MISS REBECCA LAIDLAW (Orcid ID : 0000-0002-8538-4917)

DR. VERONICA MENDEZ (Orcid ID : 0000-0001-9476-4666)

DR. CAMILO CARNEIRO (Orcid ID : 0000-0002-9803-2144)

Article type : Original Paper

Editor : Jeroen Reneerkens

Corresponding author mail id : r.laidlaw@uea.ac.uk

Vegetation structure influences predation rates of early nests in subarctic breeding waders

Running title: Subarctic wader nest predation

Rebecca A. Laidlaw[1,2], Tómas G. Gunnarsson[2], Verónica Méndez[1,2], Camilo Carneiro[2,3], Böðvar Þórisson[2], Adam Wentworth[4], Jennifer A. Gill[1] and José A. Alves[2,3]

[1]School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, NR4 7TJ, UK.

[2]South Iceland Research Centre, University of Iceland, Lindarbraut 4, 840 Laugarvatni, Iceland.

[3] Department of Biology & CESAM, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal.

[4] School of Animal Rural & Environmental Sciences, Nottingham Trent University, Brackenhurst Campus, Southwell, NG25 0QF, UK

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/IBI.12827

Abstract

Ground-nesting species are vulnerable to a wide range of predators, and often experience very high levels of nest predation. Strategies to reduce nest vulnerability can include concealing nests in vegetation and/or nesting in locations in which nests and eggs are camouflaged and less easy for predators to locate. These strategies could have important implications for the distribution of ground-nesting species, and the success rates of nests in areas with differing vegetation structure. However, the factors influencing the success of nest concealment and camouflage strategies in ground-nesting species are complex. Here we explore the effects of local vegetation structure and extent of nest concealment on nest predation rates in a range of ground-nesting, sympatric wader species with differing nest concealment strategies (open-nest species: Oystercatcher *Haematopus ostralegus*, Golden Plover *Pluvialis apricaria* and Whimbrel *Numenius phaeopus* and concealed-nest species: Black-tailed Godwit *Limosa limosa*, Redshank *Tringa totanus* and Snipe *Gallinago gallinago*) in south Iceland, in landscapes that comprise substantial variability in vegetation structure at a range of scales. We monitored 469 nests of these six wader species in 2015 and 2016 and ~40% of these nests were predated. Nest predation rates were similar for open-nest and concealed-nest species and did not vary with vegetation structure in the surrounding landscape, but nest-concealing species were ~10% more likely to have nests predated when they were poorly concealed, and the frequency of poorly-concealed nests was higher in colder conditions at the start of the breeding season. For concealed-nest species, the reduced capacity to hide nests in colder conditions is likely to reflect low rates of vegetation growth in such conditions. The ongoing trend for warmer springs at subarctic latitudes could result in more rapid vegetation growth, with consequent increases in the success rates of early nests of concealed-nest species. Temperature-related effects on nest concealment from predators could thus be an important mechanism through which climate change affecting vegetation could have population-level impacts on breeding birds at higher latitudes.

Keywords

Nest concealment; crypsis; habitat; nest predation; habitat heterogeneity; shorebird

Across arctic, subarctic and temperate landscapes, huge populations of migratory birds breed on tundra, grasslands and heathlands, and the short vegetation in these predominantly tree-less habitats means that most species are ground-nesters. Ground-nesting species are often particularly vulnerable to egg predation, as their nests can be accessible to a wide range of predators (MacDonald & Bolton 2008). Consequently, strategies employed by nesting adults to reduce nest predation risks have the potential to influence the nest site selection and breeding distribution of these species.

Among ground-nesting birds, nest camouflage and nest concealment are commonly observed, and are likely to influence vulnerability to predation. Some species, particularly wading bird species, adopt a strategy in which nests are laid on bare ground or small stones, against which adult plumage and/or egg colouration are camouflaged (Troscianko et al. 2016). These species typically rely on early detection of predators by breeding in open landscapes (Amat & Masero 2004, Bulla et al. 2016), and increased vegetation cover can delay their departure from nests when potential predators are detected (Gómez-Serrano & López-López 2014). Early predator detection and departure from nests is likely to increase the search area for predators, making it harder for nests to be located (Burrell & Colwell 2012, Troscianko et al. 2016). For species that rely on camouflage alone, nesting in open areas in which visibility of the surrounding area is not obscured might therefore be expected to increase nest success. Open-nesting species often also demonstrate anti-predator behaviour (Magnhagen 1991), including distraction displays (Byrkjedal 1987) or mobbing of predators (Jónsson & Gunnarsson 2010), and the higher use and intensity of these distracting behaviours can be associated with increased reproductive success (Gómez-Serrano & López-López 2017).

Alternatively, ground-nesting species may select nest sites in which nests and incubating adults can be concealed by the surrounding vegetation (e.g. Smart et al. 2006). This strategy is likely to result in selection of areas with sufficiently tall and dense vegetation, which may vary in availability depending on seasonal variation in vegetation height and, in farmed areas, anthropogenic activities such as livestock grazing and mechanical cutting. Nests concealed by vegetation or other microtopography (e.g. hummocks) may be less likely to be located visually by predators, but the resulting obscured visibility for incubating adults may delay their departure when a predator is detected, which may both reduce the subsequent search area for the predator and put the incubating adult at risk of capture. Although birds that flush at only short distances from predators are more likely to engage in injury-feigning or other forms of active deception of the predator (Smith & Edwards 2018).

For species relying on either camouflage or concealment, the selection of suitable nesting locations may also be influenced by vegetation structure at scales beyond the specific nest site. The probability of predators detecting a nest may be influenced by the homogeneity of vegetation structure, with nests in locations that differ from the surrounding vegetation (either open patches or patches of taller vegetation) potentially attracting predators and increasing their search efficiency (Benton et al. 2003). However, locations with a high risk of predator attraction are likely to be avoided altogether, and thus effects of vegetation structure on nest predation rates may only be apparent when opportunities to avoid risky locations are limited, for example when management results in patchy vegetation structure and/or when weather conditions constrain vegetation growth for nest concealment.

The lowlands of Iceland support high densities of a range of internationally important ground-nesting wader populations (Gunnarsson et al., 2006; Jóhannesdóttir, Arnalds, Brink, & Gunnarsson, 2014). These landscapes are comprised of large areas of semi-natural habitats interspersed with agricultural land (primarily for livestock grazing and hayfields; Jóhannesdóttir et al. 2018, 2019). At these subarctic latitudes (63°-66° North) the growing season is very short, with the onset of vegetation growth and rate of growth both being highly temperature-dependent (Thorvaldsson et al. 2005, Alves et al. 2019). These conditions provide an opportunity to explore how nest predation rates of ground-nesting birds vary in relation to vegetation height and structure, and how this varies among species that employ nest camouflage or nest concealment strategies.

METHODS

Nest finding and monitoring

Surveys to find and monitor wader nests were carried out every 7-10 days, from May to July in 2015 and 2016, two years that differed consistently in temperature. Mean monthly temperatures recorded at Eyrarbakki, south Iceland (63.8636° N, 21.1444° W) for April to July (encompassing the wader breeding season at this latitude) were cooler in 2015 (2.6, 4.4, 9.0 and 10.7°C) than in 2016 (4.1, 6.9, 10.5 and 12.8°C; www.vedur.is). Nests were located at 10 SITES (capitals at first reference indicate variables included in statistical models) across south Iceland (Fig. 1), all of which comprised open habitats (without trees) with vegetation structures ranging from bare ground to grassy areas, and in landscapes comprising a mix of semi-natural and agricultural (grass pasture and hayfields) habitats. Nests of six wader SPECIES were included in the analyses; three species classed as OPEN-NESTING because their nests are typically on bare or slightly vegetated ground (Oystercatcher *Haematopus ostralegus*, Golden Plover *Pluvialis apricaria* and Whimbrel *Numenius phaeopus*), and three classed as CONCEALED-NESTING species, as all conceal their nests in tall vegetation (Black-tailed Godwit *Limosa limosa*, Redshank *Tringa totanus* and Snipe *Gallinago gallinago*). Nests were located by surveys from vehicles and on foot, through observation of incubating adults, systematic searching and incidental flushing of incubating adults and rope-dragging (dragging a 25 m rope, held between two fieldworkers, lightly on vegetation) to flush incubating adults.

When nests were first located and measured (FIND DAY), eggs were floated in water to provide an estimated laying date (Liebezeit et al. 2007). All nests were spatially referenced using GPS, marked using a cane placed > 1 m away in a random direction and visited a minimum of every seven days to determine their fate. Nests were considered successful if one or more eggs hatched and predated nests were defined as those that were empty in advance of the predicted hatching date (laying date plus average incubation duration from Robinson, 2005) or nests without any eggshell fragments in the nest to indicate successful hatching (Green et al. 1987). To determine the time and date of nest failures, iButton dataloggers (Maxim Integrated Products Ltd, CA, USA) were placed in a randomly selected subsample of nests. These loggers recorded a temperature trace every ten minutes. For empty nests with no evidence of hatching (i.e. small fragments of shell), and no evidence of trampling (flattened nest cup) or flooding (wet nest contents), a sharp and permanent decline in nest temperature below incubation temperature indicates nest predation (Bolton et al. 2007), allowing the date, time and nest fate to be recorded. For predated nests in which the exact date of predation was not known (e.g. dataloggers not deployed), the failure day was taken as the midpoint between the final two visits.

In both study years, motion-triggered cameras (Reconyx™ PC800 HyperFire™ and Bushnell Trophy Cam HD) were deployed on a sample of open-nesting species (Table S1) to determine the predator species active on these nests. Cameras were attached to poles ~10 cm above ground level and 2 m from nests. The cameras were programmed to take ten pictures when triggered with no interval between trigger events and on the highest sensitivity level.

Nest habitat metrics

When each nest was first located, the PERCENTAGE OF EGGS VISIBLE from directly above the nest (observer standing with a leg on either side of the nest and looking down towards the nest cup) was estimated by eye in the field (i.e. the eggs of open-nesting species were predominantly 100% visible).

The habitat surrounding each nest was assessed in the field at three spatial scales: the nest cup, the 5 x 5 m and the 50 x 50 m area surrounding each nest. The NEST HABITAT of the nest cup was identified (Table 1 and see Jóhannesdóttir et al. (2014) for full definitions of the habitat types) and the percentage area of each habitat within the 5 x 5 and 50 x 50 m quadrats was visually estimated and recorded. In addition, the number of habitats (HABITAT HETEROGENEITY) within the 5 x 5 m and the 50 x 50 m areas around each nest was calculated. The habitat type which comprised the largest total area within the quadrats was considered the dominant habitat, and was classified into one of the three habitat categories of bare, short or tall (Table 1) and whether the dominant habitat category was the same (1) or different (0) to the nest habitat category was used as a binary DISSIMILARITY measure.

Statistical analyses

Variation in daily nest predation rates (DPR) were explored with Generalized Linear Mixed Models (GLMMs), using a formulation of Mayfield's (1961, 1975) method as a logistic model with a binomial error term, in which success or failure (not predated or predated) was modelled with exposure days as the binomial denominator (Aebischer 1999). Site and species were included as random factors, except for six models in which site was excluded as it explained none of the variance (Table 2, models i,ii and x-xiii). Annual and seasonal variation in visibility of concealed nests was explored in a GLMM with a normal distribution, with % eggs visible (logit scale) as the response variable and year and find day as predictors (Table 2, model iii).

Separate models were constructed for each nest scale (5 x 5 and 50 x 50 m, Table 2) as both spatial scales could not be incorporated in a single model due to collinearity. As concealed- and open-nesting species may differ in the effects of egg visibility and local habitat structure on predation risk, interactions between nesting type and habitat heterogeneity were included (Table 2). Non-significant ($P > 0.05$) variables were sequentially removed from these models (although their estimates and associated probabilities in initial maximal models are also reported, for completeness). All models were carried out in R (v 3.4.1) using the lme4 package, with model goodness-of-fit evaluated by inspecting deviance residuals.

Daily predation rates (DPR) predicted from these models were then transformed to predation probabilities by estimating nest survival rates over the incubation period (S) by raising the daily survival rate (1-DPR) to the power of the incubation period. Although species incubation durations can range from 18-20 days for Snipe up to 28-31 days for Golden Plover, an incubation period of 25 days was used as it reflected an average considering all target species (Robinson 2005), and this was used to calculate nest predation probability over the incubation period (1-S) presented in figures.

RESULTS

Over the breeding seasons of 2015 and 2016, the outcomes of 469 wader nests (predated n=190, hatched n=257, abandoned n=13, trampled n=7, mown n=2) were measured (Fig. S1) for six wader species across different habitat structures and types (Fig. S2) with varying degrees of egg visibility (Fig. S3). Daily nest predation rates were significantly higher for concealed nests in which a greater percentage of the clutch was visible (Table 3; model ii, Fig. 2), with this effect of greater percentage of the clutch visibility not apparent in open-nest species (Table 3; model i). Of the nests that were predated, both open- and concealed-nesting species were predated throughout the season and at all times of day, and both mammalian and avian predators were captured on camera (Fig. 3, Table S1). Within concealed-nest species, the visibility of nests was significantly greater in 2015 than 2016, and visibility decreased significantly as the season progressed (Table 3; model iii, Fig. 4). The higher predation rate of more visible nests of concealed-nesting species was apparent even though nests were predated up to 2-3 weeks after egg visibility was measured (Fig. S5 c & d).

Daily nest predation rates did not vary significantly in relation to the habitat heterogeneity or the extent to which the dominant habitat covered the area surrounding the nest, at either 5 x 5 or 50 x 50 m scales (Table 4). In addition, the dissimilarity between the habitat at the nest cup and in the surrounding area did not influence daily nest predation rates for open- or concealed-nest species (Table 4). Most nests were laid in habitats that were the same as the surroundings (Fig. S4e-h).

DISCUSSION

Ground-nesting waders occur at high densities in the complex of semi-natural and agricultural landscapes of lowland Iceland (Jóhannesdóttir et al. 2014), and our large-scale monitoring of over 460 nests of six wader species has shown that ~40% of nests are predated. Across this large sample of nests, the risk of predation was similar (a) in different habitats, (b) in areas with differing habitat composition at or around the nest and (c) for species that nest in the open and rely on camouflage, and species that conceal their nests in vegetation. However, among nest-concealing species, poorly-concealed nests were more likely to be predated, and poorly-concealed nests were most frequent at the start of the season and in the colder of the two years. This suggests that the risk of nest predation in these landscapes is high but unpredictable, but that the effectiveness of nest concealment can vary seasonally and with local temperatures, likely as a consequence of delayed vegetation growth in colder conditions (Thorvaldsson et al. 2005, Alves et al. 2019).

Iceland differs from many of the temperate locations of previous wader nest predation studies in having an avian-dominated predator community, a complex landscape structure and high wader nesting densities (Gunnarsson et al. 2005, Jóhannesdóttir et al. 2018, 2019). However, the level of nest predation (~40% of nests predated) in our study is similar to levels found across all geographical regions for ground-nesting waders (MacDonald & Bolton 2008, Roodbergen et al. 2012, Smith et al. 2012). Thus ground-nesting waders have a consistently high probability of having their nests located by a predator, and opportunities to reduce the likelihood of such encounters appear to be limited. Unsurprisingly, given the high latitude and lack of nocturnal darkness, there was little diurnal variation in predation rates, but the camera-captured predation events suggest that open-nesting species may be more vulnerable to avian predators, with only a single observed predation by Arctic Fox *Vulpes lagopus* (the only native mammalian predator in Iceland, although invasive American Mink *Neovison vison* are present). This may reflect a greater capacity for avian predators to locate open nests from which incubating adults have flushed early. Although predation by sheep was recorded, and has been captured on Whimbrel nest cameras previously (Katrínardóttir et al. 2015), it is likely to be incidental. We had so few cameras deployed (N=26, Table S1) we cannot explore any effect of cameras with these data.

While predator avoidance appears difficult to achieve for ground-nesting species, and both open- and concealed-nest species have similar rates of nest predation and can show predator distraction and mobbing behaviour if nests are detected (Jónsson & Gunnarsson 2010) the two strategies are likely to be subject to differing constraints. For open-nesting species with a reliance on the camouflage of eggs and incubating adults the selection of substrates that make egg camouflage effective is likely to be important (Colwell et al. 2011), and thus the spatial availability of such substrates is likely to influence nesting distribution and densities. By contrast, concealed-nest species require vegetation that is sufficiently tall and dense to conceal nests effectively (Smart et al. 2006), and the availability of such vegetation is likely to vary both spatially and seasonally (Alves et al. 2019). For both open- and concealed-nest species, we found no differences in predation rates of nests that were in habitats that were the same as or different to the dominant surrounding habitat (Table 4; models xi-xiv). However, the great majority of nests were laid in habitats that were the same as the surroundings (Fig. S4e-h). Areas of more homogenous vegetation structure (either bare/short vegetation or tall/dense vegetation) could offer better opportunities for predator detection and/or concealed departure of incubating adults while making detection harder when departure is early, and could thus be advantageous despite the stochastic risk of nest predation. For the concealed-nest strategy to be successful, however, concealment clearly needs to be effective; nests containing eggs which are visible from above are significantly more likely to be predated (Table 3). Our metric of nest concealment is related to visibility from above, but permeability of the surrounding vegetation may also influence predation risk, particularly in relation to mammalian predators. Egg visibility declined through the season in both years, and was consistently higher in the colder year (Fig. 4). This suggests that the onset and rate of vegetation growth could potentially constrain the availability of suitable nesting locations for these species, and influence nest success, particularly among early season nests (Alves et al. 2019). In agricultural habitats, these effects could be exacerbated by early or intensive grazing (Flemming et al. 2019).

These findings suggest considerable risk for concealed-nest species nesting early in the season in years when vegetation growth is delayed or slow. Given the benefits of hatching early that are observed in many migratory species, with recruitment into breeding populations typically being lower for later-hatched chicks (Harris et al. 1994, Clark et al. 2014, Visser et al. 2015, Lok et al. 2017, Alves et al. 2019), such temperature-influences on growing conditions of the vegetation used by concealed-nest species to hide their nests could be a key driver of annual variation in their breeding success (Gunnarsson et al. 2017, Alves et al. 2019). However, given the ongoing trend for warmer springs at subarctic latitudes (IPCC 2007), the conditions in which poor nest concealment occurs are likely to be reducing in frequency. Additionally, the area of vegetation in these habitats is also increasing through shrub encroachment, which may benefit concealed-nesting species in some circumstances, but could decrease the habitat available for open-nesting species (Swift et al. 2017, Alfreðsson 2018). Rapid vegetation growth as a result of warmer spring temperatures could therefore increase the likelihood of successful hatching of early concealed-nests over increasing areas of habitat, and could thus be a mechanism through which climatic conditions affecting vegetation growth could have population-level impacts on breeding birds.

This work was supported by University of Iceland Research Fund, an Icelandic Research Council (Rannís) Grant number 152470-052, a NERC Grant number NE/M012549/1, and by FCT/MCTES to CESAM (UID/AMB/50017/2019) and individual grants to CC (PD/BD/113534/2015) and JAA (SFRH/BPD/91527/2012) through national funds and ProPolar. The authors would like to thank Harry Ewing, Aldís Pálsdóttir, Catriona Morrison, Olivia Hicks, Mags Ramsey and Lilja Jóhannesdóttir for their assistance in the field, all iScreamers for fruitful discussions and to the landowners who allowed access to their land for this study. We would like to thank Jeroen Reneerkens and three anonymous reviewers for their helpful comments on the manuscript.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

Aebischer, N. J. 1999. Multi-way comparisonsand generalized linear models of nest success: extensions of the Mayfield method. *Bird Study* **46**:22–31.

Alfreðsson, S. B. 2018. The effects of shrub encroachment on avian communities in lowland Iceland. MSc Thesis. Faculty of Life and Environmental Sciences, University of Iceland.

Alves, J. A., T. G. Gunnarsson, W. J. Sutherland, P. M. Potts, & J. A. Gill. 2019. Linking warming effects on phenology, demography, and range expansion in a migratory bird population. *Ecol. Evol.* **9**:2365–2375.

Amat, J. A., & J. A. Masero. 2004. Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Anim. Behav.* **67**:293–300.

Benton, T. G., J. A. Vickery, & J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key?. *Trends Ecol. Evol.* **18**:182–188.

Bolton, M., G. Tyler, K. Smith, & R. Bamford. 2007. The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *J. Appl. Ecol.* **44**:534–544.

Bulla, M., M. Valcu, A. M. Dokter, A. G. Dondua, A. Kosztolányi, A. Rutten, B. Helm, B. K. Sandercock, B. Casler, B. J. Ens, C. S. Spiegel, C. J. Hassell, C. Küpper, C. Minton, D. Burgas, D. B. Lank, D. C. Payer, E. Y. Loktionov, E. Nol, E. Kwon, F. Smith, H. R. Gates, H. Vitnerová, H. Prüter, J. A. Johnson, J. J. H. St Clair, J. Lamarre, J. Rausch, J. Reneerkens, J. R. Conklin, J. Burger, J. Liebezeit, J. Bêty, J. T. Coleman, J. Figuerola, J. C. E. W. Hooijmeijer, J. A. Alves, J. A. M. Smith, K. Weidinger, K. Koivula, K. Gosbell, L. Niles, L. Koloski, L. Mckinnon, L. Praus, M. Klaassen, M.-A. Giroux, M. Sládeček, M. L. Boldenow, M. Exo, M. I. Goldstein, M. Šálek, N. Senner, N. Rönkä, N. Lecomte, O. Gilg, O. Vincze, O. W. Johnson, P. A. Smith, P. F. Woodard, P. S. Tomkovich, P. Battley, R. Bentzen, R. B. Lanctot, R. Porter, S. T. Saalfeld, S. Freeman, S. C. Brown, S. Yezerinac, T. Székely, T. Montalvo, T. Piersma, V. Loverti, V.-M. Pakanen, W. Tijsen, & B. Kempenaers. 2016. Unexpected diversity in socially synchronized rhythms of shorebirds. *Nature* **540**:109–113.

Burrell, N. S., & M. A. Colwell. 2012. Direct and indirect evidence that productivity of Snowy Plovers *Charadrius nivosus* varies with occurrence of a nest predator. *Wildfowl* **62**:204–223.

Byrkjedal, I. 1987. Antipredator behavior and breeding success in greater golden-plover and eurasian dotterel. *Condor* **89**:40–47.

Clark, R. G., H. Pöysä, P. Runko, & A. Paasivaara. 2014. Spring phenology and timing of breeding in shortdistance migrant birds: Phenotypic responses and offspring recruitment patterns in common goldeneyes. *J. Avian Biol.* **45**:457–465.

Colwell, M. A., J. J. Meyer, M. A. Hardy, S. E. Mcallister, A. N. Transou, R. R. Levalley, & S. J. Dinsmore. 2011. Western Snowy Plovers Charadrius alexandrinus nivosus select nesting substrates that enhance egg crypsis and improve nest survival. *Ibis (Lond. 1859).* **153**:303–311.

Flemming, S. A., E. Nol, L. V Kennedy, & P. A. Smith. 2019. Hyperabundant herbivores limit habitat availability and influence nest site selection of Arctic- - breeding birds. *J. Appl. Ecol.* **56**:976–987.

Gísladóttir, F. Ó., S. H. Brink, & A. Ólafur. 2014. Nytjaland. Rit LBHÍ nr. 49. Retrieved from http://hdl.handle.net/1946/23041.

Gómez-Serrano, M. Á., & P. López-López. 2017. Deceiving predators: linking distraction behavior with nest survival in a ground-nesting bird. *Behav. Ecol.* **28**:260–269.

Gómez-Serrano, M. Á., & P. López-López. 2014. Nest site selection by Kentish Plover suggests a trade-off between nest-crypsis and predator detection strategies. *PLoS One* **9**:e107121.

Green, R. E., J. Hawell, & T. H. Johnson. 1987. Identification of predators of wader eggs from egg remains. *Bird Study* **34**:87–91.

Gunnarsson, T. G., J. A. Gill, G. F. Appleton, H. Gíslason, A. Gardarsson, A. R. Watkinson, & W. J. Sutherland. 2006. Large-scale habitat associations of birds in lowland Iceland: Implications for conservation. *Biol. Conserv.* **128**:265–275.

Gunnarsson, T. G., J. A. Gill, J. Newton, P. M. Potts, & W. J. Sutherland. 2005. Seasonal matching of habitat quality and fitness in a migratory bird. *Proc Biol Sci* **272**:2319–2323.

Gunnarsson, T. G., L. Jóhannesdóttir, J. A. Alves, B. Þórisson, & J. A. Gill. 2017. Effects of spring temperature and volcanic eruptions on wader productivity. *Ibis (Lond. 1859).* **159**:467–471.

Harris, M. P., S. T. Buckland, S. M. Russell, & S. Wanless. 1994. Post fledging survival to breeding age of shags *Phalacrocorax aristotelis* in relation to year, date of fledging and brood size. *J. Avian Biol.* **25**:268–274.

IPCC. 2007. Intergovernmental Panel on Climate Change: Fourth Assessment Report.

Jóhannesdóttir, L., J. A. Alves, J. A. Gill, & T. G. Gunnarsson. 2018. Use of agricultural land by breeding waders in low-intensity farming landscapes. *Anim. Conserv.* **21**:291–301.

Jóhannesdóttir, L., Ó. Arnalds, S. Brink, & T. G. Gunnarsson. 2014. Identifying important bird habitats in a sub-arctic area undergoing rapid land-use change. *Bird Study* **61**:544–552.

Jóhannesdóttir, L., J. A. Gill, J. A. Alves, S. H. Brink, Ó. Arnalds, V. Méndez, & T. G. Gunnarsson. 2019. Interacting effects of agriculture and landscape on breeding wader populations. *Agric. Ecosyst. Environ.* **272**:246–253.

Jónsson, J. E., & T. G. Gunnarsson. 2010. Predator chases by breeding waders: interspecific comparison of three species nesting in Iceland. *Wader Study Gr. Bull.* **117**:145–149.

Katrínardóttir, B., J. A. Alves, H. Sigurjónsdóttir, P. Hersteinsson, & T. G. Gunnarsson. 2015. The effects of habitat type and volcanic eruptions on the breeding demography of icelandic whimbrels *numenius phaeopus*. *PLoS One* **10**:1–15.

Liebezeit, J. R., P. A. Smith, R. B. Lanctot, H. Schekkerman, S. J. Kendall, D. M. Tracy, R. J. Rodrigues, H. Meltofte, J. A. Robinson, C. Gratto-Trevor, B. J. McCaffery, J. Morse, & S. W. Zack. 2007. Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. *Condor* **109**:32–47.

Lok, T., L. Veldhoen, O. Overdijk, J. M. Tinbergen, & T. Piersma. 2017. An age-dependent fitness cost of migration? Old trans-Saharan migrating spoonbills breed later than those staying in Europe, and late breeders have lower recruitment. *J. Anim. Ecol.* **86**:998–1009.

MacDonald, M. A., & M. Bolton. 2008. Predation on wader nests in Europe. *Ibis (Lond. 1859).* **150**:54–73.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends Ecol. Evol.* **6**:183–186.

Mayfield, H. F. 1961. Nesting success calculated from exposure. *Wilson Bull.* **73**:255–261.

Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bull.* **87**:456–466.

Robinson, R. A. 2005. BirdFacts: profiles of birds occurring in Britain & Ireland. http://www.bto.org/birdfacts.

Roodbergen, M., B. van der Werf, & H. Hötker. 2012. Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: Review and meta-analysis. *J. Ornithol.* **153**:53–74.

Smart, J., J. A. Gill, W. J. Sutherland, & A. R. Watkinson. 2006. Grassland-breeding waders: identifying key habitat requirements for management. *J. Appl. Ecol.* **43**:454–463.

Smith, P. A., & D. B. Edwards. 2018. Deceptive nest defence in ground-nesting birds and the risk of intermediate strategies. *PLoS One* **13**:1–12.

Smith, P. A., I. Tulp, H. Schekkerman, H. G. Gilchrist, & M. R. Forbes. 2012. Shorebird incubation behaviour and its influence on the risk of nest predation. *Anim. Behav.* **84**:835–842.

Swift, R. J., A. D. Rodewald, & N. R. Senner. 2017. Breeding habitat of a declining shorebird in a changing environment. *Polar Biol.* **40**:1777–1786.

Thorvaldsson, G., H. Björnsson, & J. Hermannsson. 2005. The influence of weather on early growth rate of grasses. *Icelandic Agric. Stud.* **4**:65–73.

Troscianko, J., J. Wilson-Aggarwal, M. Stevens, & C. N. Spottiswoode. 2016. Camouflage predicts survival in ground-nesting birds. *Sci. Rep.* **6**:19966.

Visser, M. E., P. Gienapp, A. Husby, M. Morrisey, I. de la Hera, F. Pulido, & C. Both. 2015. Effects of spring temperatures on the strength of selection on timing of reproduction in a long-distance migratory bird. *PLoS Biol.* **13**:1–17.

Table 1. Nest habitat types (with descriptions) within the three categories of vegetation height, and the numbers of nests of open- and concealed-nest species monitored within each habitat type. Habitat descriptions follow Nytjaland classifications (Gísladóttir et al. 2014).

Category	Habitat	Description	No. concealed nests	No. open nests
Bare	Bare land	Scattered vegetation cover (0-20%)	0	17
	Gravel track	Gravelled tracks or areas alongside roadways	0	54
	Riverine gravel	Gravelled areas adjacent to rivers	0	27
	Ploughed land	Recently ploughed agricultural land	0	5
Short	Short crop	All cultivated land <10 cm high vegetation	0	23
	Partially vegetated	Scattered vegetation cover (20-50%)	0	10
	Moss	Moss species covering more than 50%	4	18
	Poor heath	Dominated by heath species, large component of moss	1	32
Tall	Tall crop	All cultivated land >10 cm high vegetation	17	6
	Grassland	Lowland plains, forbs are often prominent	47	50
	Grass tussock	Singular plants, tufts or hummocks cf. meadow	77	10
	Rich heath	Dominated by dwarf heath species, moss species and herbaceous plants (i.e. grasses and forbs)	1	19
	Shrubs	Includes land dominated by willow and mountain birch	9	18
	Wetland	Ground water level is usually high. *Carex* spp., *Equisetum* spp. and *Juncus arcticus*	23	1

Table 2. Description of the structure of models of daily nest predation rate (DPR) and percentage of eggs visible and all response and explanatory variables. The maximal models are shown and were carried out in R (v.3.4.4).

Type	Variable	Distribution (link)/ variable range of values	Explanation
Response	Daily nest predation rate (DPR)	Binomial (logit)	Nest outcome (Predated or Hatched) accounting for exposure days
	% Eggs visible	Logit proportion as response	How much of eggs are visible by eye from directly above nest
Explanatory	Year		Nests monitored in 2015 and 2016
	Site	Random	Nest site identity
	Species	Random	OC, GP, WM, BW, SN, RK (species with sample size >20)
	Find day	51-133	Day after March 1st when nest was found and vegetation measured
	Nesting type	1/0	Open or concealed nesting species
	Nest habitat	14 types	Habitat type of nest cup (i.e. gravel)
	Nest habitat category	B,S,H	Category of habitat of nest cup, by height (1-bare, 2-short,3-tall)
	Habitat heterogeneity	1 to 4/6	Number of habitats within surrounding 5 x 5 m (max 4) / 50 x 50 m (max 6)
	Dissimilarity	1/0	Nest habitat is the same (1) as the dominant habitat in surrounding 5 x 5 m / 50 x 50 m
	% Eggs visible		How much of eggs are visible by eye from directly above nest
	% Dominant habitat		Percentage value of the habitat type that covered the most area in 5 x 5 m or 50 x 50 m

Model	Response	
i	Open DPR	Year + % Egg visible +(1|Species)
ii	Concealed DPR	Year + % Egg visible + (1|Species)
iii	Concealed % Eggs visible	Year + Find date + (1|Species) + (1|Site)

iv	DPR	Year + Nest habitat + (1|Species) + (1|Site)
v	DPR	Year + Nest habitat category + (1|Species) + (1|Site)
vi	DPR	Year + Nesting type + Habitat heterogeneity 5 x 5 m + Nesting type x Habitat heterogeneity 5 x 5 m + (1|Species) + (1|Site)
vii	DPR	Year + Nesting type + Habitat heterogeneity 50 x 50 m + Nesting type x Habitat heterogeneity 50 x 50 m + (1|Species) + (1|Site)
viii	DPR	Year + % Dominant habitat 5 x 5 + (1|Species) + (1|Site)
ix	DPR	Year + % Dominant habitat 50 x 50 + (1|Species) + (1|Site)
x	Open DPR	Year + Dissimilarity 5 x 5 m + (1|Species)
xi	Concealed DPR	Year + Dissimilarity 5 x 5 m + (1|Species)
xii	Open DPR	Year + Dissimilarity 50 x 50 m + (1|Species)
xiii	Concealed DPR	Year + Dissimilarity 50 x 50 m + (1|Species)

Table 3. Results of generalised linear mixed models exploring the influences of year and proportion of egg visible on daily nest predation rates (DPR) in i) open and ii) concealed nests and (iii) year and season on the proportion of eggs visible within nests of waders in lowland Iceland (see Table 2 for model details). The maximal model is shown above the dashed lines and factors retained in minimum models are shown below the dashed lines. Significant effects (P < 0.05) are highlighted in bold.

Model	Fixed effects	Estimate	SE	*z* value		*p*
I	*Initial linear mixed effects model (BIC=645.9)*					
OPEN	(Intercept)	-3.576	0.218	-16.380		**<0.001**
NESTS DPR	Year	0.241	0.186	1.298		0.194
(n=290)	% egg visible	0.210	0.144	1.463		0.143
	Minimal linear mixed effects model (BIC=638.8)					
	(Intercept)	-3.491	0.167	-20.890		**<0.001**
ii	*Minimal linear mixed effects model (BIC=335.5)*					
CONCEALED	(Intercept)	-3.070	0.188	-16.315		**<0.001**
NESTS DPR	Year	-0.618	0.269	-2.295		**0.022**
(n=179)	% egg visible	0.541	0.153	3.544		**<0.001**
		Estimate	SE	*df*	*t*	*p*
iii CONCEALED	(Intercept)	0.809	0.622	2.348	1.302	0.306
NESTS % Egg visible	Year	-1.974	0.283	174.605	-6.964	**<0.001**
(n=179)	Find day	-0.742	0.140	174.251	-5.312	**<0.001**

Table 4 Results of generalised linear mixed models exploring the factors influencing daily nest predation rates of open- and concealed-nesting waders in lowland Iceland (see Table 2 for model details). The maximal model is shown above the dashed lines and factors retained in minimum models are shown below the dashed lines. Significant effects (P < 0.05) are highlighted in bold.

Model	Fixed effects	Estimate	SE	*z* value	*p*
iv	*Initial linear mixed effects model (BIC=1043.1)*				
ALL	(Intercept)	-3.734	0.443	-8.430	**<0.001**
NESTS DPR	Year	-0.216	0.181	-1.193	0.233
N=469	Nest habitat	Chi squared = 19.622		df =13	0.105
	Minimal linear mixed effects model (BIC=982.8)				
	(Intercept)	-3.453	0.177	-19.472	**<0.001**
	Year	-0.360	0.168	-2.139	**0.032**
v	*Initial linear mixed effects model (BIC=993.4)*				
ALL	(Intercept)	-3.723	0.223	-16.713	**<0.001**
NESTS DPR	Year	-0.382	0.166	-2.302	**0.021**
N=469	Nest habitat category	Chi squared = 2.614		df =2	0.271
	Minimal linear mixed effects model (BIC=982.8)				
	(Intercept)	-3.453	0.177	-19.472	**<0.001**
	Year	-0.360	0.168	-2.139	**0.032**
vi	*Initial linear mixed effects model (BIC=997.8)*				

ALL	(Intercept)	-3.517	0.268	-13.142	**<0.001**
NESTS DPR	Year	-0.363	0.175	-2.070	**0.039**
N=469	Nesting type	0.044	0.269	0.165	0.869
	Habitat heterogeneity **5 x 5 m**	0.049	0.122	0.398	0.691
	Nesting type*Habitat het **5 x 5 m**	-0.265	0.170	-1.562	0.118
	Minimal linear mixed effects model (BIC=982.8)				
	(Intercept)	-3.453	0.177	-19.472	**<0.001**
	Year	-0.360	0.168	-2.139	**0.032**
vii	*Initial linear mixed effects model (BIC=1001.2)*				
ALL	(Intercept)	-3.473	0.245	-14.151	**<0.001**
NESTS DPR	Year	-0.357	0.170	-2.104	**0.035**
N=469	Nesting type	0.028	0.244	0.113	0.910
	Habitat heterogeneity **50 x 50 m**	0.034	0.143	0.237	0.813
	Nesting type*Habitat het **50 x 50 m**	-0.029	0.170	-0.168	0.866
	Minimal linear mixed effects model (BIC=982.8)				
	(Intercept)	-3.453	0.177	-19.472	**<0.001**
	Year	-0.360	0.168	-2.139	**0.032**
viii	*Initial linear mixed effects model (BIC=988.5)*				
ALL	(Intercept)	-3.450	0.182	-18.957	**<0.001**
NESTS DPR	Year	-0.370	0.169	-2.189	0.029
N=469	% Dominant habitat **5 x 5 m**	0.052	0.079	0.662	0.508
	Minimal linear mixed effects model (BIC=982.8)				
	(Intercept)	-3.453	0.177	-19.472	**<0.001**
	Year	-0.360	0.168	-2.139	**0.032**
ix	*Initial linear mixed effects model (BIC=988.0)*				
ALL	(Intercept)	-3.455	0.183	-18.845	**<0.001**
NESTS DPR	Year	-0.383	0.170	-2.253	0.024
N=469	% Dominant habitat **50 x 50 m**	0.075	0.078	0.952	0.341
	Minimal linear mixed effects model (BIC=982.8)				
	(Intercept)	-3.453	0.177	-19.472	**<0.001**
	Year	-0.360	0.168	-2.139	**0.032**

x	*Initial linear mixed effects model (BIC=649.0)*				
OPEN	(Intercept)	-3.559	0.276	-12.897	**<0.001**
NESTS DPR	Year	0.202	0.185	1.094	0.274
n=290	Dissimilarity **5 x 5 m**	-0.021	0.246	-0.086	0.932
	Minimal linear mixed effects model (BIC=638.8)				
	(Intercept)	-3.491	0.167	-20.890	**<0.001**
xi	*Initial linear mixed effects model*	Model does not converge			
CONCEALED	(Intercept)				
NESTS DPR	Year				
n=179	Dissimilarity **5 x 5 m**				
xii	*Initial linear mixed effects model (BIC=645.1)*				
OPEN	(Intercept)	-3.861	0.238	-16.209	**<0.001**
NESTS DPR	Year	0.150	0.186	0.805	0.421
n=290	Dissimilarity **50 x 50 m**	0.417	0.216	1.931	0.053
	Minimal linear mixed effects model (BIC=638.8)				
	(Intercept)	-3.491	0.167	-20.890	**<0.001**
xiii	*Initial linear mixed effects model (BIC=347.7)*				
CONCEALED	(Intercept)	-3.416	0.631	-5.414	**<0.001**
NESTS DPR	Year	-0.859	0.267	-3.221	0.001
n=179	Dissimilarity **50 x 50 m**	0.549	0.604	0.908	0.364
	Minimal linear mixed effects model (BIC=343.5)				
	(Intercept)	-2.885	0.224	-12.880	**<0.001**
	Year	-0.904	0.263	-3.440	**<0.001**

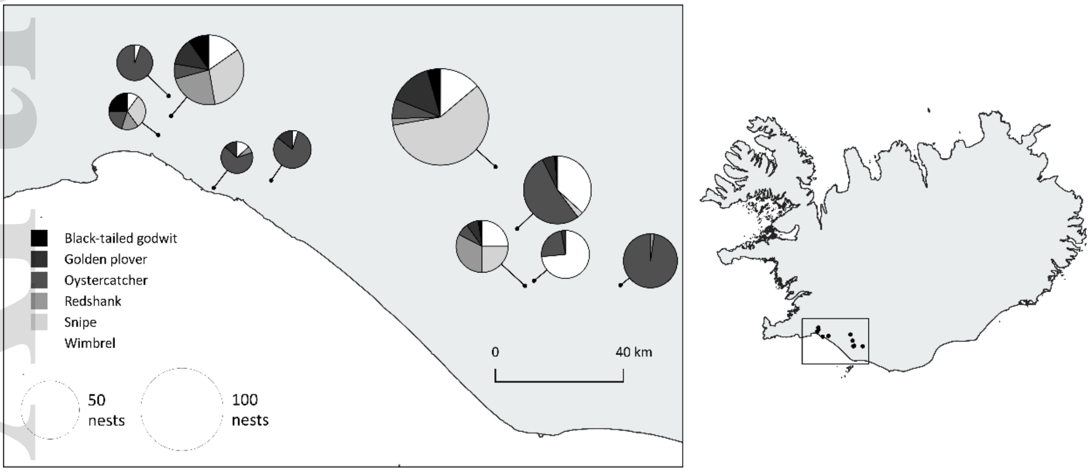

Figure 1. Locations of the 10 study areas in which wader nests were monitored in southern Iceland. The size of each pie charts represents the number of nests at each site (range 15 – 137) and colours represent the species composition of monitored nests at each site.

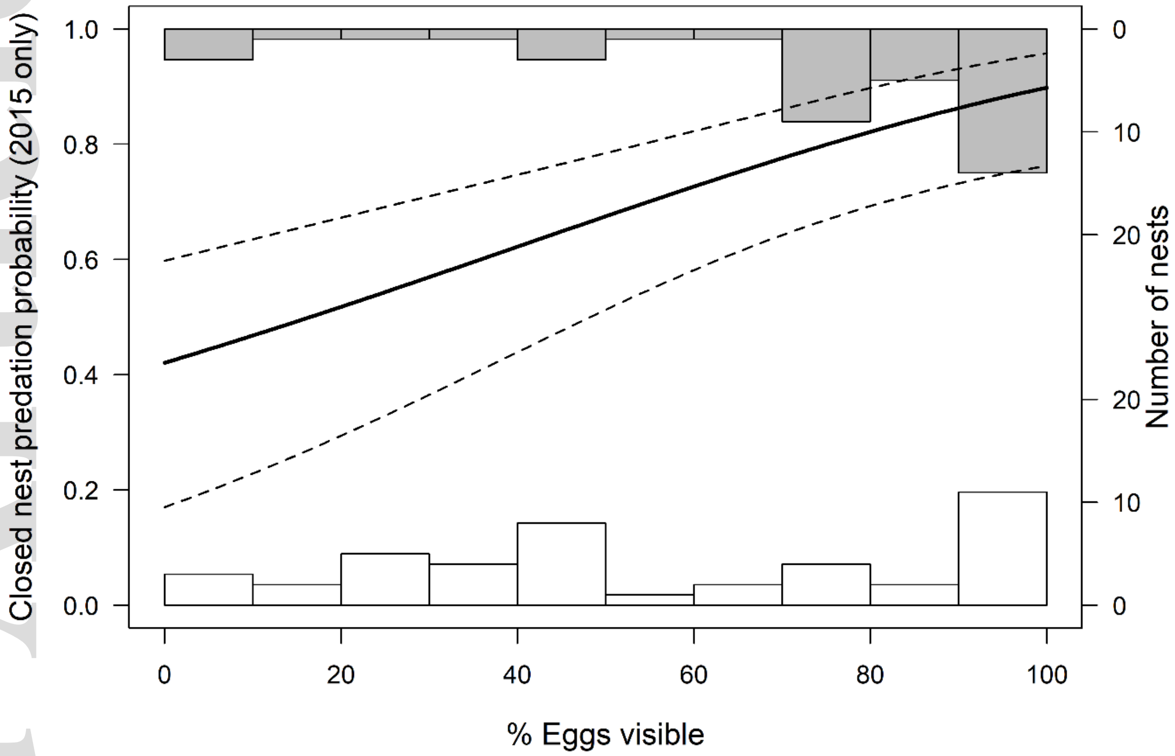

Figure 2. Changes in the predicted probability of nest predation with increasing percentage of eggs visible for concealed-nest species in 2015 only. Predictions (with dashed 95% CI) from model ii in Table 2. Bars represent number of nests that were predated (closed bars) or not predated (open bars) at different egg visibilities.

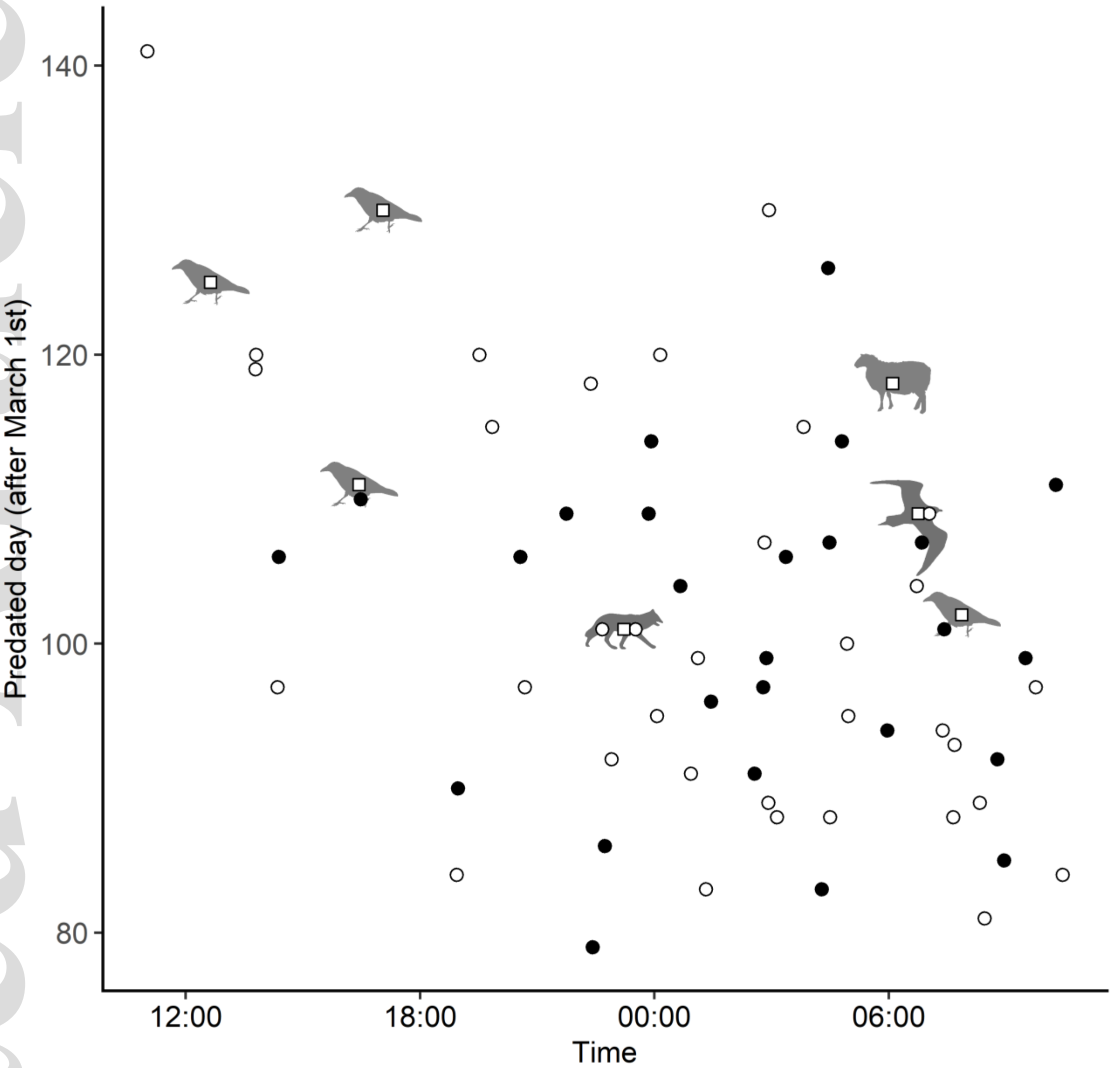

Figure 3. Time of nest predation events (determined via ibutton temperature logger traces) over the 24 hour cycle for open- (empty circles) and concealed- (filled circles) nest wader species (n=60 nests). Identified predators of open nests recorded on camera (empty squares, n=7) are denoted by animal symbols (single predation events by Arctic Fox, Arctic Skua *Stercorarius parasiticus*, Sheep *Ovis aries* and four predation events by Raven *Corvus corax*; Table S1).

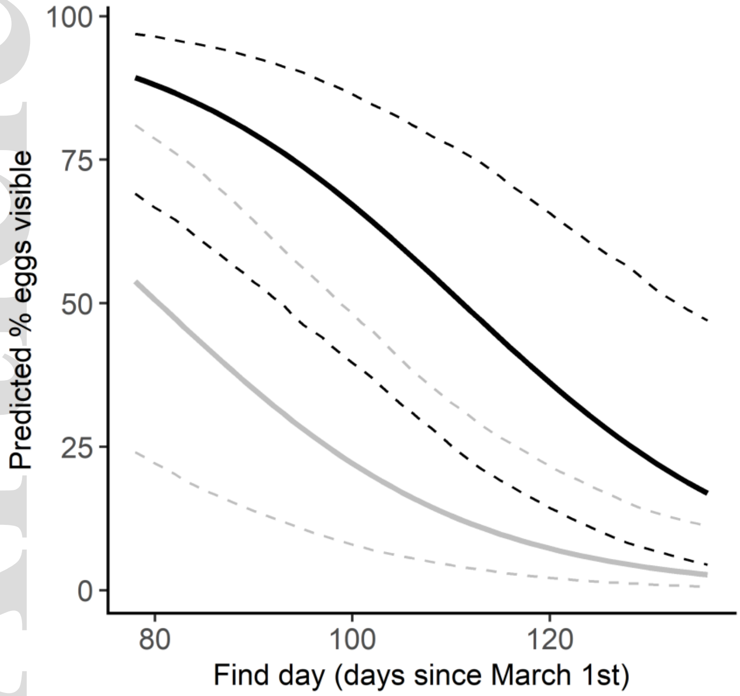

Figure 4. Seasonal changes in the predicted percentage of eggs visible (± 95% CI) for concealed-nest species in 2015 (black) and 2016 (grey). Back-transformed predicted values from logit transformation of percentage eggs visible; Table 3; model iii).

Supplementary material

Table S1 Outcome of open nesting species with nest cameras

Figure S1 Distribution of lay dates of wader nests in a) 2015 and b) 2016 that were either predated (closed bars) or not predated (open bars).

Figure S2 Number of nests predated (closed bars) and not predated (open bars) in 2015 and 2016 of (a) each species (total nest numbers: Oystercatchers (OC):163, Golden plover (GP):47, Whimbrel (WM):101, Black-tailed godwit (BW):20, Snipe (SN):121 and Redshank (RK): 38), (b) in differing vegetation heights and (c) in differing habitats (see Table 1 for details).

Figure S3 Boxplot showing the percentage of eggs visible for each species using combined data from 2015 and 2016 (total nest numbers: Oystercatchers (OC):152, Golden plover (GP):42, Whimbrel (WM):96, Black-tailed godwit (BW):20, Snipe (SN):121 and Redshank (RK): 38). Given are the median, interquartile range, range and outliers (grey points). Mean ± SE is also displayed for each species (black points)

Figure S4 Number of nests predated (closed bars) and not predated (open bars) for open- and concealed-nest species in areas with differing number of habitats and same or different habitats to the nest in the surrounding 5 x 5 m and 50 x 50 m.

Figure S5 Proportion of eggs visible for concealed nests that were either predated (filled) or not predated (open) in relation to their find day in a) 2015 and b) 2016, and number of monitored exposure days (days between nest finding and nest outcome) in c) 2015 and d) 2016.