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RESEARCH ARTICLE

Adult survival and annual movement patterns of common snipe in Iceland

Aevar Petersen,[1] Sverrir Thorstensen,[2] Ib K. Petersen,[3] Scott W. Petrek,[4] Kane Brides,[5] Anna M. Calvert,[6] Mark L. Mallory,[7] Gregory J. Robertson[8] & Sarah E. Gutowsky[7]

[1]Reykjavik, Iceland
[2]Akureyri, Iceland
[3]Department of Ecoscience, Aarhus University, Aarhus, Denmark
[4]Wildfowl and Wetlands Trust, Slimbridge Wetland Centre, Slimbridge, UK
[5]Wildfowl and Wetlands Trust, Conservation Evidence Department, Slimbridge, UK
[6]Landscape Science and Technology Division, Environment and Climate Change Canada, National Wildlife Research Centre, Carleton University, Ottawa, Ontario, Canada
[7]Biology, Acadia University, Wolfville, NS, Canada
[8]Wildlife Research Division, Environment and Climate Change Canada, Mount Pearl, NL, Canada

Abstract

The common snipe (*Gallinago gallinago*) is a wader that breeds in subarctic regions from Iceland to Russia, and for which global populations are in decline. We studied snipe breeding in western Iceland between 1998 and 2020, locating nests and ringing birds annually. In 2019 and 2020, we deployed geolocators on nesting adults to estimate the timing of their annual migration and the location of overwintering areas. Birds moved principally between breeding locations in Iceland to wintering areas in Ireland, although some birds may winter farther north. We also found that apparent annual adult survival averaged 66%, but was higher in years with warmer, wetter winters. Given the similarity of our survival estimates to those from snipe elsewhere, we suggest that adult survival is unlikely a major contributor to declining populations, and other factors like habitat loss may be of more concern.

Keywords

Gallinago gallinago; wintering; geolocator; NAO; Ireland; habitat loss

Correspondence

Mark L. Mallory, Biology, Acadia University, 15 University Ave., Wolfville B4P 2R6, NS, Canada. E-mail: mark.mallory@acadiau.ca

Abbreviations

AIC: Akaike information criterion
ANODEV: analysis of deviance
CI: confidence interval
GLS: global location sensor (also known as light-level geolocator)
IUCN: International Union for the Conservation of Nature
KDE: kernel density estimate
NAO: North Atlantic Oscillation
P: probability
PLI: profile likelihood interval
SE: standard error

Introduction

Wildlife monitoring programmes run through government, academics and community science are providing convincing and consistent evidence that many bird populations are in decline (e.g., Paleczny et al. 2015; Horns et al. 2018; Rosenberg et al. 2019; Neate-Clegg et al. 2020; Hertzog et al. 2021). Particularly pronounced are declines found in waders, which have witnessed greater declines than other species (Rosenberg et al. 2019; Burns et al. 2021; Koleček et al. 2021). While natural fluctuations in bird populations occur, notably in response to long-term drivers such as climate (e.g., Duda et al. 2021), the widespread and consistent declining trends in recent decades across different groups of birds are principally attributable to anthropogenic threats, including habitat development (alteration, fragmentation or loss), climate change, pollution and extractive industries like agriculture, mining, forestry and fisheries (e.g., Calvert et al. 2013; Reif 2013). Furthermore, understanding drivers and managing populations of broadly distributed migratory birds that cross international borders present an additional set of logistical, political and regulatory challenges, especially if they are harvested (Nichols et al. 1995; Elmberg et al. 2006). Consequently, understanding factors that influence different bird populations will be the key to our ability to manage, recover or sustain them in the future.

In many parts of Europe and North America, a subset of the waders—the snipes and woodcocks—have seen

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populations in decline (Ferrand 2006; Franks et al. 2018) and, indeed, are amongst the most threatened bird guilds in Europe (Zmilhorski et al. 2018). For example, long-term declines in these species have been found in Northern Ireland (Henderson et al. 2002), Great Britain (Heward et al. 2015), Sweden (Svensson 2000) and Poland (Żmihorski et al. 2018). Many factors are known to negatively influence the breeding success and, ultimately, population numbers of waders and waterbirds, including changes in land-cover to intensify agriculture (e.g., Colhoun et al. 2015), increasing numbers of predators (MacDonald & Bolton 2008), habitat losses at migratory stop-over and wintering sites (Iwamura et al. 2013), and warming climate patterns influencing moisture (Weiser et al. 2018). Sæther & Bakke (2000) showed that, for most bird populations, population growth is most sensitive to changes in annual adult survival. More recently, Weiser et al. (2020) showed that better information on vital rates for most wader species is required to improve demographic, model-based estimates of population trends, and in particular, measures of annual adult survival were a key need for all species.

The common snipe (*Gallinago gallinago*), herein snipe, is distributed across Europe from Iceland through Russia, and the IUCN not only lists it as of ‘least concern’ as of 2021 but also notes that the global population is decreasing (Birdlife International 2021). In Iceland, which hosts the *faeroeensis* subspecies (Brehm 1831), it is amongst the most common and widely distributed of waders (Asbirk et al. 1997; Gunnarsson et al. 2006; Jóhannesdóttir et al. 2014). Most of the Iceland population is migratory, with available recoveries of ringed birds suggesting overwintering in the British Isles, but there is some variation in migratory strategies, as some birds remain in southern Iceland (Petersen 1998; Henderson 2002; Svazas & Paulauskas 2006). Population trends in Iceland as a whole have not been published (Wentworth 2015), although local studies are found (e.g., Ragnarsdóttir et al. 2021). Studies on nesting birds, population trends as well as ringing of adult females and chicks, have been undertaken for several decades as part of long-term studies of birds on the island of Flatey in western Iceland (Petersen 1979; Petersen & Thorstensen 2003).

Here, we use more than 20 years (1998–2020) of ringing data to estimate apparent adult survival rate of snipe breeding on Flatey. Moreover, encouraged by the results of GLS technology in bird research (e.g., Stutchbury et al. 2009), we deployed GLSs on nesting females in 2019 and 2020 and recovered them in subsequent years. Those results, reported here, provide insights into the wintering range of this breeding population of snipe. With this additional information on wintering range, we relate apparent annual survival rates to climate conditions experienced by snipe to examine their potential to influence snipe survival.

Methods

Study site and data collection

This study was carried out on Flatey, a small island (total area of 0.5 km^2) in the bay of Breiðafjörður in western Iceland (65.37°N, 22.92°W; Fig. 1). The main study area is restricted to the western third of the island, which is mostly a mixture of meadows and dry hummocky moorland. A single gravel road runs through the middle of that part of the island, which has two farms, including buildings, gardens, small hayfields and grazing sheep. The island is visited by thousands of tourists every summer, and a few cruise liners call in for parts of days. A small village, with a hotel, is located on the island, with most houses occupied by summer residents.

Likely on account of the site’s adequate cover for nesting, moist soils for feeding and a total lack of terrestrial predators, the snipe breeding population density is exceptionally high on Flatey. There are about 90 pairs on the island, or about 180 pairs/km^2, recorded during several breeding seasons. Breeding occurs throughout the season from May through August in four nesting ‘waves.’

Snipes are most reliably caught during incubation on the nest, and only the female snipe incubates, so most live captures are females. From 1998 to 2020,

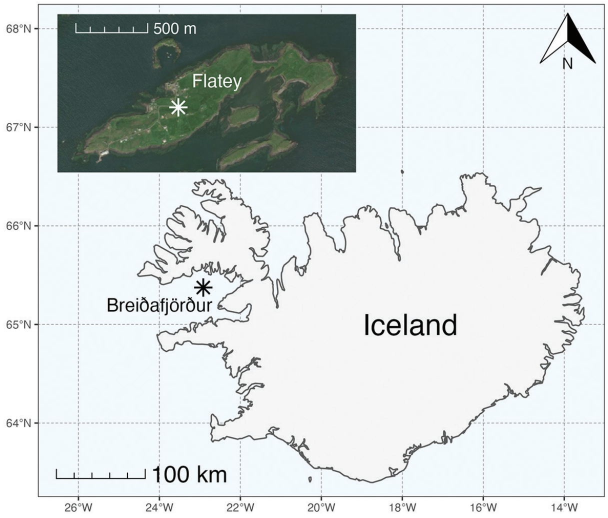

Fig. 1 Map of Iceland, showing the location of the study site, Flatey island (asterisk), in the bay of Breiðafjörður. The inset satellite image of Flatey and surrounding islets was obtained from the Esri map service (“world imagery” layer) using the basemaps R package (Schwalb-Willmann 2021).

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efforts were made each breeding season in two field excursions, in June and again in July, to find nests by flushing incubating birds and ringing as many as possible. Nests were found using two main search methods: (1) unsystematic searching through suitable habitat on foot; and (2) systematic searching via 'rope-dragging,' whereby a 20-m long rope strung with pebble-filled cans was dragged by two persons walking parallel, such that any incubating birds between them would flush, which was recorded by one to four persons walking a short distance behind the rope (see Jackson 2004). Nests were also found incidentally, either during other research activities or as reported by local people. Once nests were located, hand-held nets were placed over the nest, and the area was left for 15–30 minutes to allow the female time to return. When approached, the snipe usually flew straight up from the nest and into the net. Captured snipe were measured, weighed and ringed with a uniquely numbered metal ring. All live recoveries were from nest trapping; dead recoveries from ringed birds were found through chance by researchers and residents, or they were reported to the Icelandic bird-ringing office in Reykjavik.

Attempts were made each year to find as many nests and to capture as many females as possible, but variable weather conditions (e.g., we avoided disturbing birds during periods of substantial rain) and logistical constraints meant that nest finding effort and capture rates varied annually. To quantify nest finding effort each year, the total 'personnel days' (i.e., number of days conducting research on snipe multiplied by the number of field personnel during each campaign) was tabulated. Additionally, 'search effort' was scored according to a scale from 1 to 7, representing the search methods used and the proportion of the island searched in each of the two excursions (Table 1). Total 'search effort' was taken as the sum of scores from each field trip, creating a relative ordinal search effort index ranging from 2 to 14. The search effort index was linearly correlated with personnel days ($R^2 = 0.72$, $P < 0.0001$), as larger teams and longer field trips allowed

Table 1 Criteria for scoring of nest-finding 'search effort' for common snipe (*Gallinago gallinago*) on Flatey, Iceland, during the breeding seasons from 1998 to 2020. Search effort was scored independently for two field campaigns each year (June and July) based on the search methods used and the proportion of the island searched in each campaign, then summed to create an annual relative search effort index ranging from 2 to 14.

Score	Search methods	Proportion of island searched (%)
1	Unsystematic, incidental	<100
2	Unsystematic, incidental	100
3	Rope-dragging	33
4	Rope-dragging, incidental	33
5	Rope-dragging, incidental	50
6	Rope-dragging, incidental	66
7	Rope-dragging, incidental	100

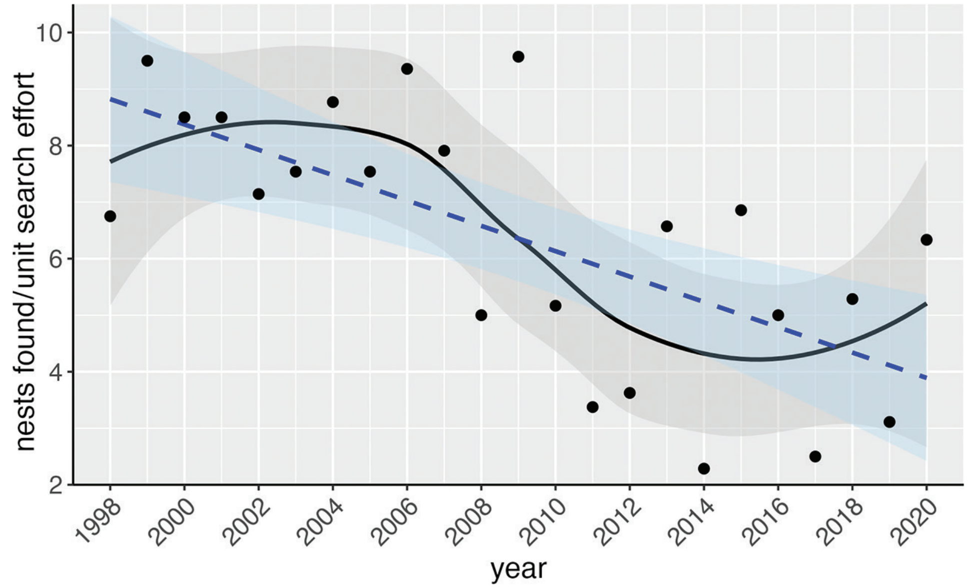

Fig. 2 Time series of nests found per unit search effort for common snipe (*Gallinago gallinago*) on Flatey, Iceland. Linear regression indicated an overall decline over the study period ($R^2 = 0.44$, slope estimate = -0.22 ± 0.05 SE, $P < 0.001$, dashed blue line). LOESS smoother is shown with a solid line (the 95% CI indicated with grey shading), where the intersection with the linear trend corresponds to the changepoint identified at 2009 (95% CI = 2005–2013, $P < 0.001$).

for greater search effort. Furthermore, there was a strong linear relationship between the number of nests found and the search effort index ($R^2 = 0.84$, $P < 0.0001$), but less so between the number of nests found and personnel days ($R^2 = 0.47$, $P = 0.023$). We therefore scaled the number of nests found by search effort and used the proportion of captured females relative to total nests found scaled for effort as an annual index of capture effort and success (Fig. 2).

Non-breeding distributions by geolocation

In June and July 2019, 17 Biotrack Ltd. GLS devices (model MK5090) were deployed on captured female snipe. Devices were leg-mounted using a modified colour ring with a flag. The mass of the ring, device, tie and glue was ca. 1.35g (based on other studies), representing <1.5% of the body mass of equipped birds (range 100–135 g, $n = 21$). In 2020, five devices were recovered, four of which provided reliable data. New GLS devices were deployed on each of these five recaptured females in 2020, and two were recaptured in June 2021 (one from the initial failed logger bird), providing data for a total of six non-breeding seasons from five individual females. At recapture in 2020, three of five birds had developed skin lesions of varying severity on the tibia due to the device attachment. We did not include capture histories from individuals fitted with GLS in the analysis of survival in case of device effects on breeding behaviour or return rates.

The devices measured light levels and recorded maximum levels at two-minute intervals. Data were downloaded and decompressed using the BAS Track software (Biotrack Ltd.). Data were limited to the period between 1 August in 2019 and 15 May 2020, when positional estimates stabilized in the expected general latitudinal and longitudinal range of the breeding site. We excluded data from a six-week window around the fall and spring equinox before processing (e.g., Gutowsky et al. 2021). The species' tendency to remain hidden in vegetation (Van Gils et al. 2020) renders positional estimation from light level data challenging, and error around positional estimates is assumed to be substantial, likely to be at the upper end of the estimated GLS error, which is between ca. 140 and 200 km (Lisovski et al. 2012).

Using data from six snipe-years, we estimated general distributions and migratory movements for birds breeding at Flatey as follows. Twilight events were using the findTwilights function in the TwGeos package (Wotherspoon et al. 2016) in programme R (R version 2.15.2), with a light threshold of 2 and a minimum darkness period between sunset and sunrise of 3 hours to filter spurious twilight transitions caused by shading, weather or light pollution. Transitions were examined to filter or remove incorrect sunrise/sunset times with the twilightEdit function, based on the following: (1) if a transition had a time difference of >60 minutes from transitions within a two-day window on either side, and the transitions within that window were all within 30 minutes of one another, then the transition time was flagged and adjusted to the median of the window; and (2) if a transition time was >60 minutes different to the window, but the transitions within the window were more variable than expected for stationary behaviour, the transition was flagged as a candidate for removal.

For positional estimation from sunrise/sunset transition events, the coord function in the Geolight package, version 2.0 (Lisovski & Hahn 2012), was used based on a range of potential sun elevation angles (-5 to 5°). For each angle, we plotted the estimates and selected the sun angle that resulted in the closest match in latitude estimates before and after equinoxes, the highest proportion of positions fitted within a reasonable latitudinal and longitudinal range of the breeding area during the post-breeding and pre-breeding periods, and the best fit over land within the known overwintering range. Final sun angles were chosen between -2.5 and -0.5°. Stationary periods were delineated based on patterns of sunrise and sunset using the function changeLight, with a minimum stationary duration of 10 days. Stationary periods less than two days and 150 km apart were merged, and the overwinter phase was identified as the longest duration stationary period. To illustrate distributions of birds during overwintering, we generated individual KDEs with the adehabitatHR package (Calenge 2006), using a smoothing parameter of two and a 2° × 2° grid cell size, based on the mean accuracy of the GLS devices (Delord et al. 2019). Five-day rolling means of longitude plotted against time were used to estimate the timing of east–west migratory movements, as longitude estimates are prone to lower error and allowed us to approximate movements to and from the general breeding area in west Iceland as well as movements across Iceland before and after migrating.

Nesting population and survival analysis

To examine potential temporal trends in the nesting population over the course of the study period, a linear regression and breakpoint regression were fitted to a time-series of nests found per unit search effort using the package chngpt (Fong et al. 2017). Breakpoints are determined using a piecewise linear regression that fits two linear regressions split at a non-continuous break point (i.e., "stegmented" or stepped and segmented) estimated to minimize residual variance.

To analyse the ringing data, we implemented joint live encounter–dead recovery Burnham models (Burnham 1993) in Program MARK, version 6.0, using the package RMark (Laake 2014). This model allows estimation of apparent survival (S_t; probability an individual survives the interval from year t to year $t + 1$), live recapture rate (p_t; probability of live encounter and capture in year t given that the individual survived the preceding interval and is in the study area) and fidelity to the study area (F_t; probability that an individual present in the study area in year t is also present in the study area in year $t + 1$, given that it is alive in year $t + 1$), as well as the Seber dead recovery rate (r_t; the probability that an individual that dies in year i is found and reported).

The set of candidate models to be considered was based on a priori expectations. Because of the sparseness of recoveries, we restricted the dead recovery parameter r to be constant over our study period in all models. Live recaptures and dead recoveries within the study period were restricted to the study site, so we fixed the fidelity parameter F to 1 in all models (Cooch & White 2017). Parameter S therefore did not represent true survival but instead 'local' or 'apparent' survival, which could be confounded with permanent emigration from the study site. S and p were allowed to vary annually (t).

The fully saturated general model $\{S_t\ p_t\ F_{F=1}\ r.\}$ had 46 parameters, and most S_t and p_t were poorly estimated or inestimable. Live recapture rate p was expected to vary with time, as the number of field days, size of field crews, nest search effort and nests found varied considerably amongst field seasons over the course of the study. To reduce the dimensionality of the parameter space, we explored reduced parameter models of p and saw clear evidence that the annual index of capture effort improved model fit over the time-variant model. Our starting model then included time-varying survival with recapture constrained to co-vary with capture effort $\{S_t\ p_{effort}\ F_{F=1}\ r.\}$.

To test the hypothesis that snipe apparent annual survival co-varied with broad weather patterns, we looked for a relationship between apparent survival and the NAO during three annual periods: the full year (NAO_{yr}) from May (in year t) to April (in year $t + 1$); the breeding season (NAO_{br}) from May to August (in year t); and the overwinter months (NAO_{ow}) from November (in year t) to March (in year $t + 1$; Fig. 3). The NAO is the most dominant teleconnection pattern in the North Atlantic, describing the strength of the sea-level pressure difference between the Icelandic Low and the Azores High (Krueger et al. 2019). During a positive NAO, conditions in northern Europe are warmer and wetter than average, whereas during negative NAO, conditions are colder and drier than average (Visbeck et al. 2001). The NAO is also positively correlated with increased winter storm activity in the north-east Atlantic, particularly since the 1970s in northern Europe (Krueger et al. 2019).

Prior to model selection, we examined the live encounter data to identify any biologically explicable sources of poor model fit (Pradel et al. 2003) using the R2ucare package to test Cormack-Jolly-Seber goodness-of-fit (Gimenez et al. 2018). Tests for transience of individuals (TEST3.SR) and trap-dependence (TEST2.CT) were non-significant. We also tested the fully saturated general live encounter–dead recovery Burnham model without covariates for overdispersion ($\hat{c} > 1.00$) by calculating Fletcher $\hat{c}$ (Fletcher 2012), bootstrap goodness of fit $\hat{c}$ and the median $\hat{c}$ (White & Burnham 1999). None of these goodness-of-fit assessments indicated the data were over-dispersed (Fletcher $\hat{c} = 0.99$, bootstrap goodness-of-fit $\hat{c} = 0.95$, median $\hat{c} = 0.98$), so AIC adjustments were not needed (Burnham & Anderson 2002). The models in the candidate model set were compared via differences in sample-size-corrected AIC values (ΔAIC_c, where the best-fit model has the lowest AIC_c value) as well as relative Akaike model weights (w_i, which sum to 1 and provide an index of support for each model relative to the total candidate model set [Akaike 1973; Burnham & Anderson 2002]). We applied ANODEV to assess the statistical significance and the fraction of temporal variation explained by covariates in the top models (Lebreton et al. 1992; Skalski 1996). Support for specific predictors was also evaluated from effect sizes evaluated at the scale (logit) of the linear predictor. Finally, we derived an apparent mean apparent survival rate calculated with a variance components approach using the var.covar function via a $\{S_t\ p_{effort}\ F_{F=1}\ r.\}$ model structure, which provides an estimates of time-dependent process variation (σ^2) in apparent annual survival probabilities. Estimates and effect sizes are all presented as means ± SE, along with associated 95% PLIs.

Results

Non-breeding distributions

From the geolocator data recovered from six individuals, KDE indicated the overwinter distribution for female snipe equipped with GLSs in the breeding season of 2019 fell primarily along the west coast of Ireland for three birds, and likely in the Faroe Islands for the fourth (Fig. 4). For snipe equipped in 2020, the central overwinter distribution shifted north towards Northern Ireland and Scotland, with one bird likely spending some time in the Faroe Islands as well (Fig. 2). Migration from Iceland occurred before the fall equinox for two birds (C-2019 and D-2020), and during or after the fall equinox for the other four (Fig. 5). One bird remained in Iceland until late October (E-2020),

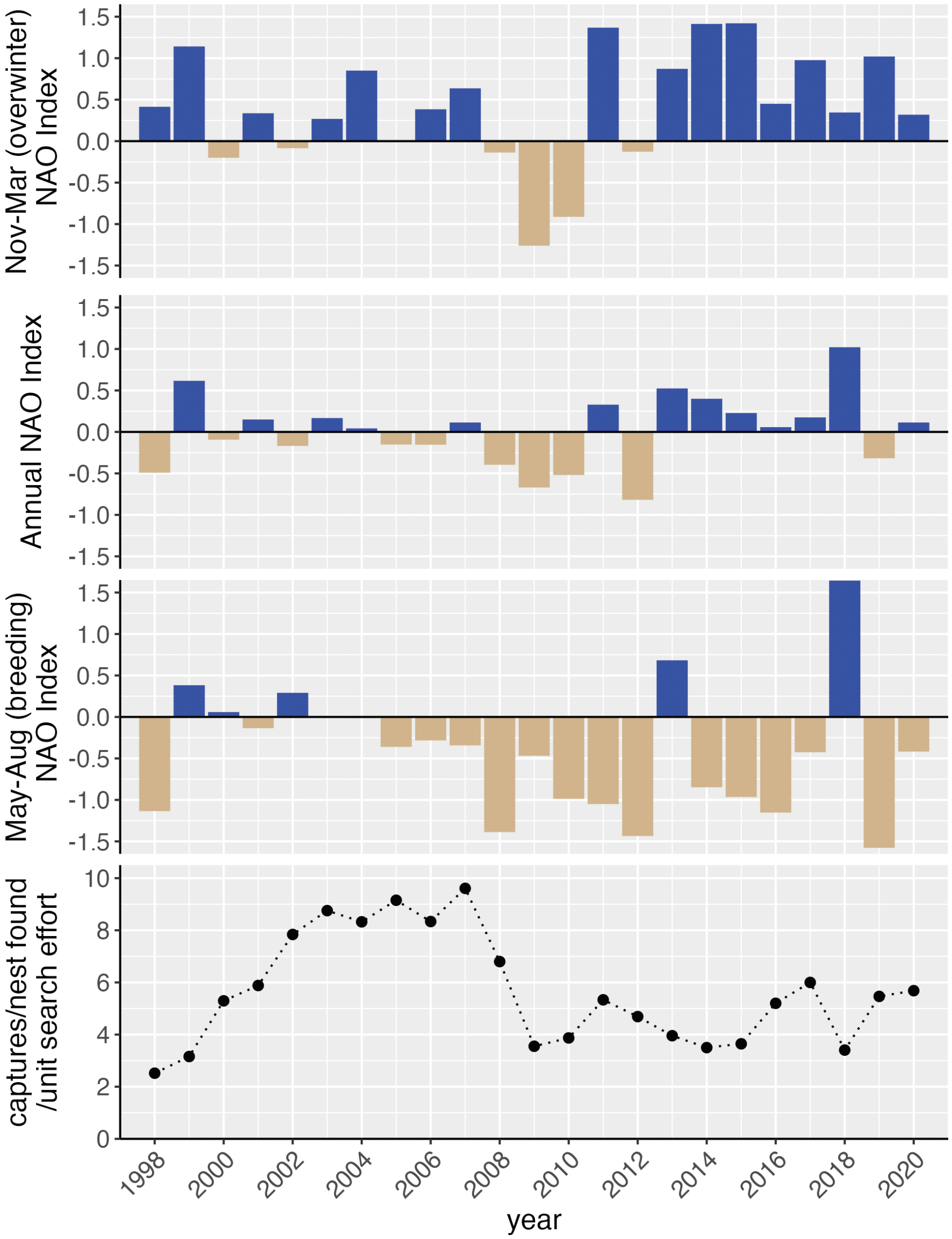

Fig. 3 Time series of covariates used in joint live encounter–dead recovery Burnham models to estimate common snipe (*Gallinago gallinago*) adult female survival. Live recapture (*p*) is constrained in all models to vary with an index of capture effort (captures/nest found/search effort). Survival covariates include the NAO index during the breeding months, the overwinter months and the full year.

while the others initiated migration between late August and early October (Fig. 5). The stationary overwinter period lasted 109 ± 45 days, beginning between 9 October and 30 November and ending between 6 February and 14 April. Mean distances travelled between the study area and the centroids of overwinter KDE contours were 1369 ± 251 km. Spring return migration was initiated in April, with all birds returning to Iceland by May (Fig. 5).

Female apparent adult survival

During the study period (1998–2020), a sample of 455 adult female snipe provided 830 live recaptures and 10 dead recoveries. The number of nests found, and the number of females recaptured ranged from 16 nests and eight females in 2014 to 131 nests and 78 females in 2006. The number of nests found relative to the amount of nest search effort exhibited an overall linear decline

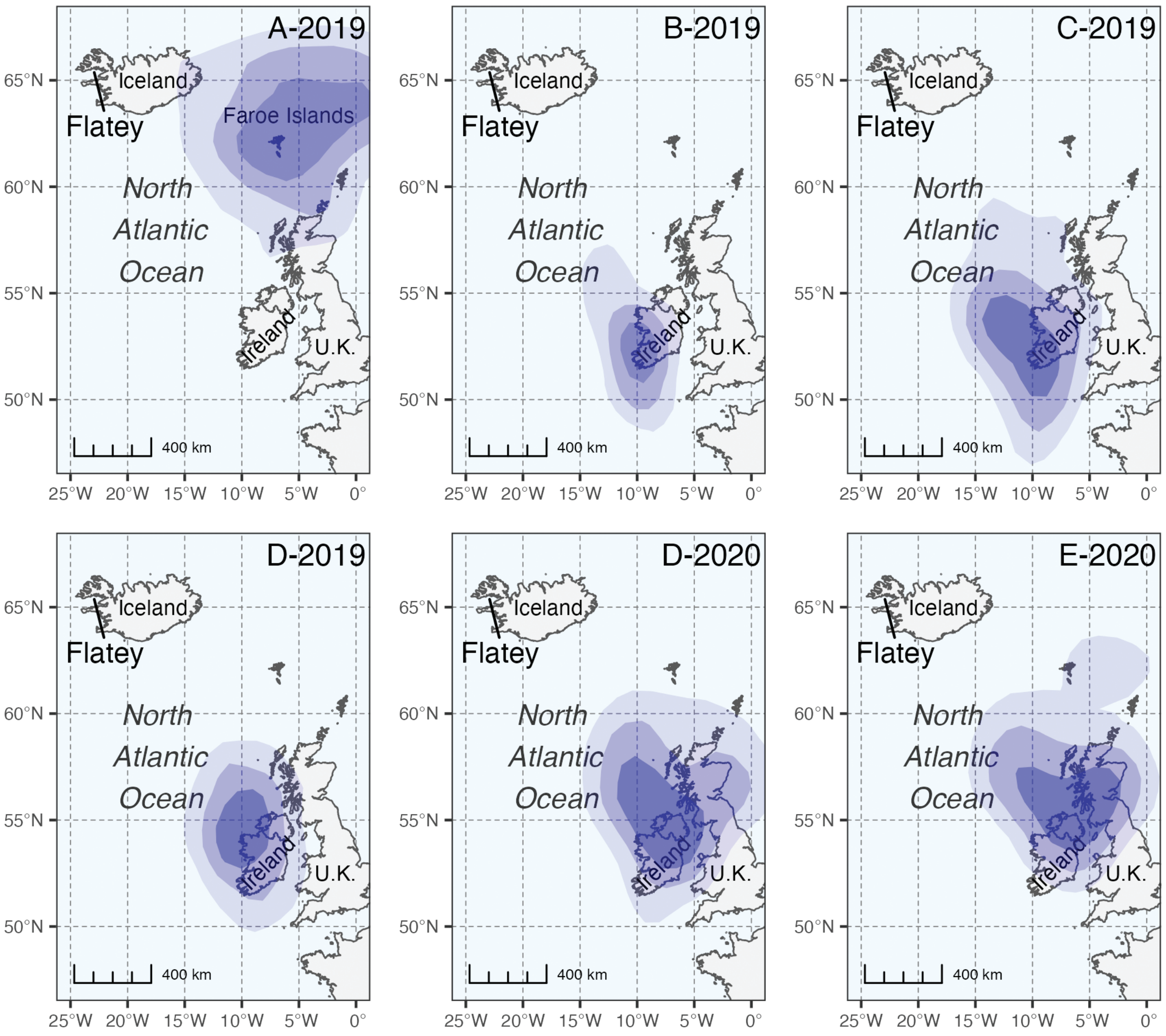

Fig. 4 Overwintering distribution of female adult common snipe (*Gallinago gallinago*; $n = 5$, individual D tracked twice) during the period October to April determined using GLSs deployed during the 2019 and 2020 breeding seasons on Flatey, Iceland. Distributions are shown based on the 25% (light purple shading) to 75% (dark purple shading) contours (from kernel density estimation.

over the study period ($R^2 = 0.44$, slope estimate = -0.22 ± 0.05, $P < 0.001$) with a changepoint identified at 2009 (95% CI = 2005–2013, $P < 0.001$; Fig. 2).

The top-ranked joint live encounter–dead recovery Burnham model, where apparent survival probability co-varied with winter NAO and live recapture probability co-varied with capture effort {$S_{NAOwin}\ p_{effort}\ F_{F=1}\ r.$}, garnered 52% of the model support (Table 2). Unconstrained live recapture probability ranged $P = 0.24$–0.54, and the effect size of capture effort was small but did not bound zero ($\beta_{effort} = 0.20$, SE = 0.04, 95% PLI = 0.12–0.27). The probability of recovering a marked bird if it died during the study was low (mean $r = 0.02$, SE = 0.01, 95% CI = 0.01–0.04). While the effect size of winter NAO on apparent survival did not bound zero ($\beta_{NAOwin} = 0.33$, SE = 0.16, 95% CI = 0.03–0.64), ANODEV indicated that the percentage of annual variation in apparent survival explained by winter NAO variability was small (7.1%; Fig. 6). Predicted apparent survival estimates varied from 0.76 ± 0.04 (0.68–0.82) in 2015 when winter NAO reached a high of 1.42, to 0.57 ± 0.06 (0.45–0.68) in 2009 when NAO was lowest at -1.26.

The second-ranked model with 23% of model weight included apparent survival varying with annual NAO and live recapture probability varying with effort {$S_{NAOyr}\ p_{effort}\ F_{F=1}\ r.$} ($\Delta AIC_c = 1.58$, Table 2). However, the annual NAO

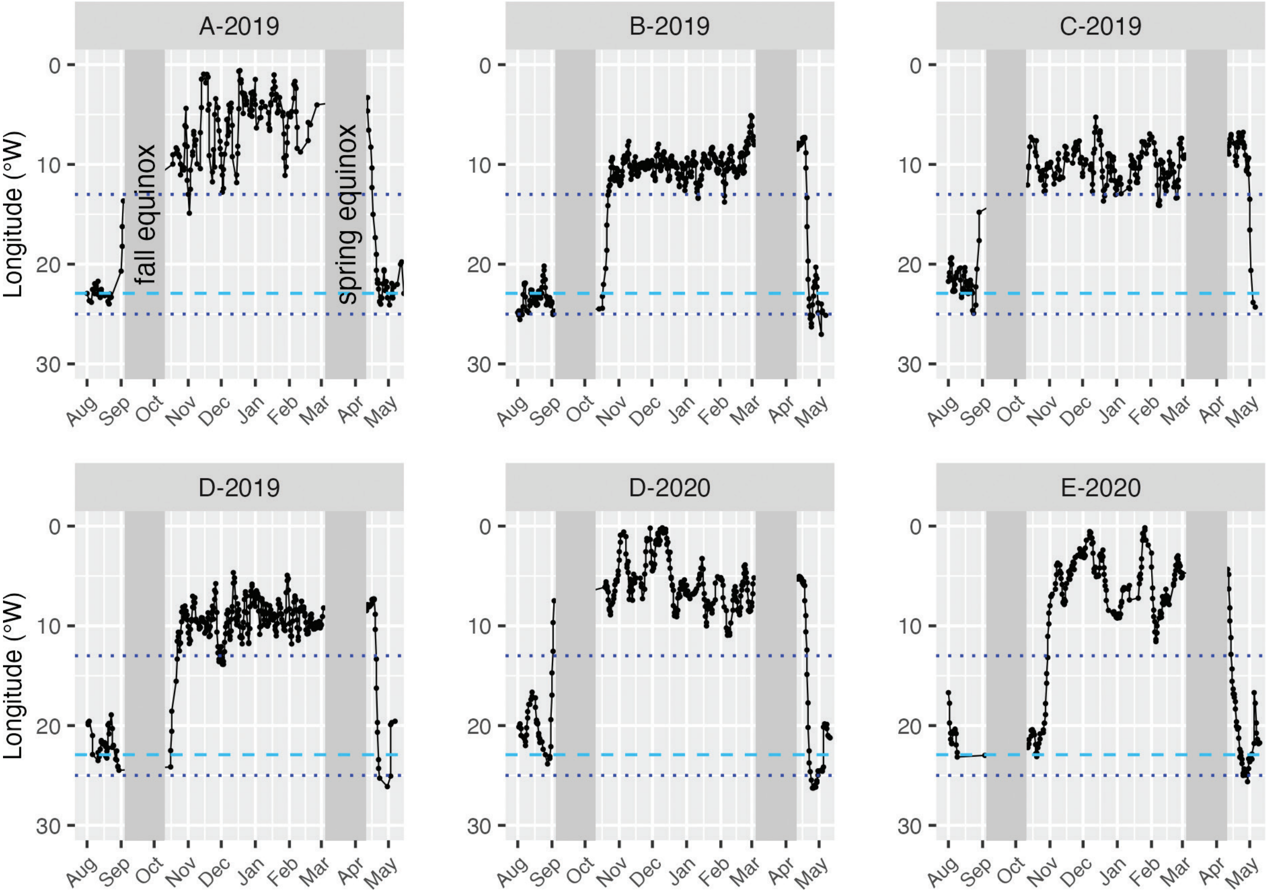

Fig. 5 Longitudinal position over time of female adult common snipe (*Gallinago gallinago*; *n* = 5, individual D tracked twice) determined using GLSs deployed during the 2019 and 2020 breeding seasons on Flatey, Iceland. Dark blue dotted lines represent the longitudinal limits of Iceland, and the light blue dashed line indicates the longitude of the study site. Coordinates are shown as five-day rolling mean values of longitude.

Table 2 Joint live encounter–dead recovery Burnham model (Seber parameterization) results used to estimate common snipe (*Gallinago gallinago*) adult female survival on Flatey, Iceland, with AIC adjusted for small sample size (ΔAIC_c) and Akaike weight (*w*). Model parameters include apparent survival (*S*), live recapture (*p*), fidelity (*F*) and dead recovery (*r*) probabilities. Live recapture (*p*) is constrained to vary with capture effort (*effort*). *F* is fixed to 1 and *r* is constant in all models. Because all models are of the form $\{S(\,)\ p_{effort}\ F_{F=1}\ r.\}$, only the *S* parameter is shown in the table. The notation (.) indicates the parameter is treated as constant, and (*t*) indicates full time dependence (different values for each year). Covariates include NAO index during the breeding months (NAO_{br}), overwinter months (NAO_{win}) and year (NAO_{yr}), and an effect of a changepoint at 2009 (cp_{2009}).

Model	ΔAIC_c	*w*	Deviance	Parameters
$\{S_{NAOwin}\}$	0.00	0.52	673.01	5
$\{S_{NAOyr}\}$	1.58	0.23	674.59	5
{S.}	2.10	0.18	677.12	4
$\{S_{cp2009}\}$	3.98	0.07	676.99	5
$\{S_t\}$	21.21	0.00	650.55	26
$\{S_{NAObr}\}$	39.46	0.00	712.47	5

effect on *S* did not differ from zero (β_{NAOyr} = 0.48 ± 0.30, 95% CI = -0.10–1.06). The majority of the remaining model support (18%) went to a model that held apparent survival constant over time $\{S.\ p_{effort}\ F_{F=1}\ r.\}$, with ΔAIC_c = 2.10 (Table 2). Time-invariant apparent survival probability was estimated as 0.69 ± 0.02.

It is possible to provide a mean apparent survival rate from our top model; however, the estimate would be constrained by the winter NAO covariate. Instead, we used the variance components method to take into account annual variance and sampling variance in apparent survival rate. The time-varying survival model $\{S_t\ p_{effort}\ F_{F=1}\ r.\}$ failed to estimate *S* in five of the later years (Fig. 6). From the remaining estimates, our mean estimate of apparent survival from the time-varying model considering sampling error was 0.66 ± SE 0.03, with a process variance (σ^2 = 0.005, 95% CI = -0.001–0.03) accounting for a small proportion of the total annual variance (process + sampling variance) in the data.

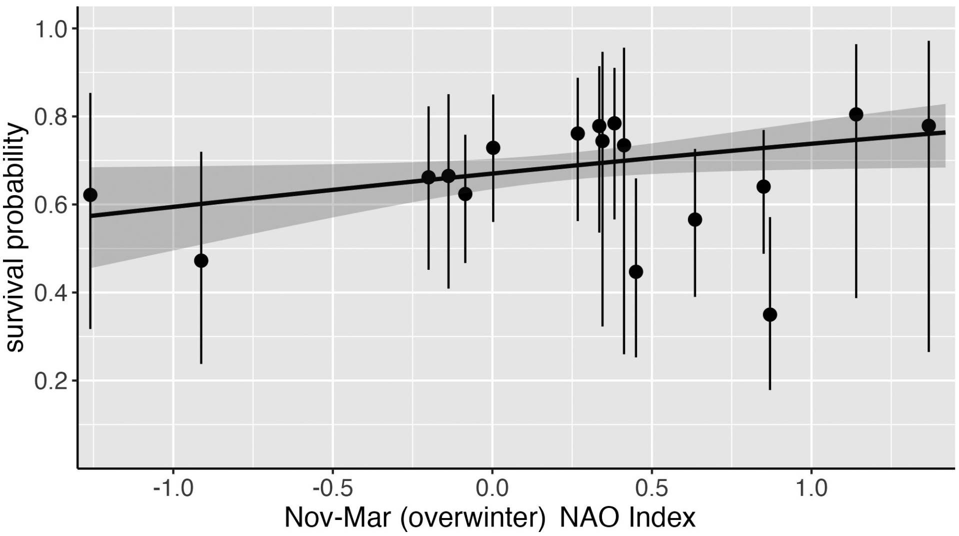

Fig. 6 Unconstrained survival probability of adult female common snipe (*Gallinago gallinago*) according to the model {S_t p_{effort} $F_{F=1}$ r.} relative to winter NAO index during the overwinter season (November–March) from 1998 to 2019 (points with 95% CI error bars). Boundary estimates for years when the model failed to estimate S are not shown. Shown as upward-trending horizontal line (with the 95% confidence interval indicated in grey) are predicted values of survival generated from the model {S_{NAOwin} p_{effort} $F_{F=1}$ r.} for a range of NAO values.

Discussion

This study provides novel insights into the biology of the common snipe breeding in western Iceland. Our geolocator data confirm what limited ringing data previously suggested, that is, some snipe from Iceland winter in Ireland (Petersen 1998; Henderson 2002), although some ringed birds have been found as far south as Portugal (Asensio & Carrasca 1987). Boyd & Petersen (2006) found that spring arrival dates at the breeding grounds had advanced in the 20th century, presumably influenced by global warming. When we estimated apparent annual adult survival for female snipe, we also found that climate patterns had a small but significant effect, with warmer, wetter winters, resulting in higher apparent survival. Snipe are harvested in parts of their winter range (Tapper 1992), and changing climate patterns that influence overwinter survival may have important implications for conservation management of this species in the future.

Our tracking confirmed that common snipe that breed in Iceland overwinter mainly in Ireland, although we suggest that they may also winter in Scotland. Snipes are hunted in Ireland and Scotland, but harvest statistics are not collected in Ireland. Estimates for the UK as a whole in 1995 were 30 000 hunted birds (e.g., Murray & Simcox 2003). Better data, especially from Ireland, would help determine whether harvest pressure varies annually and, consequently, whether human hunting contributes to variation in snipe survival (which we could not account for in our analysis). Moreover, researchers have suggested that large-scale habitat changes, notably drainage of agricultural land (about 1.4 million ha, 1950–1979), contributed to declines of snipe in Ireland (Lang 1988; Colhoun et al. 2015). Consequently, the evidence for strong migratory connections between the British Isles and Iceland highlights the importance of international coordination to manage snipe populations.

We also found that one snipe wintered farther north than the others. While the snipe is a common breeding bird on the Faroe Islands, with 1500–3000 breeding pairs recorded there, numbers increase during the migratory periods, presumably due to migrants passing through from Iceland and possibly also from the northernmost regions of Europe (Hammer et al. 2014). Our results support the notion that Icelandic birds likely use the Faroes as a migratory stop-over, with some electing to remain for the winter, as some do in Iceland (Petersen 1998; Svazas & Paulauskas 2006). Further tracking work, perhaps with more precise locations from GPS loggers deployed at multiple sites in Iceland, will confirm the migratory routes of Icelandic snipe.

We estimated apparent adult survival of female common snipe nesting in western Iceland as 0.66 ± SE 0.03, which yields an average lifespan of about 2.4 years (the oldest bird was one adult recaptured 12 years after ringing). This rate is similar to, or higher than, those reported in earlier studies. For example, common snipe wintering in France had survival rates of 0.44–0.52, depending on whether they wintered at interior or coastal regions (Péron et al. 2013), and populations were considered stable. Spence (1988) estimated survival of UK snipe at 62.5%, using less advanced statistical approaches. Arnold et al. (2016) reported a remarkably similar survival rate of 0.653 for the closely related Wilson's snipe (*Gallinago delicata*) in North America, where the population appears to be increasing (BirdLife International 2021). Survival rates for the American woodcock (*Scolopax minor*) have been estimated as 0.49 (Krementz et al. 2003), and Tavecchia et al. (2002) reported adult survival of 0.44 for Eurasian woodcock (*Scolopax rusticola*). Therefore, while we lack adult survival rates from other sites in Iceland, the rates from Flatey appear similar to or greater than what has been reported for similar species elsewhere. Variable survival rates between study populations may be related to the intensity of mortality, such as due to hunting.

Although the overall apparent annual survival rate was consistent with other studies, we found substantial annual variation in survival. Some variation may have been due to emigration (which we could not measure well but which could confound mortality estimates); we recorded one instance of an adult ringed at the nest and recovered alive seven years later at a site 29 km north during the breeding season. However, variation was also explained by climate indices, in particular the NAO. This index had its absolute minimum in 2010 over the period 1875–2020, and in the years thereafter, the NAO was mostly positive (Krueger et al. 2019). The winter of 2009/10 was the coldest winter in 50 years in Ireland, and the following year (November/December 2010) experienced another severe cold spell (Irish Meteorological Service data at https://www.met.ie/climate/major-weather-events), corresponding to the two lowest winter NAO indices during the study period (Fig. 3). This also corresponds to the sustained decline in the number of nests found on Flatey beginning in 2010, even after accounting for search effort. Following 2010, the diminished nesting population and subsequent low capture rates at Flatey impeded our ability to obtain estimates for survival in most years. Nonetheless, we interpret these results as suggesting that winters of extreme low NAO and cold, dry conditions have had a greater negative effect on snipe survival than years of high winter storm activity. Our data are consistent with other studies that have shown that extreme weather events can have important consequences for abundance, survival and overall population demography in a variety of bird species (e.g., Frederiksen et al. 2008; Gardner et al. 2017; Cohen et al. 2021).

We caution that the unique attributes of our study site should be considered when interpreting the results, which may not apply to the entire Icelandic snipe population. For example, two farms operate on Flatey. Common eider (*Somateria mollissima*) resources, including eiderdown, are collected (Petersen 1979), and avian predators such as ravens (*Corvus corax*) and great black-backed gulls (*Larus marinus*) are actively deterred. Our nesting snipe may experience lower risks of predation than snipe elsewhere; they may also experience greater disturbance from people and sheep, as both can move freely over much of the core nesting area (Petersen 1979). Disturbance can negatively influence nesting success (Götmark 1992), although it is less likely to affect adult survival (but see Gibson et al. 2018). We suspect that disturbance is not a major factor, as snipe nesting density is much higher on the western, inhabited part of the island than the eastern, uninhabited area, which is also a nature reserve and closed to visitors for most of the summer. For snipe nesting on Flatey, disturbance by people and livestock may not pose a problem because of the lack of predators, in contrast to what has been found for waders elsewhere (e.g., St. Clair et al. 2010). For context, we recently examined adult survival in Arctic terns (*Sterna paradisaea*) and common eiders nesting on Flatey, and estimated rates were amongst the highest reported for each species (Petersen et al. 2020; Wood et al. 2021). The snipe apparent survival rate on Flatey could be a bit higher than elsewhere on mainland Iceland, where nesting birds may experience predation pressure from feral American mink (*Neovison vison*) and Arctic fox (*Vulpes lagopus*).

While extreme years may have important impacts on survival that could be having long-term impacts on the population, snipe appear to be highly resilient and adapted to harsh breeding and overwintering conditions. For the Icelandic breeding population, migration is relatively short and quick, so perhaps it is not surprising that apparent survival is relatively consistent and high; short-distance migrants likely face fewer challenges from the effects of warming climates than long-distance migrants (e.g., Both et al. 2010; Clausen & Clausen 2013; Rotics et al. 2017). Perhaps of more immediate concern for snipe is the pattern of habitat change, as climate warming dries out their preferred moist sites or as people drain land for agriculture or urban expansion (reviewed by Green et al. 2017). We recommend additional tracking studies, particularly using GPS technology, to increase sample size and identify more precisely stop-over and wintering areas for common snipe from Iceland, with a goal of identifying and conserving internationally important habitat sites in the face of habitat change.

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Compliance with ethical standards

All work was conducted under approved ringing permits in Iceland.

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