not been reseeded or ploughed at any time prior to the survey. Other habitat categories included bog (B), forestry (F), and upland mosaic (bog and rough grassland; UM).

In addition, field size (m^2), distance to the nearest main roost (m), and distance to nearest road (m) were measured in QGIS (2014). Distance to the nearest main roost was measured as the linear distance from the field centroid to both of the two regularly used roost sites (Figure 2(a)), and the shortest distance was used in the analysis. Distance to the nearest road was measured as the linear distance from the field centroid to the nearest public road.

We used a five-year field count dataset between 2011/2012 and 2015/2016, as this dataset was (a) contemporaneous to the field habitat data (collected in 2013) and (b) included a corresponding five-year

Figure 1. The Slamannan Plateau study area showing the Site of Special Scientific Interest (SSSI)/Special Protection Area (SPA) designated for Taiga Bean Geese (hatched area) in relation to human settlements (solid grey areas) and main roads (black lines). Inset shows the location in central Scotland.

period matching that of the five years' data used to identify the original protected area boundary (2000/2001–2004/2005).

Although there was some variation in the route taken for each count, complete survey coverage of the Plateau was achieved, either whilst driving between flocks or during scans from vantage points. All counts were completed between September and February inclusive, during the five winters between 2011/2012 and 2015/2016. Counts were completed on average over 59 days (range 48–80) per winter, or two days per week, and each count usually took between four and six hours to complete.

Geese were counted from vehicles, using binoculars and spotting scopes at distances of between 200 and 700 m. As this study was investigating foraging habitat selection, the field count dataset was limited to counts made between 09:00 and 15:00 h, in accordance with daylight hours on the shortest winter day. The flock size and field number, as well as the time of observation were recorded. A total of 19 numbered fields, amounting to 2.9% of the field area, were not counted in any survey year due to access restrictions (Figure 2(a)).

Bean Geese were caught under licence using cannon nets in early October, soon after arrival from their breeding grounds in 2012, 2013, and 2015 (Mitchell *et al.*, 2016). They were marked with British Trust for Ornithology metal rings and plastic neck collars integrated with solar GPS – global system for mobile communications (GSM)/ultra high frequency (UHF) loggers. The total mass of each collar and logger was 27–42 g, approximately 0.8–1.3% of the body mass of the nine male and three female Bean Geese tagged (Table 1). We excluded the locations from the first three days after logger attachment, to allow for habituation to the collars. Our sample included six birds tracked for one winter, four for two winters, and two for three winters, a total of 20 bird-seasons. Location data were retrieved either via Short Message Service (SMS) or via a hand-held UHF receiver. GPS logger location accuracy was estimated using stationary GPS loggers located in a field in Fife, Scotland (56.29N, 2.65W) and on a building in Reykjavik, Iceland

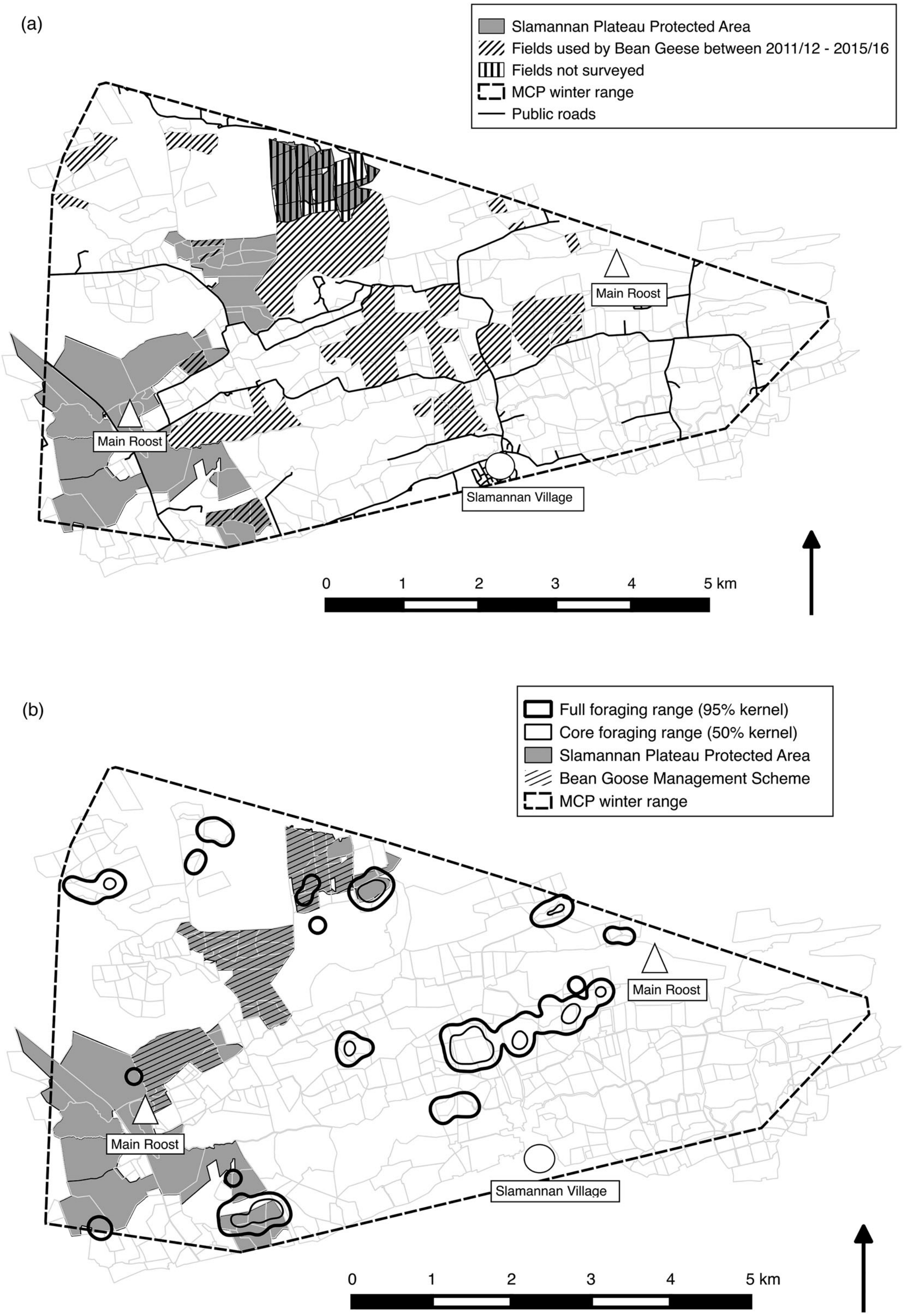

Figure 2. (a) Foraging range based on field count data (20011/2012–2015/2016) in relation to the protected area and (b) full (95% kernel) and core (50% kernels) foraging ranges in relation to the protected area and Bean Goose management scheme. The full and core foraging ranges are based on one bird season with a protected area overlap of 19.5% and 32.9% respectively, which most closely matched the median overlap across all 20 bird seasons (21% [range 9.5–31.9%] and 30% [range 0.3–44.9%] for full and core foraging ranges respectively). Kernels were based on GPS data collected between 09:00 and 15:00 h. Blank gaps between fields were considered to be unavailable to foraging geese, consisting of open water, forestry, and urban areas.

Table 1. Summary details of the GPS/UHF telemetry devices deployed on Taiga Bean Geese caught at Slamannan, near Falkirk in 2012, 2013, and 2015. The number of GPS fixes used to generate the fixed kernels is provided for each bird.

Bird ID	Tag type	Body mass (g)	Age and sex	Date of deployment	Bird Season	No. GPS fixes for foraging range estimation
UCOL06a	GPS/GSM	3375	Adult male	14/10/2012	2012/13	254
UCOL07	GPS/GSM	3350	Adult male	14/10/2012	2012/13	274
					2013/14	196
UCOL08	GPS/GSM	3175	1st winter male	14/10/2012	2012/13	115
TAG16	GPS/UHF	3250	1st winter male	14/10/2012	2012/13	195
TAG02	GPS/UHF	3025	1st winter female	14/10/2012	2012/13	817
UHF04	GPS/UHF	3175	Adult male	07/10/2013	2013/14	701
UCOL06b	GPS/GSM	3050	Adult male	07/10/2013	2013/14	250
UCOL03	GPS/GSM	3375	Adult male	14/10/2012	2012/13	152
Tag replacement UCOL10	GPS/GSM/UHF			09/10/2015	2015/16	404
					2016/17	239
UCOL27	GPS/GSM/UHF	3175	Adult female	09/10/2015	2015/16	436
					2016/17	364
UCOL29	GPS/GSM/UHF	3535	Adult male	09/10/2015	2015/16	366
					2016/17	294
UCOL30	GPS/GSM/UHF	2875	Adult female	09/10/2015	2015/16	284
					2016/17	263
FAB13	GPS/UHF	3425	Adult male	07/10/2013	2013/14	391
					2014/15	699
					2015/16	428

(64.13N, 21.90W). Location data from the loggers were combined. The GPS loggers provided an estimated latitude location error of 15.6 m (0.63 m se, $n = 1327$) and an estimated longitude location error of 8.9 m (0.32 m se, $n = 1327$), and this was deemed accurate enough at the foraging range scale.

We collected location data for each bird every three hours (daylight schedule = 09:00, 12:00, 15:00 h) during the birds' wintering period on the Slamannan Plateau. However, during mid-winter, when solar charging potential was low, many tags gave locations every six hours or less, with some providing no location data on some days.

Population foraging range habitat selection – statistical analysis

Generalized linear models (GLMs) with a binomial error distribution were used to analyse the influence of the field characteristic variables (distance to nearest road, distance to nearest main roost, and field size) on the probability of field use by foraging geese. For each field, and for each of the five winters within the study period, we recorded whether the field was used (1) or not detected as used (0; for brevity called 'unused'). The binomial numerator for each field was the number of years it was detected as used (between 0 and 5) and the binomial denominator for each field was the number of years it was available in the study (in each case five). Predicted values from models could thus be interpreted as annual probabilities of detected use. We checked for multicollinearity in the explanatory variables by creating a global model containing each explanatory variable and calculating the variance inflation factor (VIF) for each, using the *car* package in R (Fox & Weisburg, 2019). A generally accepted threshold for VIF is that if they are >2.5 it indicates 'considerable collinearity', while some authorities use a higher threshold (Johnston *et al.* 2018); we took a conservative approach and used the lower 2.5 threshold. All VIFs in the global model were <1.15 and, therefore, we considered multicollinearity in the explanatory variables to be low and not an issue in our models.

We tested for the possible presence of over-dispersion in each GLM using the ratio of residual deviance to residual degrees of freedom, considering that over-dispersion may be present where this was ≥2 (Lindsey 1999). Ratios of residual deviance to residual degrees of freedom for all models in the candidate set ranged between 1.4 and 1.6, so we considered this did not meet the criterion for further checking for the presence of over-dispersion (Lindsey 1999). To reduce heavy positive skew within the explanatory variables, field size was natural logarithm transformed, while distance to road was square-root transformed. Because the analysis was exclusively investigating foraging distribution, any habitats considered to be unavailable to foraging geese, such as forestry, bog, and upland mosaic, were excluded from the models.

A set of 11 *a priori* hypotheses, based on previous studies, was used to build a set of candidate models explaining the foraging distribution of the geese (Table 2). These models were based on biologically plausible hypotheses identified in the literature as

Table 2. Candidate set of *a priori* hypotheses tested in the population foraging range analysis, based on factors reported to influence the foraging distribution of geese in the literature. Codes for model formula: FS = field size; FH = field habitat; DMR = distance to nearest main roost; and DR = distance to road.

Model	Model formula	Hypothesis (based on previous studies)	References
1	Null model	No field variable explains the probability of field use. Distribution is apparently random with respect to the variables considered (null hypothesis).	
2	FS	Geese select larger field sizes as this provides greater 360° lines of sight and reduces predation risk.	Gill (1996), Chudzinska *et al.* (2015), Jensen *et al.* (2017), Rosin *et al.* (2012)
3	FH	Geese select more nutritious grassland swards such as recently improved pasture and avoid rough grassland.	Smith *et al.* (1995)
4	DMR	Geese select fields closer to a main roost site to reduce energy expenditure associated with travel from roost sites.	Chudzinska *et al.* (2015), Jensen *et al.* (2017), Harrison *et al.* (2018)
5	DR	Geese avoid roads to reduce predation/disturbance risks.	Keller (1991), Gill (1996), Chudzinska *et al.* (2015), Jensen *et al.* (2017), Smith *et al.* (1995), Madsen (1985)
6	FH+DR	Geese select more nutritious grassland swards to maximize energy intake, and select fields further away from roads to minimize predation/disturbance risks.	Chudzinska *et al.* (2015), Smith *et al.* (1995)
7	FH x DR	As per model 6, but these effects interact to mean more nutritious field habitats further from roads are disproportionately used.	Chudzinska *et al.* (2015), Jensen *et al.* (2017)
8	FH+DMR	Geese select more nutritious improved grassland swards to maximize energy intake and select fields closer to a main roost site to reduce energy expenditure associated with travel from roost sites.	Jensen *et al.* (2017), Harrison *et al.* (2018), Chudzinska *et al.* (2015)
9	FH x DMR	As per model 8, but these effects interact to mean more nutritious field habitats closer to a main roost site are disproportionately used.	Chudzinska *et al.* (2015), Jensen *et al.* (2017), Harrison *et al.* (2018)
10	FH+FS	Geese select more nutritious improved grassland swards to maximize energy intake and bigger fields to reduce predation risk.	Gill (1996), Stenhouse (1996), Chudzinska *et al.* (2015), Jensen *et al.* (2017), Chudzinska *et al.* (2015)
11	FH x FS	As per model 10 but these effects interact to mean that more nutritious improved grassland swards in bigger fields are disproportionately used.	Chudzinska *et al.* (2015), Jensen *et al.* (2017)

being important in influencing the distribution of foraging geese. As with previous studies, field size (Smith *et al.* 1995, Gill 1996, Stenhouse 1996, Chudzińska *et al.* 2015, Jensen *et al.* 2017) and distance to road (Madsen 1985, Keller 1991, Smith *et al.* 1995, Gill 1996, Chudzińska *et al.* 2015, Jensen *et al.* 2017) were used as proxies for perceived predation or disturbance risk. We also used distance to the nearest main roost site as an explanatory variable in the models, to test whether roost location was influencing foraging site selection (Hamilton & Watt 1970, Johnson *et al.* 2014, Chudzińska *et al.* 2015, Jensen *et al.* 2017, Harrison *et al.* 2018).

All models were ranked by their small-sample Akaike information criterion (AIC) and inferences were taken from a confidence set of models which was the smallest set of models with a summed Akaike's weight of $w_i \geq 0.95$ (Johnson & Omland 2004).

We report goodness-of-fit measures for each model, including the negative log-likelihood of each model. Because we were using binomial GLMs, we report two pseudo-R^2 values: McFadden's and Nagelkerke's using the *rcompanion* package (Mangiafico 2019) in R version 3.4.1 (R Core Development Team 2015). We selected two pseudo-R^2 to represent a more conservative and less conservative estimate of goodness-of-fit; pseudo-R^2 values for logistic regression tend to be more conservative in general than R^2 values in original least squares regression (Smith & McKenna 2013).

We tested for spatial autocorrelation in the confidence set of models by plotting the model residuals as spline correlograms with Moran's *I*, using the *ncf* package (Bjørnstad *et al.* 1999). For the confidence set of models, there was a weak positive spatial autocorrelation between model residuals below approximately 2000 m. The maximum correlation coefficient for these models (at 0 m) was only 0.2. However, the correlation between the model residuals falls away rapidly and is not significantly different from zero after approximately 2000 m (Figure 3(a, b)). Given the median field size used (0.06 km^2, equivalent to a circle of diameter 286 m), this localized spatial autocorrelation was not expected to have had a major impact on the model parameter estimates.

Individual foraging range habitat selection – statistical analysis

Foraging ranges were determined for all tagged birds (*n* = 12; 20 bird-seasons; Table 1) using a 95% and 50% fixed kernel estimator with a least-squares cross-validation smoothing parameter (Worton 1989) representing full and core foraging ranges respectively. In accordance with daylight hours on the shortest winter day, only GPS fixes between 09:00 and 15:00 h were sampled to ensure no nocturnal roost sites were included in the dataset. All kernels were checked in QGIS to ensure no roost sites were included in the sample.

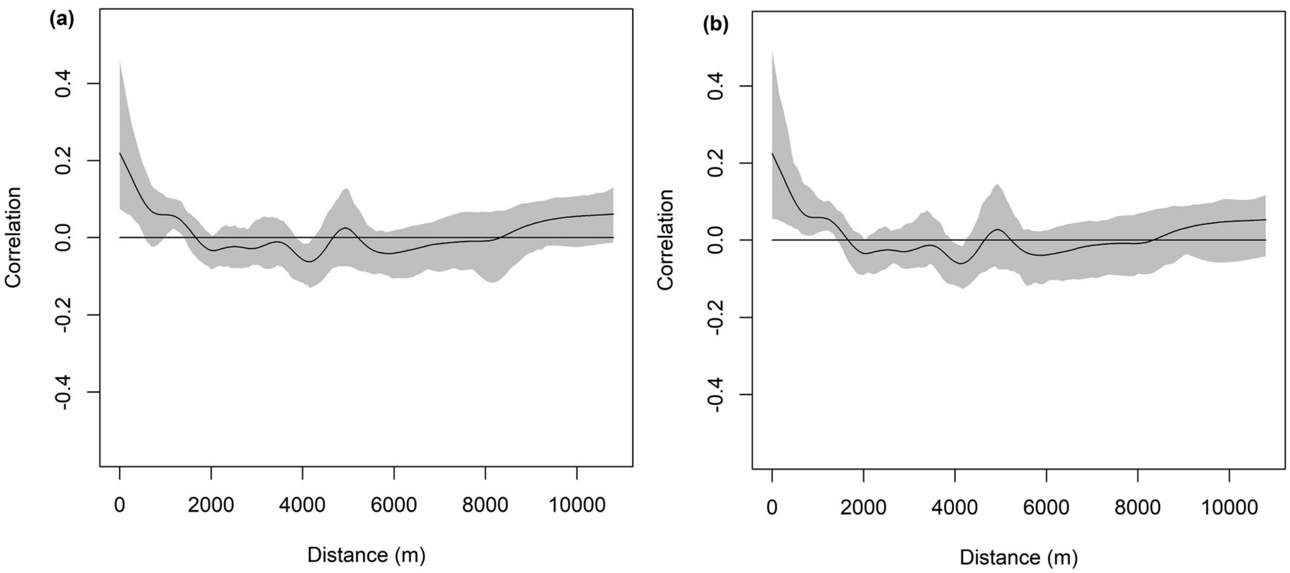

Figure 3. Correlograms for the confidence set of models testing for spatial auto-correlation including (a) model 6 and (b) model 7. Model numbers refer to those in Tables 2 and 3. The shaded areas represent 95% pointwise confidence intervals.

We used a 100% minimum convex polygon (MCP) to define the approximate winter range of the whole flock, representing an estimate of habitat availability at the scale of the study area (Aebischer *et al.* 1993) (Figure 2(b)). This was based on all fields known to be used by the geese since 1993/1994 (Minshull *et al.* 2014). The field habitat data used for the population scale analysis were also used to assess individual foraging range habitat selection.

To assess whether 50% and 95% kernels represented stable estimates of core and full foraging range sizes respectively, we carried out a randomized range stabilization analysis (Kenward 2004). For each bird-season with at least 300 fixes ($n = 8$), 10 GPS fixes were randomly selected and 95% and 50% fixed kernels with least-squares cross-validation smoothing parameter were calculated (Worton 1989). This was repeated by incrementally adding 10 additional random GPS fixes, up to a maximum of 300 fixes, and estimating the 95% and 50% fixed kernel areas at each iteration. This method produces a plot of range size against number of GPS fixes, and an approximation of the number of GPS fixes required for range stabilization can be determined when this reaches an asymptote. For comparison across ranges (separately for full and core), areas of ranges were indexed such that the area at 300 fixes was set to 1.

For both core and full foraging range sizes, analyses revealed stabilization was achieved at approximately 100 GPS locations (Figure 4(a, b)). The minimum number of locations we used to estimate any one foraging range was 115, with a median of 289 (inter-quartile range, IQR: 247–410) locations, so we considered our kernels to be stable representations of foraging ranges.

Compositional analysis was used to assess apparent habitat selection by comparing habitat use with availability (Aebischer *et al.* 1993). Compositional analysis was carried out at two scales: (i) full foraging range (95% kernel) within the study area (100% MCP of whole flock) and (ii) core foraging range (50% kernel) within the full foraging range, representing second- and third-order habitat selection respectively (Johnson 1980, Aebischer *et al.* 1993).

Because habitat components within a composite are non-independent, all habitat data were rendered linearly independent by taking natural log-ratios of the proportions of each but one habitat against that of the remaining habitat (here forestry, but the choice of habitat does not impact the results), and substituting zero values with 0.01% (Aebischer *et al.* 1993). The null hypothesis that habitat use did not significantly differ from availability was tested with a MANOVA using the test statistic Wilks' Lambda (Λ), with the multiple log-ratios as response variables and used/available as a binary explanatory variable (Aebischer *et al.* 1993). If the null hypothesis was rejected, indicating apparent habitat selection, then habitats were ranked by relative position on the selection-avoidance spectrum by comparing the difference in the log-ratios of proportional use/availability of all pairs of habitats, ranking each in turn by the number of other habitats they exceeded in this ratio. Because we could not assume normality of errors, permutational linear models were used to determine whether pairwise differences between habitats in the use/availability ratio were significant at $P = 0.05$, using the

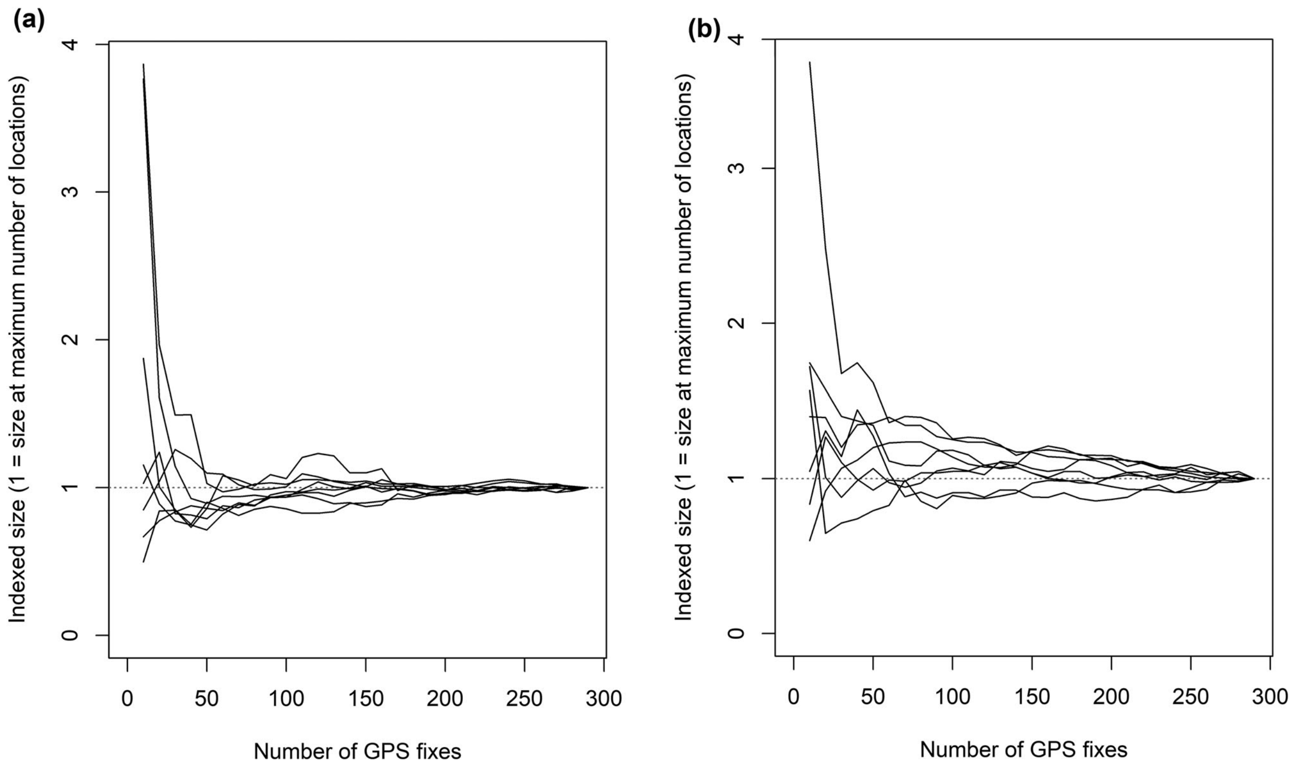

Figure 4. Range stabilization analysis showing the relationship between the number of GPS fixes and range size where the range had at least 300 fixes for (a) full foraging ranges ($n = 8$ bird seasons) and (b) core foraging ranges ($n = 8$ bird seasons).

lmPerm package in R (Wheeler & Torchiano 2016). All results were displayed as ranking matrices, where habitats were ranked according to their relative position on the selection-avoidance spectrum.

Population foraging range overlap with protected area

We investigated what the protected area boundary might look like if it were based on our more recent field count data from the five winters 2011/2012 to 2015/2016, rather than the original five years of data used to select the protected area boundary. We used the same method that was applied to select the protected area boundary (SNH 2007). For each field, the total counts made on each count visit, on each year were summed. The fields were ranked in order of this count. The selected area was then taken as the smallest set of fields that contained at least 99% of all geese counted across the 5-year period, hereafter called the ‘99 percentile criterion’.

Individual foraging range overlap with protected area

The percentage area of each full and core foraging range within the protected area was calculated for each bird season in QGIS ($n = 20$). Overlap was then calculated as the area shared by each foraging range and the protected area divided by the total foraging range for each bird season separately, multiplied by 100. If all goose activity was contained within the protected area, then we would expect a value of 100%, and if no goose activity was contained within the protected area, 0%.

Results

Population foraging range habitat selection

Of 304 fields surveyed in the available grassland foraging area (including all OIP, RIP, and RG fields), 48 (16%) were observed to be used by foraging geese (Figure 2(a)). The mean number of fields used per annum was 19 (range 14–29), or 6% of all available grassland fields surveyed. The frequency of field use was highly skewed, with 10 fields accounting for 59% of all goose use, and 20 fields accounting for 83% of all goose use. A greater number of fields were used as the winter progressed, with a mean of only 1.25 (±se 0.3) fields used in September, rising to a mean of 20 (±se 2.6) fields in February.

Bean Geese used larger fields (Used median: 0.059 km^2 [IQR: 0.042–0.092]; Unused median: 0.044 km^2 [IQR: 0.028–0.070]), and fields further away from

Table 3. Model results for a set of *a priori* hypotheses based on the previous studies investigating foraging distribution in geese that were tested using generalized linear models with a binomial error distribution. Model hypotheses are given in Table 2 matched by model number. k = number of estimated parameters, $-\ln(L)$ = negative log-likelihood of model, AIC = Akaike's information criterion; Δ_{AIC} = difference between the AIC for given model and best model; w_i = relative likelihood model is best model given data and candidate model set; R^2_{McF} = McFadden's pseudo-R^2; R^2_{Nag} = Nagelkerke's psuedo-R^2; $\hat{c}$ = ratio of residual deviance to residual degrees of freedom. The confidence set of models is indicated in bold (with a summed w_i of >0.95).

Model	Explanatory variables	k	$-\ln(L)$	AIC	Δ_{AIC}	w_i	R^2_{McF}	R^2_{Nag}	$\hat{c}$
6	**Field habitat + distance to road**	**4**	**−235.1**	**478.24**	**0.00**	**0.630**	**0.103**	**0.204**	**1.418**
7	**Field habitat * distance to road**	**6**	**−233.7**	**479.31**	**1.07**	**0.369**	**0.108**	**0.214**	**1.417**
10	Field habitat + field size	4	−241.7	491.38	13.14	0.001	0.078	0.158	1.464
5	Distance to road	2	−244.8	493.57	15.33	<0.001	0.066	0.135	1.476
11	Field habitat * field size	6	−241.6	495.17	16.93	<0.001	0.078	0.159	1.474
2	Field size	2	−247.0	498.08	19.84	<0.001	0.057	0.118	1.492
8	Field habitat + distance to nearest main roost	4	−255.8	519.69	41.45	<0.001	0.024	0.050	1.565
9	Field habitat * distance to nearest main roost	6	−254.8	521.67	43.43	<0.001	0.027	0.058	1.569
3	Field habitat	3	−258.4	522.79	44.55	<0.001	0.014	0.030	1.577
4	Distance to nearest main roost	2	−259.4	522.79	44.55	<0.001	0.010	0.022	1.579
1	Null	1	−262.0	526.05	47.81	<0.001	0.000	0.000	1.592

roads (Used median: 294.2 m [IQR: 184.5–399.8]; Unused median: 147.7 m [IQR: 97.7–268.8]). However, distances to the nearest main roost between used (median 2.2 km; IQR: 1.1–2.8) and unused (median 2.1 km; IQR: 1.4–2.6) fields were similar.

For habitat selection at the population foraging range scale, two models formed the confidence set (Table 3). The best model ($w_i = 0.63$) predicted that field use would increase with distance to road for agriculturally improved pasture (OIP and RIP) (Figure 5(a)). The second-best model ($w_i = 0.37$) predicted that field use would increase with distance to road; however, the relative probability of use was greater for RIP than OIP at greater distances from roads (Figure 5(b)). Model parameter estimates can be found in Table 4.

Individual foraging range habitat selection

The median core foraging range size (0.31 km^2; IQR: 0.24–0.37) was 17% of the full foraging range size (1.80 km^2; IQR: 1.21–2.27) (Figure 2(b)). There was a clear difference between habitat availability and use at the individual foraging range scale, with greater use of both old and recently improved pastures relative to their availability (Figure 6). This difference was even more pronounced when comparing core foraging habitat use with available habitats, than it was when comparing full foraging habitat use with available habitats.

There was significant habitat selection, both at the scale of the full foraging range within the whole flock MCP (Wilks' $\Lambda = 0.018$ $P = 0.002$) and at the scale of the core foraging range within the full foraging range (Wilks' $\Lambda = 0.150$, $P = 0.002$).

The ranking matrix results for full foraging range within the study area showed an apparent selection-avoidance spectrum as follows (where > indicates higher apparent selection and >>> significantly higher apparent selection at $P = 0.05$): recently improved pasture (RIP) > old improved pasture (OIP) >>> rough grassland (RG) > bog (B) > upland mosaic (UM) > forestry (F) (Table 5(a)). Selection for core foraging range within full foraging range showed an apparent selection-avoidance spectrum as follows: RIP > OIP >>> UM > B > RG >>> F (Table 5(b)).

Foraging range overlap with protected area

The protected area boundary is based on the 35 fields that contained at least 99% of all geese counted across the original 5-year period (2000/2001–2004/2005). Repeating this method for 2011/2012–2015/2016, we selected 38 fields, although only 12 of these were the same fields across both periods (note that one field included originally has since been split, but we treated it as a single field for comparison) (Figure 7). Therefore, 23 fields (66%) within the protected area would not have been designated as such if it had been based on the 2011/2012–2015/2016 data. Using the GPS location data, a median of 21% (range 9.5–31.9) and 30% (range: 0.3–44.9) of the individual full and core foraging ranges respectively, fell within the protected area over all the study years.

Discussion

Habitat selection

This study showed that Bean Geese foraged almost exclusively on agriculturally improved pasture at the population and individual foraging range scales. In common with our study, Smith *et al.* (1995) reported that the Slamannan population largely exploited agriculturally improved pasture for foraging in the

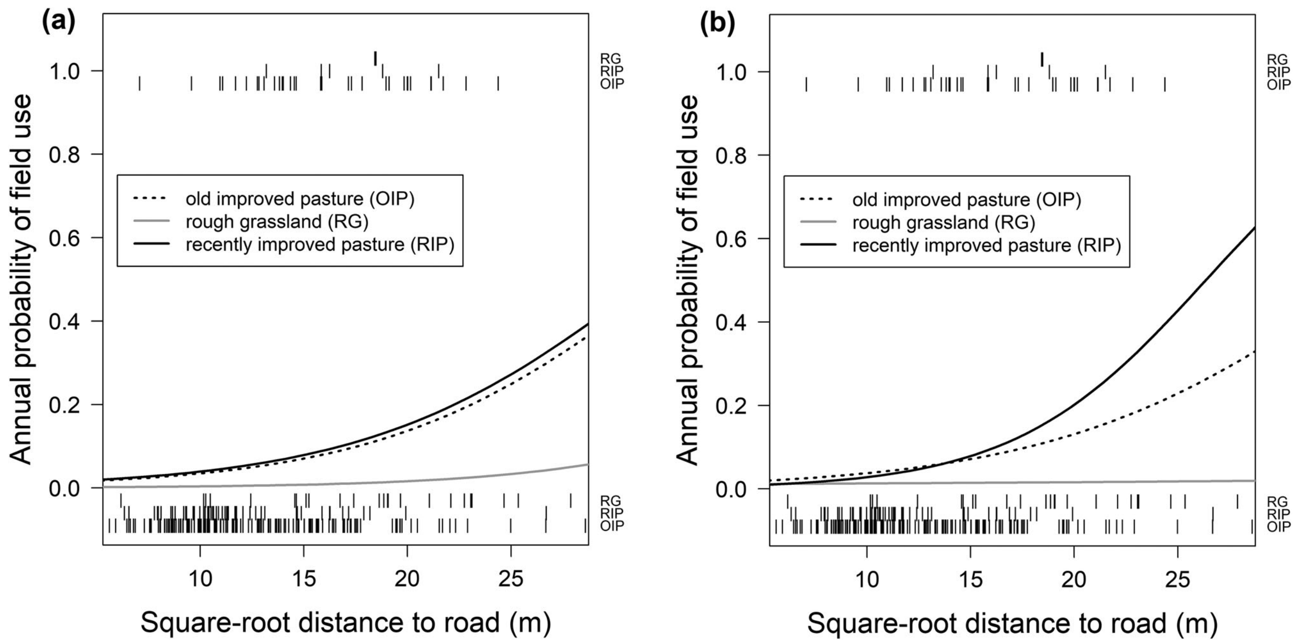

Figure 5. Modelled probabilities of population scale field use by Bean Geese on the Slamannan Plateau in relation to (a) field habitat and distance to road (Model 6); and (b) the interaction between field habitat and distance to road (Model 7). Model numbers refer to those in Table 3. Parameter estimates with standard errors are given in Table 4. The distributions of raw data of used (top) and unused (bottom) fields are shown using vertical bars, categorized by habitat type: RIP = recently improved pasture, OIP = old improved pasture, RG = rough grassland. These are just shown for illustration and indicate if a field was used or unused during the five-year study period, while models are based on annual probabilities of use (see text).

early 1990s. However, the selection of agricultural pasture reported in our study is in contrast to other studies in their European wintering range. In Norfolk, England, Bean Geese have been reported foraging in old, less intensively farmed pastures (Allport 1991, Ben Lewis, RSPB, pers. comm.). Elsewhere in Europe, Bean Geese have been reported foraging in a diverse range of agricultural crops such as Sugar Beet *Beta vulgaris*, Potato *Solanum tuberosum*, Maize *Zea mays* stubbles, and winter cereals (Rosin *et al.* 2012, Nilsson & Kampe-Persson 2013). At a previously occupied

Table 4. Parameter estimates and standard errors for confidence set models from Table 3. The null model is shown for comparison.

Model	Parameter	Estimate	Standard error
6	Intercept	−4.792	0.367
	Field type RG	−2.265	0.735
	Field type RIP	0.120	0.276
	$\sqrt{}$ Distance to any road (m)	0.148	0.021
7	Intercept	−4.593	0.398
	Field type RG	0.044	2.715
	Field type RIP	−1.123	0.918
	$\sqrt{}$ Distance to any road (m)	0.135	0.024
	$\sqrt{}$ Distance to any road (m): Field type RG	−0.114	0.142
	$\sqrt{}$ Distance to any road (m): Field type RIP	0.082	0.056
1 *[null]*	Intercept	−2.725	0.110

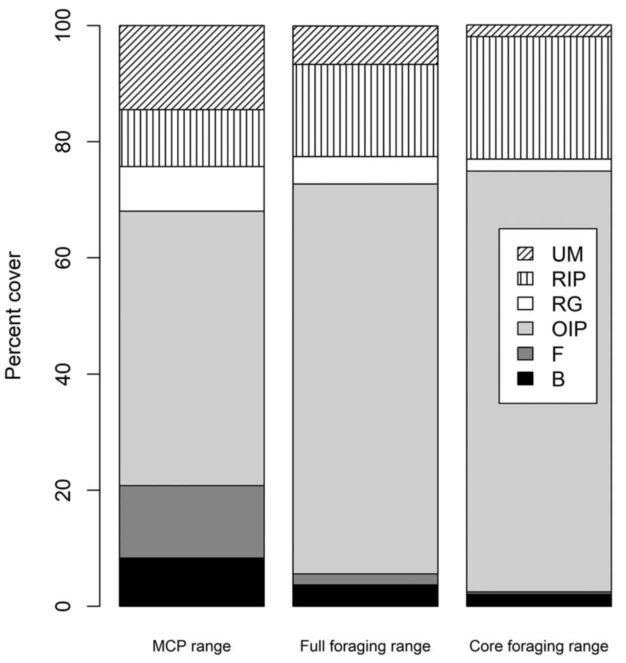

Figure 6. Habitat compositions in MCP range for whole flock (representing habitat availability in the study area), full foraging ranges (mean for 20 bird-seasons), and core foraging range (mean for 20 bird-seasons). Habitats are UM = upland mosaic, RIP = recently improved pasture, RG = rough grassland, OIP = old improved pasture, F = forestry, and B = bog.

Table 5. Habitat selection ranking matrices for two different compositional analyses. The + or - sign shows that the row habitat was higher (+)/lower (-) ranked than the column habitat and therefore demonstrated more or less apparent selection. The + or - sign is tripled (+++ or ---) where the pairwise difference was significant at $P < 0.05$. Row habitats are ranked according to the number of higher rank (+ or +++) positions, with 1 indicating most selected and 6 most avoided.

	Column habitat						
Row habitat	B	F	OIP	RG	RIP	UM	RANK
(a) Full foraging range (95% fixed kernel) within study area (MCP).							
Bog (B)		+++	---	-	---	+	4
Forestry (F)	---		---	---	---	-	6
Old improved pasture (OIP)	+++	+++		+++	-	+++	2
Rough grassland (RG)	+	+++	---		---	+	3
Recently improved pasture (RIP)	+++	+++	+	+++		+++	1
Upland mosaic (UM)	-	+	---	-	---		5
(b) Core foraging range (50% fixed kernel) within full foraging range (95% fixed kernel).							
Bog (B)		+++	---	+	---	-	4
Forestry (F)	---		---	---	---	---	6
Old improved pasture (OIP)	+++	+++		+++	-	+++	2
Rough grassland (RG)	-	+++	---		---	-	5
Recently improved pasture (RIP)	+++	+++	+	+++		+++	1
Upland mosaic (UM)	+	+++	---	+	---		3

wintering site in south-west Scotland, Bean Geese foraged on marshes, stubbles, and grassland, and were not exclusively foraging on agriculturally improved pasture (Watson 1986). Away from their wintering site, the Slamannan population have been reported foraging on nutrient-rich agricultural crops, such as stubbles, winter cereals, and grassland at their main spring and autumn staging sites (Mitchell *et al.* 2016).

A previous study, which analysed Bean Goose droppings from agriculturally improved pasture on the Slamannan Plateau, revealed that perennial rye-grass *Lolium perenne* was the dominant food plant, consisting of up to 87% composition in most samples (Percival & Votier 1996). More recent data have shown that sward composition at Bean Goose foraging locations on the Slamannan Plateau was dominated by perennial rye-grass (unpubl. data 2018).

In common with many other global populations of geese, it would appear that Bean Geese wintering on the Slamannan Plateau have made the transition from foraging on semi-natural wetlands, to exploiting highly nutritious agriculturally improved grassland, dominated by perennial rye-grass (Owen 1980, Van Eerden *et al.* 2005, Owen & Black 2008, Fox & Abraham 2017). Heavily fertilized, modern cultivars of perennial rye-grass in agricultural grassland can be sequentially defoliated and still produce high quality leaf tissue for grazers, including geese, for prolonged periods of time (Davies 1988, Lestienne *et al.* 2006).

At the individual foraging range scale, recently improved pasture (<5 years old) was ranked above old improved pasture (>5 years old) in the compositional analysis, suggesting the geese were selecting more palatable and nutritious swards to maximize their nutrient intake (Percival 1993), although a pairwise comparison indicated this difference was not significant. In addition, at the population foraging range scale, geese favoured recently improved pasture, with stronger selection for recently improved pasture, relative to old improved pasture, further away from roads. This suggests that habitat selection at the population foraging range scale is shaped by a trade-off between maximizing nutrient intake and minimizing perceived predation or disturbance risk (Gill 1996, Chudzińska *et al.* 2015, Jensen *et al.* 2017).

Although field size has been shown to be an important spatial variable, influencing the foraging distribution of geese (Gill 1996, Stenhouse 1996, Rosin *et al.* 2012), field size was not included in the confidence set of models in our population foraging range analysis (Table 3). We included field size as a broad proxy for perceived predation risk; however, it is possible that perceived predation risk is influenced by other factors that we did not record, such as field boundary type (hedge, ditch, or fence), or field topography, which may influence sight lines for foraging geese (Madsen 1985, Chudzinska *et al.* 2016, Jensen *et al.* 2017).

Roost location has been identified as an important factor influencing habitat selection in geese, with several studies showing that geese preferentially use suitable foraging habitats closer to roost sites to minimize energy expenditure associated with flying to foraging sites (Hamilton & Watt 1970, Johnson *et al.* 2014). However, distance to the nearest main roost site in this study did not appear to strongly influence goose foraging locations (Table 3). Foraging fields were close to the nearest main roost site (median: 2.2 km, IQR 1.1–2.8) and, therefore, foraging flight distances were relatively short when compared with the mean for nine other goose species (7.8 km, Johnson *et al.* 2014). Furthermore, all foraging locations based on field use and GPS fixes, were less than 7.7 km from all known contemporary roost sites, suggesting the geese did not expend significant amounts of energy travelling from roost sites to foraging fields, and the population may exist well within the energetic carrying capacity of the landscape (Johnson *et al.* 2014).

The small individual foraging ranges occupied by the geese within the whole flock MCP, revealed by the GPS data and field counts, suggest that foraging resource

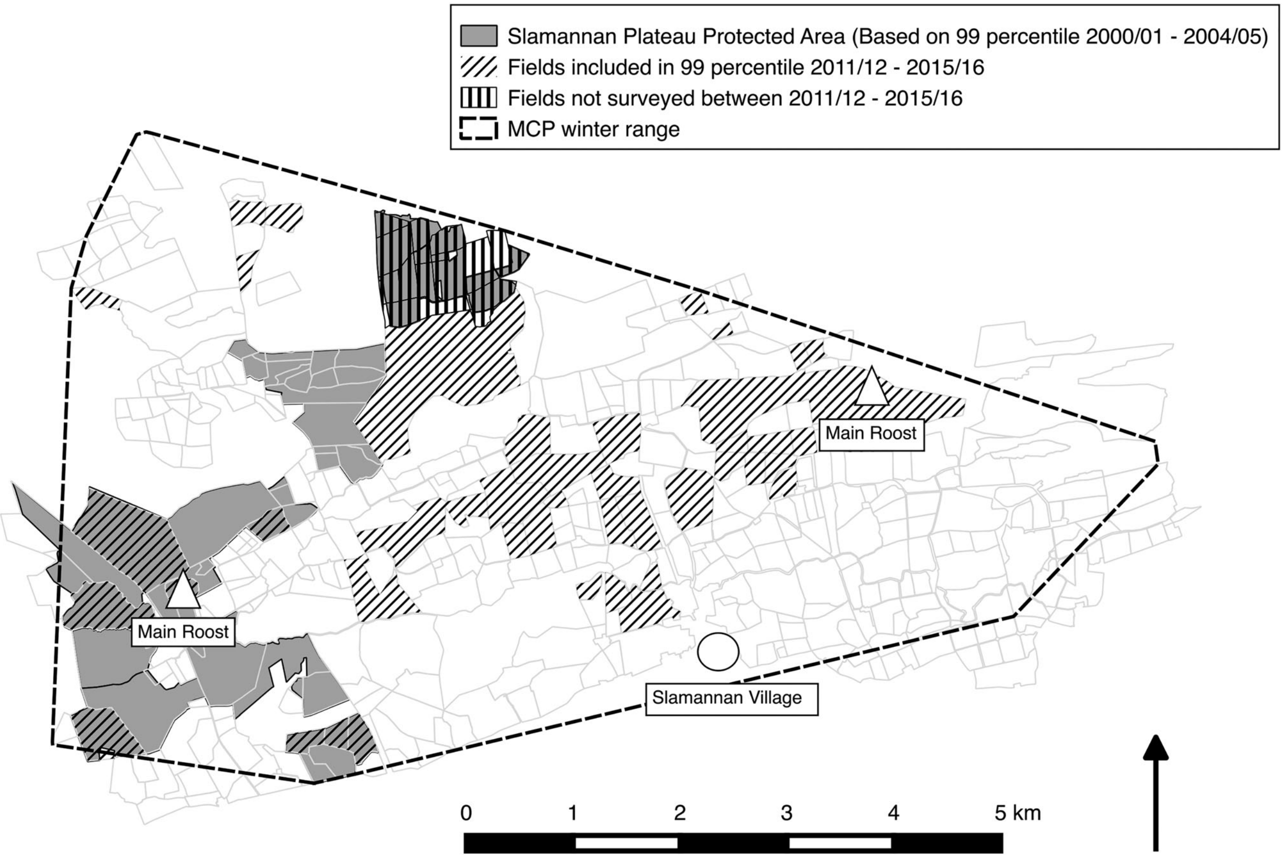

Figure 7. Geographical comparison of the protected area footprint (which was based on data from 2000/2001–2004/2005) with field use between 2011/2012 and 2015/2016 using the same 99-percentile selection criterion that was used to select the original protected area boundary (see text for method).

availability is not limiting the population. This is supported by the fact that the geese used only 23% of the agriculturally improved grassland (RIP and OIP) field area within their entire MCP winter range during our study period. However, some of this grassland may have been unavailable to the geese due to a high-perceived predation or disturbance risk close to roads. Furthermore, the median core foraging range (median = 0.31 km^2, IQR: 0.24–0.37) occupied only 17% of the median full foraging range (median = 1.80 km^2, IQR: 1.21–2.27), suggesting that the geese regularly used a few favoured foraging areas within their winter range. This is supported by the fact that only 20 out of 304 available fields accounted for 83% of all goose foraging activity.

The seasonal increase in the number of fields used by foraging geese reported here is possibly linked to agricultural management. After their arrival, the majority of the flock uses a small number of fields between late September and October, and then the geese disperse across the Plateau by November, possibly in response to the introduction of livestock grazing and the associated disturbance. As our population foraging range model was at the scale of field-within-year, any seasonal analysis of foraging distribution was not possible using this model structure. However, a seasonal analysis of foraging distribution, investigating whether selection of field type changes over the course of the winter, would be a useful future study.

Mitchell *et al.* (2016) noted that the geese usually leave the Slamannan Plateau in February, an earlier spring departure than other migratory species, at a time when the rate of grass growth is increasing. They suggested that this might indicate competition for foraging resources is not driving departure, and therefore not limiting the population. However, a wider scale analysis of spatio-temporal variation in resource use and availability within the global flyway may reveal foraging resource constraints elsewhere for the Slamannan population (Davis *et al.* 2014).

Foraging range overlap with protected area

In common with many other migratory waterfowl, the Bean Goose population at Slamannan has shown a high degree of winter site fidelity at the landscape scale, returning to the same small area since the 1980s, a strategy that is likely to confer individual fitness benefits (Robertson & Cooke 1999). However, our study has shown that there has been a shift in foraging distribution within the landscape since the classification of the protected area in 2006.

When we applied the same 99 percentile selection criterion used to identify the protected area boundary, using our more recent field count dataset (2011/2012–2015/2016), there was a substantial difference in the range of fields which would have been included in the protected area, with only 34% of fields shared between them (Figure 7). A previous study, which took the same approach, but compared the protected area to 99 percentile data from the preceding five years (with one year's overlap 2000/2001), also found substantial geographical differences, reporting that 23 fields were included within the 99 percentile criterion across both periods, with 22 and 10 fields unique to each period respectively (SNH 2007).

It would appear, therefore, that the mismatch between the population foraging range and the protected area boundary reported in this study is due to the fact that the protected area boundary was based on a limited range of fields used as foraging habitat between 2001/2002 and 2004/2005, and this failed to fully capture the long-term spatio-temporal foraging dynamics of the population. The individual foraging range analysis also revealed this mismatch with the protected area, with a maximum of 32% and 45% of the full and core foraging ranges respectively, falling inside the protected area. Less than 6% of the population foraging range fell within the management scheme area, revealing a mismatch between scheme payments and the principal foraging areas used by the geese. This ultimately led to the management scheme being discontinued in 2018, as it was agreed that the scheme was no longer delivering value for money.

It is likely that the geese have gradually shifted their foraging range to use additional fields outside of the protected area. This has probably been facilitated by exploratory flights by the geese to sample new fields, as 17% of their foraging fields were irregularly used by the geese and fell outside their core foraging areas.

The exact cause of this shift in foraging distribution remains unknown; however, it is unlikely to be due to density-dependent factors, as the population size has remained relatively stable since the designation of the protected area in 2006 (Peak count 2005/2006 = 300; peak count 2015/2016 = 263). Furthermore, this range shift has occurred despite the fact that the protected area consisted of 1.7 km^2 (30%) of apparently suitable agriculturally improved pasture foraging habitat in 2018, a greater proportion than in 2008 (20%), when the SPA was classified (Joint Nature Conservation Committee 2008). Several studies have shown that the application of fertilizer as a pasture management tool can increase grazing intensity by geese (Owen 1973, Williams & Forbes 1980, Percival 1993, Vickery & Gill 1999); therefore, changes in the pattern of fertilizer application across the landscape may have caused the shift to areas outside of the protected area.

Management implications

The majority of non-breeding goose SPAs in the UK only include important roost sites; however, there have been recommendations that SPA boundaries should be extended to include 'functionally-linked' goose foraging areas (Rowell & Robinson 2006). Our study suggests that this approach may fail to fully account for the spatio-temporal foraging dynamics of geese, and that a more appropriate conservation measure would be the use of flexible management schemes to maintain their foraging areas both within and beyond SPA boundaries. This issue may also apply to other threatened bird species liable to change their ranges in response to cropping regimes, such as the Corncrake *Crex crex* (Berg & Hiron 2012), Black Grouse *Lyrurus tetrix* (White *et al.* 2013), and Stone-curlew *Burhinus oedicnemus* (Green & Griffiths 1994).

More broadly, this case study stresses the importance of developing dynamic conservation strategies, particularly for species liable to undergo range shifts. Structured decision-making processes have been applied to identify optimal conservation strategies for species recovery (Gregory & Long, 2009, O'Donnell *et al.* 2017), protected area design (Converse *et al.* 2020), and species translocations (Schwartz & Martin 2013). We recommend that complex species conservation strategies are informed by structured decision-making, using the most up-to-date monitoring data, to ensure that effective conservation measures continue to be implemented at the correct spatio-temporal scales.

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References

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74:** 1313–1325.

Allport, G.A. 1991. The feeding ecology and habitat requirements of overwintering western Taiga Bean Geese (*Anser fabalis fabalis*). PhD thesis, University of East Anglia.

Bainbridge, I. 2017. Goose management in Scotland: an overview. *Ambio* **46:** 224–230.

Bainbridge, I., Brown, A., Burnett, N., Corbett, P., Cork, C., Ferris, R., Howe, M., Maddock, A., Mountford, E. & Pritchard, S. 2013. Guidelines for the selection of biological SSSIs Part 1: rationale, operational approach and criteria for site selection. Peterborough.

Baker, H. & Stroud, D. 2007. An assessment of the use of cropped habitats by bird species represented in the UK special protection area network. JNCC paper to Natura 2000 & Ramsar Steering Committee.

Berg, A. & Hiron, M. 2012. Occurrence of Corncrakes Crex crex in mosaic farmland landscapes in south-central Sweden - effects of habitat and landscape structure. *Bird Conserv. Int.* **22**: 234–245.

Bjørnstad, O.N., Ims, R.A. & Lambin, X. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends Ecol. Evol.* **14:** 427–432.

Chudzińska, M., Ayllón, D., Madsen, J. & Nabe-Nielsen, J. 2016. Discriminating between possible foraging decisions using pattern-oriented modelling: the case of Pink-footed Geese *Anser brachyrhynchus* in mid-Norway during their spring migration. *Ecol. Modell* **320:** 299–315.

Chudzińska, M.E., van Beest, F.M., Madsen, J. & Nabe-Nielsen, J. 2015. Using habitat selection theories to predict the spatio-temporal distribution of migratory birds during stopover – a case study of Pink-footed Geese *Anser brachyrhynchus*. *Oikos* **124:** 851–860.

Conover, M.R. 1991. Herbivory by Canada Geese *Branta canadensis:* diet selection and effect on lawns. *Ecol. Appl.* **1:** 231–236.

Conover, M.R. 2011. Population growth and movements of Canada Geese *Branta canadensis* in New Haven County, Connecticut, during a 25-year period. *Waterbirds* **34:** 412–421.

Converse, S.J., Garner, B. & Morey, S. 2020. Reserve network design for prairie- dependent taxa in south Puget Sound. In S. J. Converse, B. Garner & S. Morey. (eds) *Structured Decision Making: case studies in natural resource management*, 124–134. John Hopkins University Press, Baltimore.

Davies, A. 1988. The regrowth of grass swards. In Jones, M.B. & Lazenby, A. (eds) *The Grass Crop (The Physiological Basis of Production)*, 85–127. Springer, Dordrecht.

Davis, J.B., Guillemain, M., Kaminski, R.M., Arzel, C., Eadie, J.M. & Rees, E.C. 2014. Habitat and resource use by waterfowl in the northern hemisphere in autumn and winter. *Wildfowl* **4:** 17–69.

European Environment Agency (EEA). 2012. Protected areas in Europe – an overview. EEA Report No 5/2012, EEA Report No. 5/2012.

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., Elmberg, J., Tombre, I.M. & Hessel, R. 2017. Agriculture and herbivorous waterfowl: a review of the scientific basis for improved management. *Biol. Rev.* **92:** 854–877.

Fox, A.D. & Madsen, J. 2017. Threatened species to super-abundance: the unexpected international implications of successful goose conservation. *Ambio* **46:** 178–187.

Fox, J. & Weisberg, S. 2019. *An {R} Companion to Applied Regression*, 3rd edn. Sage, Thousand Oaks, CA.

Fuller, R.J. 2012. *Birds and Habitat: relationships in changing landscapes, ecological reviews.* Cambridge University Press, New York.

Gauthier, G. & Bedard, J. 1991. Experimental tests of the palatability of forage plants in Greater Snow Geese *Anser caerulescens. J. Appl. Ecol.* **28:** 491–500.

Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M. & Burgess, N.D. 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biol. Conserv.* **161:** 230–238.

Gill, J.A. 1996. Habitat choice in Pink-footed Geese *Anser brachyrhynchus*: quantifying the constraints determining winter site use. *J. Appl. Ecol.* **33:** 884–892.

Green, R.E. & Griffiths, G.H. 1994. Use of preferred nesting habitat by stone curlew Burhinus oedicnemus in relation to vegetation structure. *J. Zool.* **233**: 457–471.

Gregory, R. & Long, G. 2009. Using structured decision making to help implement a precautionary approach to endangered species management. *Risk Anal.* **29:** 518–532.

Guixé, D. & Arroyo, B. 2011. Appropriateness of special protection areas for wide-ranging species: the importance of scale and protecting foraging, not just nesting habitats. *Anim. Conserv.* **14:** 391–399.

Hamilton, W.J. & Watt, K.E.F. 1970. Refuging. *Annu. Rev. Ecol. Syst.* **1:** 263–286.

Harrison, A.L., Petkov, N., Mitev, D., Popgeorgiev, G., Gove, B. & Hilton, G.M. 2018. Scale-dependent habitat selection by wintering geese: implications for landscape management. *Biodivers. Conserv.* **27:** 167–188.

Jensen, G.H., Pellissier, L., Tombre, I.M. & Madsen, J. 2017. Landscape selection by migratory geese: implications for hunting organisation. *Wildlife. Biol.* **2017:** 1–12.

Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61:** 65–71.

Johnson, R., Jones, K. & Manley, D. 2018. Confounding and collinearity in regression analysis: a cautionary tale and an alternative procedure, illustrated by studies on British voting behaviour. *Qual. Quant. Int. J. Methodol.* **52:** 1957–1976.

Johnson, J.B. & Omland, K.S. 2004. Model selection in ecology and evolution. *Trends Ecol. Evol.* **19:** 101–108.

Johnson, W.P., Schmidt, P.M. & Taylor, D.P. 2014. Foraging flight distances of wintering ducks and geese: a review. *Avian Conserv. Ecol.* DOI: 10.5751/ACE-00683-090202.

Joint Nature Conservation Committee. 2008. Natura data form - Slamannan Plateau SPA.

Joint Nature Conservation Committee. 2010. *Handbook for Phase 1 Habitat Survey: a technique for environmental audit*. JNCC, Peterborough.

Keller, V.E. 1991. The effect of disturbance from roads on the distribution of feeding sites of geese (*Anser brachyrhynchus, A. anser*), wintering in north-east Scotland. *Ardea* **79:** 229–231.

Kenward, R. 2004. Radio tracking. In Sutherland, W., Newton. & Green, R.E. (eds) *Bird Ecology and Conservation (A Handbook of Techniques)*, 141–159. Oxford University Press, Oxford.

Lestienne, F., Thornton, B. & Gastal, F. 2006. Impact of defoliation intensity and frequency on N uptake and mobilization in *Lolium perenne*. *J. Exp. Bot.* **57:** 997–1006.

Lindsey, J.K. 1999. On the use of corrections for overdispersion. *J. R. Stat. Soc. Ser. C Appl. Stat.* DOI: 10.1111/1467-9876.00171.

Madsen, J. 1985. Impact of disturbance on field utilization of Pink-footed Geese *Anser brachyrynchus* in West Jutland, Denmark. *Biol. Conserv.* **33:** 53–63.

Madsen, J., Bjerrum, M. & Tombre, I.M. 2014. Regional management of farmland feeding geese using an ecological prioritization tool. *Ambio* **43:** 801–809.

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.

Mangiafico, S. 2019. Functions to support extension education program evaluation. R package version 2.3.7.

Marjakangas, A., Alhainen, M., Fox, A.D., Heinicke, T., Madsen, J., Nilsson, L. & Rozenfeld, S. (Compilers) 2015. International single species action plan for the conservation of the Taiga Bean Goose *Anser fabalis fabalis*. Bonn.

Mason, T.H.E., Keane, A., Redpath, S.M. & Bunnefeld, N. 2017. The changing environment of conservation conflict: geese and farming in Scotland. *J. Appl. Ecol.* **55:** 651–662.

McKenzie, R. & Shaw, J.M. 2017. Reconciling competing values placed upon goose populations: the evolution of and experiences from the Islay Sustainable Goose Management Strategy. *Ambio* **46:** 198–209.

Minshull, B.C., Mitchell, C., Maciver, A. & Griffin, L. 2014. Report on the collation of field use data relating to wintering Bean Geese *Anser fabalis* on the Slamannan Plateau, SNH Commissioned Report No. 711.

Mitchell, C., Griffin, L., Maciver, A., Minshull, B. & Makan, N. 2016. Use of GPS tags to describe the home ranges, migration routes, stop-over locations and breeding area of Taiga Bean Geese *Anser fabalis fabalis* wintering in central Scotland. *Bird Study* **63:** 437–446.

Nilsson, L. & Kampe-Persson, H. 2013. Field choice of autumn staging and wintering geese in southwestern Sweden. *Ornis Svec.* **22:** 46–60.

O'Donnell, K.M., Messerman, A.F., Barichivich, W.J., Semlitsch, R.D., Gorman, T.A., Mitchell, H.G., Allan, N., Fenolio, D., Green, A., Johnson, F.A., Keever, A., Mandica, M., Martin, J., Mott, J., Peacock, T., Reinman, J., Romañach, S.S., Titus, G., McGowan, C.P. & Walls, S.C. 2017. Structured decision making as a conservation tool for the recovery planning of two endangered salamanders. *J. Nat. Conserv.* **37:** 66–72.

Owen, M. 1971. The selection of feeding site by White-fronted Geese *Anser albifrons* in winter. *J. Appl. Ecol.* **8:** 905–917.

Owen, M. 1973. The management of grassland areas for wintering geese. *Wildfowl* **24:** 123–130.

Owen, M. 1977. The role of wildfowl refuges on agricultural land in lessening the conflict between farmers and geese in Britain. *Biol. Conserv.* **11:** 209–222.

Owen, M. 1980. *Wild Geese of the World*. B. T. Batsford Ltd, Fakenham.

Owen, M. 1990. The damage-conservation interface illustrated by geese. *Ibis* **132:** 238–252.

Owen, M. & Black, J.M. 2008. Geese and their future fortune. *Ibis* **133:** 28–35.

Patterson, I.J. & Fuchs, R.M.E. 2001. The use of nitrogen fertilizer on alternative grassland feeding refuges for Pink-footed Geese *Anser brachyrynchus* in spring. *J. Appl. Ecol.* **38:** 637–646.

Percival, S.M. 1993. The effects of reseeding, fertilizer application and disturbance on the use of grasslands by Barnacle Geese *Branta leucopsis*, and the implications for refuge management. *J. Appl. Ecol.* **30:** 437–443.

Percival, S. & Votier, S. 1996. A dietary analysis of Bean Geese *Anser fabalis* on the Slamannan Plateau and Whooper Swans *Cygnus cygnus* at Inchinnan/Black Cart. Report to SNH.

QGIS. 2014. Quantum Geographic Information System. Open Source Geospatial Foundation Project. [WWW Document].

R Core Development Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. htto://www.R-project.org.

Robertson, G. & Cooke, F. 1999. Winter philopatry in migratory waterfowl. *Auk* **116:** 20–34.

Rosin, Z.M., Skórka, P., Wylegała, P., Krąkowski, B., Tobolka, M., Myczko, Ł, Sparks, T.H. & Tryjanowski, P. 2012. Landscape structure, human disturbance and crop management affect foraging ground selection by migrating geese. *J. Ornithol.* **153:** 747–759.

Rowell, H. & Robinson, J. 2006. Identifying and characterising the feeding areas of Dark-bellied Brent Geese *Branta bernicla bernicla* in and around special protection areas in the UK. In Boere, G.C., Galbraith, C.A. & Stroud, D.A. (eds) *Waterbirds Around the World*, 517–518. TSO Scotland Ltd, Edinburgh.

Schwartz, M. & Martin, T. 2013. Translocation of imperilled species under changing climates. *Ann. N. Y. Acad. Sci.* DOI: 10.1111/nyas.12050.

Smith, T., Bainbridge, I. & O'Brien, M. 1995. Distribution and habitat use by Bean Geese *Anser fabalis* in the Slamannan area. Second year 1994/95, RSPB Report to SNH.

Smith, T.J. & McKenna, C.M. 2013. A comparison of logistic regression pseudo R2 indices. *Mult. Linear Regres. Viewpoints* **39**(2): 17–26.

SNH. 2005. *The Slamannan Plateau SSSI Scientific Case for Notification*. SNH, Edinburgh.

SNH. 2006. Slamannan Plateau SSSI Citation, SNH internal document.

SNH. 2007. Advisory committee on Sites of Special Scientific Interest. Report to SNH.

SNH. 2017. Review of the Slamannan Bean Goose management scheme. SNH report to the National Goose Management Policy Review Group.

Stenhouse, I.J. 1996. The feeding behaviour of Greylag *Anser anser* and Pink-footed Geese *Anser brachyrynchus* around the Moray Firth, 1992-93. *Scott. Birds* **18:** 222–230.

Stroud, D.A., Bainbridge, I.P., Maddock, A., Anthony, S., Baker, H., Buxton, N., Chambers, D., Enlander, I., Hearn, R.D., Jennings, K.R, Mavor, R., Whitehead, S. & Wilson, J.D. – on behalf of the UK SPA & Ramsar Scientific Working Group (eds) 2016. *The Status of UK SPAs in the 2000s: The Third Network Review*. JNCC, Peterborough.

Tombre, I.M., Eythórsson, E. & Madsen, J. 2013. Towards a solution to the goose-agriculture conflict in north Norway, 1988-2012: the interplay between policy, stakeholder influence and goose population dynamics. *PLoS One* **8.** DOI: 10.1371/journal.pone.0071912.

Van Eerden, M.R., Drent, R.H., Stahl, J. & Bakker, J.P. 2005. Connecting seas: western Palearctic continental flyway for water birds in the perspective of changing land use and climate. *Glob. Chang. Biol.* **11:** 894–908.

Vickery, J.A. & Gill, J.A. 1999. Managing grassland for wild geese in Britain: a review. *Biol. Conserv.* **89:** 93–106.

Watson, D. 1986. Bean Geese in southwest Scotland. *Scott. Birds* **14:** 17–24.

Wheeler, B. & Torchiano, M. 2016. Permutation tests for linear models. R package version 2.1.0.

White, P.J.C., Warren, P. & Baines, D. 2013. Forest expansion in Scotland and its potential effects on Black Grouse Tetrao tetrix conservation. *Forest Ecol. Manageme*. **308**: 145–152.

Wiens, J.A. 1989. *The Ecology of Bird of Communities (Two Volumes)*. Cambridge University Press, Cambridge.

Williams, G. & Forbes, J.E. 1980. The habitat and dietary preferences of Dark-bellied Brent Geese *Branta bernicla* and Wigeon *Anas penelope* in relation to agricultural management. *Wildfowl* **31:** 151–157.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home- range studies. *Ecology* **70:** 164–168.