


Long-term data reveal contrasting impacts of native versus invasive nest predators in Iceland

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Abstract

Bird species on islands are strongly impacted by biological invasions, with the Icelandic common eider (*Somateria mollissima borealis*) being particularly threatened. Down collection by local families in Breiðafjörður, West Iceland, provided long-term datasets of nests from two archipelagos, covering 95 islands over 123 years and 39 islands over 27 years, respectively. Using these exceptional datasets, we found that the arrival of the invasive semi-aquatic American mink (*Neogale vison*) was a more impactful driver of population dynamics than climate. This invasive predator heavily reduced eider nest numbers by ca. 60% in the Brokey archipelago. In contrast, we detected an apparently adaptive response to the return of the native fox in the Purkey archipelago, with dense nests on islands inaccessible to the fox and no apparent impact on eider populations. This difference might be due to the eiders lacking a joint evolutionary history with the mink and therefore lacking appropriate antipredator responses.

KEYWORDS

American mink, arctic fox, Atlantic multidecadal oscillation index (AMO), biological invasions, citizen science, common eider duck, Iceland, long-term data, nesting behaviour, time series

INTRODUCTION

How fleeting are all human passions compared with the massive continuity of ducks.

Dorothy L. Sayers (Sayers, 1935).

The ways in which humans shape ecosystems worldwide are diverse, fast and drastic, with species introductions being amongst the most important factors threatening biodiversity (IPBES, 2019; Pyšek et al., 2020). Species invasions interact with other biodiversity threats like climate change, further exacerbating extinction risk (Macinnis-Ng et al., 2021). These interactions are often difficult to disentangle, as long-term data, including the pre-invasion stage, are typically missing. This lack of long-term data has been recognized as a key limitation

in the field of invasion science (e.g. Pergl et al., 2020; Strayer et al., 2006).

Climate is a bottom-up driver of population dynamics, and its effects are widely studied. In the southern hemisphere, anomalies in sea surface temperature (SST) were shown to influence krill population dynamics and, in turn, populations of their mammalian and bird predators (Murphy et al., 2007). In the northern hemisphere, nutrient flow and thus species abundance and migration was shown to be linked to the Atlantic Multidecadal Oscillation index (Alvarez-Fernandez, 2012; Hátún et al., 2016), which is the de-trended mean of North Atlantic (0–60°N) SST anomalies (Alheit et al., 2014). The AMO has implications for a trophic cascade through plankton to crustaceans and molluscs to seabirds (Drinkwater & Kristiansen, 2018).

Jón Einar Jónsson, Fiona S. Rickowski and Florian Ruland contributed equally to this work.

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Conversely, predation pressure can act as a top-down driver on nest numbers and distribution of seabirds (Barros et al., 2016; Gerell, 1985; Nordström & Korpimäki, 2004), and the impacts of native and introduced predators can differ vastly (Salo et al., 2007). In New Zealand, for instance, we can clearly contrast the role of native predators such as the weka (*Gallirallus australis*; Carpenter et al., 2021) from the negative impacts of invasive mammalian predators such as dogs (*Canis familiaris*, Greig & Rawlence, 2021), cats, stoats and rats. As New Zealand previously had no terrestrial mammalian predators, native bird species were naïve and defenceless towards them (Banks & Dickman, 2007), leading to strong population declines and extinctions (Robertson et al., 2021). Furthermore, species communities on islands generally have smaller population sizes and geographic ranges or lack antipredator responses, rendering them more vulnerable to negative impacts of invaders than those on mainlands (Blumstein & Daniel, 2005), especially bird species impacted by invasive mammals (Dueñas et al., 2021).

Another interesting island impacted by invasive species is Iceland. Iceland is a relatively young volcanic island more than 300 km from the next landmass. Its terrestrial productivity is low, but it is an important breeding ground for a large number of migrating and resident bird species, due to highly productive coastal waters. This makes the Icelandic flora and fauna vulnerable to (i) climate change, especially those affecting marine biota, and (ii) introductions of terrestrial and freshwater species by humans. There are only two wild non-marine mammalian predators: the native arctic fox (*Vulpes lagopus*, hereafter fox), which is the most significant predator on ground-nesting birds in the Arctic (Petersen et al., 2015; Waltho & Coulson, 2015) and colonized Iceland before human settlement (Hersteinsson, 2004) and the invasive American mink (*Neogale vison*, hereafter mink), which was introduced to Iceland in 1932 and, like elsewhere in Europe (Jónsson, 2001; Nordström & Korpimäki, 2004; Stefánsson et al., 2016), has been detrimental for bird populations. Both fox and mink predate on eggs, chicks and breeding females, which can elicit nest site relocation (Dall, 1875; Petersen et al., 2015), delayed nest initiation or even nest abandonment (Chen, 2016; Jónsson, 2001).

A species of very high social-ecological relevance in Iceland is the common eider (*Somateria mollissima*, hereafter eider)—16% of its world population and 32% of its European population can be found in Iceland (BirdLife International, 2019), where it has undergone several episodes of population decline over the past century. These declines were documented by local people who have a strong cultural connection to the eider colonies. Eiderdown has been collected in Iceland for centuries, and numbers of nests per island are meticulously documented per year by local families (Chen, 2016). These citizen science data are highly valuable, due to the long

time periods they cover combined with their high quality. The families gathering these data do not only know their islands (which they typically own for generations) better than anyone but also the eider, their predators and other animals inhabiting the islands.

Here, we analysed these long-term data from two archipelagos within Breiðafjörður Bay in West Iceland, with one dataset covering 95 islands in the Brokey archipelago and the time period from 1892 to 2014 (123 years), and the other dataset covering 39 islands in the Purkey archipelago from 1986 to 2012 (27 years). These data allowed us to investigate the influence of the invasive mink and the native fox on eiders, as the dataset for Brokey covers time periods before and after the arrival of the mink in 1948, and the one for Purkey covers time periods before and after the return of the fox in 1994. Other predators of eiders in Breiðafjörður are the common raven (*Corvus corax*), gulls (*Larus* spp.) and white-tailed sea eagles (*Haliaeetus albicilla*). Previous studies have shown that the mink reduced bird populations on islands in Breiðafjörður, including those of eiders, black guillemot (*Cephus grylle*) and Atlantic puffin (*Fratercula arctica*; Ásgeirsson, 2011; Johannesson & Guðjonsdóttir, 2007; Stefánsson et al., 2016). One reason for these declines is that their evolved defences against the native fox are insufficient against the non-native mink. For example: nesting on more distant islands provides protection against the terrestrial fox (Schamel, 1977) but significantly less so against the aptly swimming mink (Björns-son & Hersteinsson, 1991; Jónsson, 2001). However, even though the mink is a recent colonizer of Breiðafjörður, it is possible that eiders already show some anti-predator responses.

Our goal was to investigate changes in eider nest numbers and distribution as a response to changes in climate and predator presence, comparing the effects of invasive mink versus native fox. Our research hypotheses and predictions were: (1) Bottom-up control of eiders: cooler temperatures in the sea around Iceland are related to more nutrients, which has a positive bottom-up effect on seabirds. Following this hypothesis, we predicted a negative correlation between eider nest numbers and AMO. (2) Top-down control by a novel predator: invasive mink are very efficient and impactful seabird predators in Iceland. They are capable of reaching remote islands and swimming in strong currents, which are both novel predator traits in this ecosystem. Following this hypothesis, we predicted eider nest numbers to be lower after the arrival of the mink in Iceland compared to the decades before. (3) Rapid response to a novel predator: while mink are efficient swimmers, it is possible that very remote islands may provide eiders a degree of safety, and large islands could provide safer nesting sites away from the sea, as mink tend to hunt in the intertidal zone rather than across the island. Following this hypothesis, we predicted more nests on (i) more remote and (ii) larger islands in Brokey after the arrival of the mink as compared

to before. (4) Retained response to a native predator: fox predation on islands is limited by geographic factors, which eiders can take advantage of. Islands can be far from the mainland; inaccessible to foxes due to strong tidal currents; large enough to enable colonial breeding, leading to a safety-in-numbers effect; or a combination of these. Following this hypothesis, for the Purkey archipelago we predicted that: (i) the proportion of eider nests on islands where one or more of these isolation factors are met to increase after the return of the fox; and (ii) total nest numbers to decrease less strongly compared to the mink's arrival in the Brokey archipelago.

MATERIALS AND METHODS

Data sources

Unique datasets exist about the eider populations in Iceland due to generations of meticulous documentation. Eider colonies are defined and censused/counted by ownership (Chen, 2016; Jónsson et al., 2013), which in our study corresponds to the two archipelagos Brokey and Purkey in the south-east of Breiðafjörður Bay in West Iceland (Figure S1, Björnsson et al., 1989; Jónsson et al., 2013). Each archipelago belongs to one family, and ownership did not change over our study period for either archipelago. Owners maintain their ancestral homes, that is, the Brokey and Purkey properties, for summer farming, such as small-scale sheep husbandry, traditional egg harvesting of gulls and eiderdown collection (Björnsson et al., 1989). We used nest counts done annually in a consistent manner in the field by the respective local eiderdown collectors (see Jónsson et al., 2013). The strategy was to collect a natural resource with optimal effort, and records were carefully kept. All islands were visited over the span of 1–2 weeks every breeding season each year, depending on weather and the number of people available. For Brokey and Purkey, nests were counted and located by 6–12 and 2–5 people per year, respectively. The only years missing were 1946–1950 in the Brokey archipelago. Later in the season, down was removed from the nests and replaced with hay, a procedure that has no negative impact on fledging success (Kristjánsson & Jónsson, 2011).

Icelandic eiderdown collectors commonly possess ecological knowledge about predators on and near their properties (Chen, 2016). We based our predator indices on interviews (our own and interviews with local eider farmers found in the Icelandic newspaper database timarit.is), personal accounts, and journals of land-owners in Brokey 1892–2014 and Purkey 1986–2012. Consequently, we were able to use precise presence/absence temporal data for the mink and the fox, specific to each archipelago. For Brokey, we marked all years prior to the well-documented mink introduction in 1948 as “mink absent” (0) and all subsequent years as “mink present” (1). For Purkey, the local

farmers reported that mink were ever-present 1986–2012, and thus, no mink index was employed for Purkey. The fox was absent in Purkey in the years from 1986 to 1993 (which we marked as “fox absent” (0)), and present in the years from 1994 to 2012 (which were marked as “fox present” (1)). There are 14 islands in Purkey that are not fox-accessible and were therefore marked as “fox-inaccessible” (0), while the other 25 islands were marked as “fox-accessible” (1). All inaccessible islands are located in the south-east of Purkey and are surrounded by strong tidal currents (Jón Helgi Jónsson of Purkey, pers. obs.).

For both the Brokey and Purkey archipelagos, we created complete and accurate maps which we publish along with this manuscript. Previously published maps of the area either had island or islet names missing or had smaller islands insufficiently labelled. Our maps were created in close collaboration with the families owning the islands and incorporating their knowledge on location and names, island by island. These maps were important to accurately assess the area of each island on which nests were counted.

The geographic data—linear distance from mainland and area-shoreline ratio of islands—were measured using the browser tool on map.is (2022). Linear distance from the mainland was used as a proxy of isolation from terrestrial predation analogous to Björnsson and Hersteinsson (1991). The area-shoreline ratio is the area in m² divided by the shoreline in m. This parameter provides us with a proxy of relative inland safety, with mink predation mostly occurring in the intertidal zone around the island (Ireland, 1990). Islands with a larger area-shoreline ratio are typically larger and provide eiders with more breeding ground away from the shore and therefore away from the typical mink foraging route.

The AMO data were retrieved from Trenberth and Zhang (2021).

Statistical analyses

For the analyses focusing on changes in nest numbers over time, we pooled for each year all nest counts from all islands in the Brokey archipelago for the period 1892–2014 and the Purkey archipelago for 1986–2012. We performed change-point analyses using these total nest numbers in each archipelago, with plateaus of a minimum length of 3 years and no overlapping confidence intervals. We used the commands `ts()`, `breakpoints()` and `confint()` of the `strucchange` package in R (Zeileis et al., 2003).

For the analyses focusing on nest-site changes, we fitted generalized linear mixed effects models with negative binomial error distribution to predict eider nest numbers per year per island in the Brokey archipelago (*model 1*) and Purkey archipelago (*model 2*), respectively. θ was approximated using intercept and random island effect. We tested for the relative safety that remote or

large islands could provide (hypotheses 3 and 4) by using distance from mainland (distanceFromMainland) and area-shoreline ratio (asRatio) of each island as fixed effects. Island was used as a random effect in both models.

The Atlantic Multidecadal Oscillation index (AMO) was used in the Brokey archipelago, but not in Purkey because the latter timeline (27 years) was too short for the AMO's 50–70-year cycle. The presence of mink (minkPresent) was a fixed effect for *model 1*. We controlled for a potential interaction between AMO and mink arrival, as the role of AMO could shift for the eider due to indirect effects, although we do not currently have a defined hypothesis for this. Thus, the interactions of minkPresent with AMO, asRatio and distanceFromMainland were fixed effects in *model 1* for Brokey, and island was a random effect:

Model 1: BrokeyNests ~ minkPresent + AMO
+ asRatio + distanceFromMainland
+ minkPresent: AMO + minkPresent: asRatio
+ minkPresent: distanceFromMainland + (1 | island)

In *model 2* for Purkey, the return of the fox (foxPresent) was used instead of the mink's arrival. In addition to distance from mainland and island shape (asRatio) as isolation factors, we used fox accessibility (foxAccessible), which accounts for strong tidal currents running between islands making them inaccessible to the fox. To test the predictions outlined in hypothesis 4 in the Introduction, we included interactions of foxPresent and the three isolation factors foxAccessible, asRatio and distanceFromMainland in *model 2*. Island was again included as a random effect:

Model 2: PurkeyNests ~ foxPresent + foxAccessible
+ asRatio + distanceFromMainland
+ foxPresent: foxAccessible + foxPresent: asRatio
+ foxPresent: distanceFromMainland + (1 | island)

θ was approximated using the glm.nb() and theta.md() commands of the MASS package (Venables & Ripley, 2002). Models were fitted using the glmer() command of the lme4 package (Bates et al., 2015), and model comparisons were performed using the dredge() command of the MuMIn package (Barton, 2009).

RESULTS

Brokey

There was a total of eight change points in the common eider nest numbers within Brokey from 1892 to 2014 (Figure 1). After the increase beginning in 1896, nest numbers were highest in the early 20th century, followed by a series of declines, beginning in 1917, 1933, 1939, 1953 and 1970, reaching the lowest numbers around 1980. In 1985, nest numbers increased again from under 500 to more than 1000, followed by another, smaller decline in 2001.

Model comparisons revealed that one model was clearly best supported by the data, with an AIC weight of 0.929 and a Δ -AIC for the second-best model of 5.15 (Table 1). The marginal and conditional R^2 values of this best-supported model were 0.40 and 0.54, respectively. In support of our Bottom-up control hypothesis (H1), AMO was negatively correlated to overall nest numbers in Brokey before the arrival of the mink. There was a significant interaction between AMO and mink presence, as the correlation of AMO and nest numbers was positive after the arrival of the mink (Figure 1). Consistent with the Top-down control hypothesis (H2), nest numbers decreased with the arrival of the mink. Islands closer to the shore and smaller in size suffered greater losses (Table 1; Figure 2), supporting our Novel predator rapid response hypothesis (H3) that large remote islands provided relative safety from mink predation.

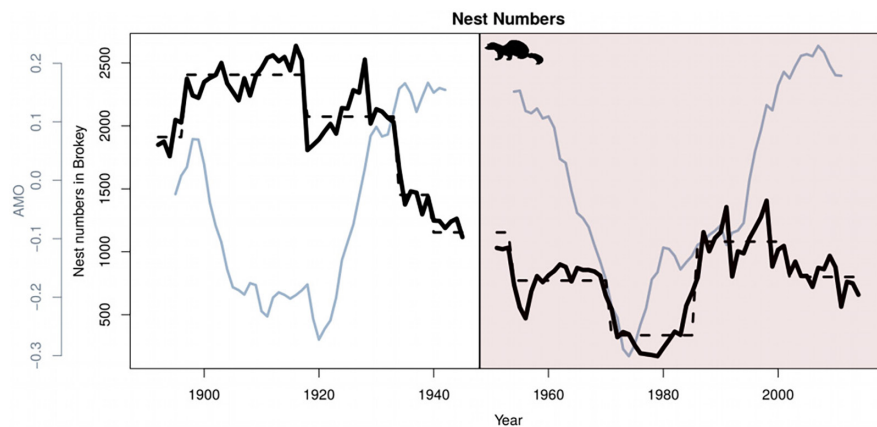


FIGURE 1 Total eider nest changes in the Brokey archipelago from 1892 to 2014 (solid black line). Dashed black line shows stable periods and change points. The solid grey line indicates the smoothed Atlantic Multidecadal Oscillation index (AMO). The arrival of the mink in 1948 is indicated by the pictogram and the red background.

TABLE 1 The results of model comparisons among all combinations for the Brokey archipelago (*model 1*). Shown are models with an accumulated AIC weight of >0.95.

Model (fixed effects)	AIC _c	Δ-AIC	AIC weight	Deviance	logLik
-minkPresent -AMO+asRatio (-distanceFromMainland) + minkPresent:AMO + minkPresent:asRatio +minkPresent:distanceFromMainland	52718.9	0.0	0.941	52,698.9	-26,349.5
-minkPresent -AMO+asRatio (-distanceFromMainland) + minkPresent:AMO + minkPresent:distanceFromMainland	52724.5	5.54	0.059	52,706.5	-26,353.2

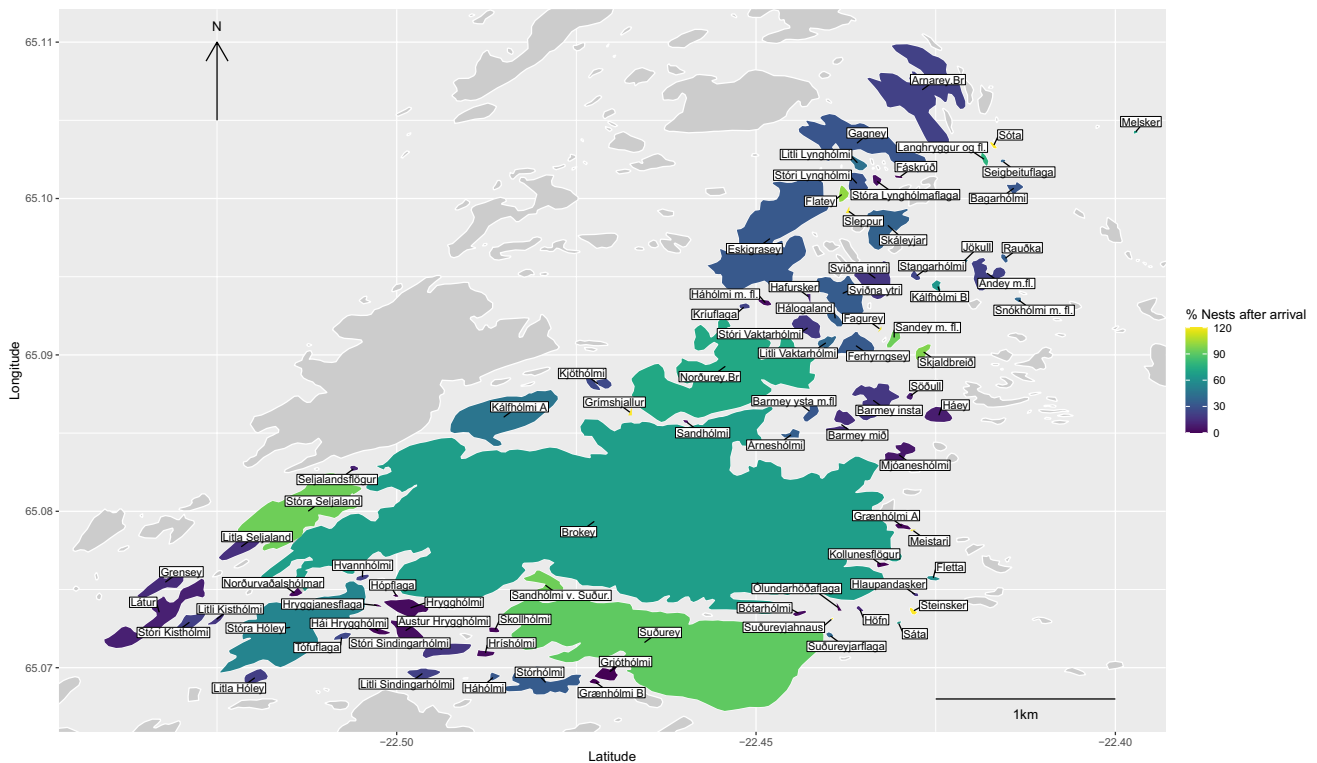


FIGURE 2 Percentage of average yearly nest numbers after the arrival of the American mink in the Brokey archipelago, indicated separately for each of the 95 islands. Dark blue shades indicate heavier losses, while green shades and yellow shades indicate constant numbers or even a mild increase. The direct distance to the mainland from the southernmost point of Suðurey southward is 2 km. The direct distance to the mainland from the northernmost point of Arnarey Br. northward is 4 km. We therefore expect the typical route of access for the mink into the archipelago to be from the mainland in the south.

Purkey

In contrast to Brokey, total nest numbers in Purkey increased over the observed period 1986–2012. The overall nest numbers increased after 1990 and remained at that level, despite the return of fox to the archipelago in 1994 (Figure 3).

Nests were more evenly distributed across fox-accessible and fox-inaccessible islands of different sizes before the return of the fox (Figure 4 and Table 2). The best model had marginal and conditional R^2 values of 0.15 and 0.26, respectively. In support of our Native predator retained response hypothesis (H4), fox-accessible islands suffered massive declines, whereas fox-inaccessible islands increased in nest counts after the return of the fox in 1994. In three of the four best-supported models, there was a negative interaction between the return of the

fox and area-shoreline ratio (Table 2). This means that nest numbers were higher on islands with a large area-shoreline ratio, but significantly less so in presence of the fox. In contrast to Brokey, the distance from mainland was never a significant predictor of nest numbers in Purkey, neither was the interaction between distance to mainland and the return of the fox.

DISCUSSION

Our results suggest that eiders in Breiðafjörður select their nest sites depending on predator presence. We detected an apparently adaptive response to the return of the native fox in the Purkey archipelago, with dense nests on islands inaccessible to the fox and no apparent impact on eider populations. Conversely, the arrival

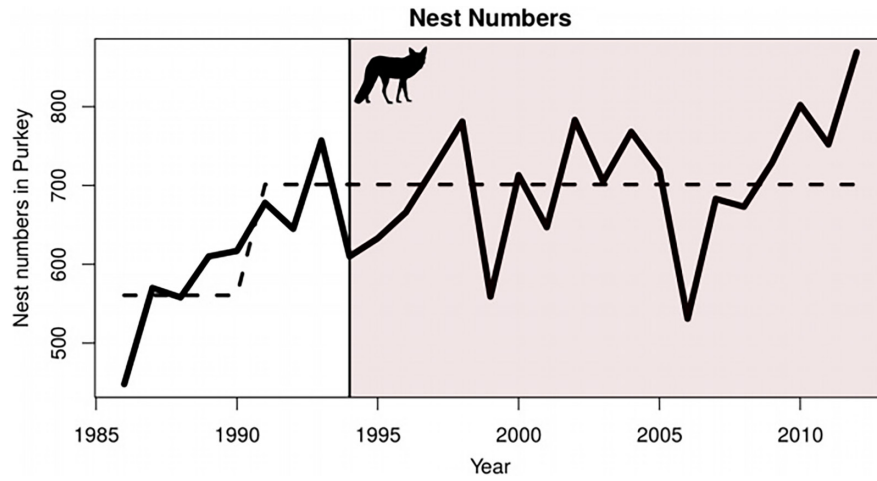


FIGURE 3 Total nest numbers in the Purkey archipelago from 1986 to 2012 (solid black line). The change point in the year 1990 is indicated (dashed black line). The return of the arctic fox in 1994 is highlighted in red.

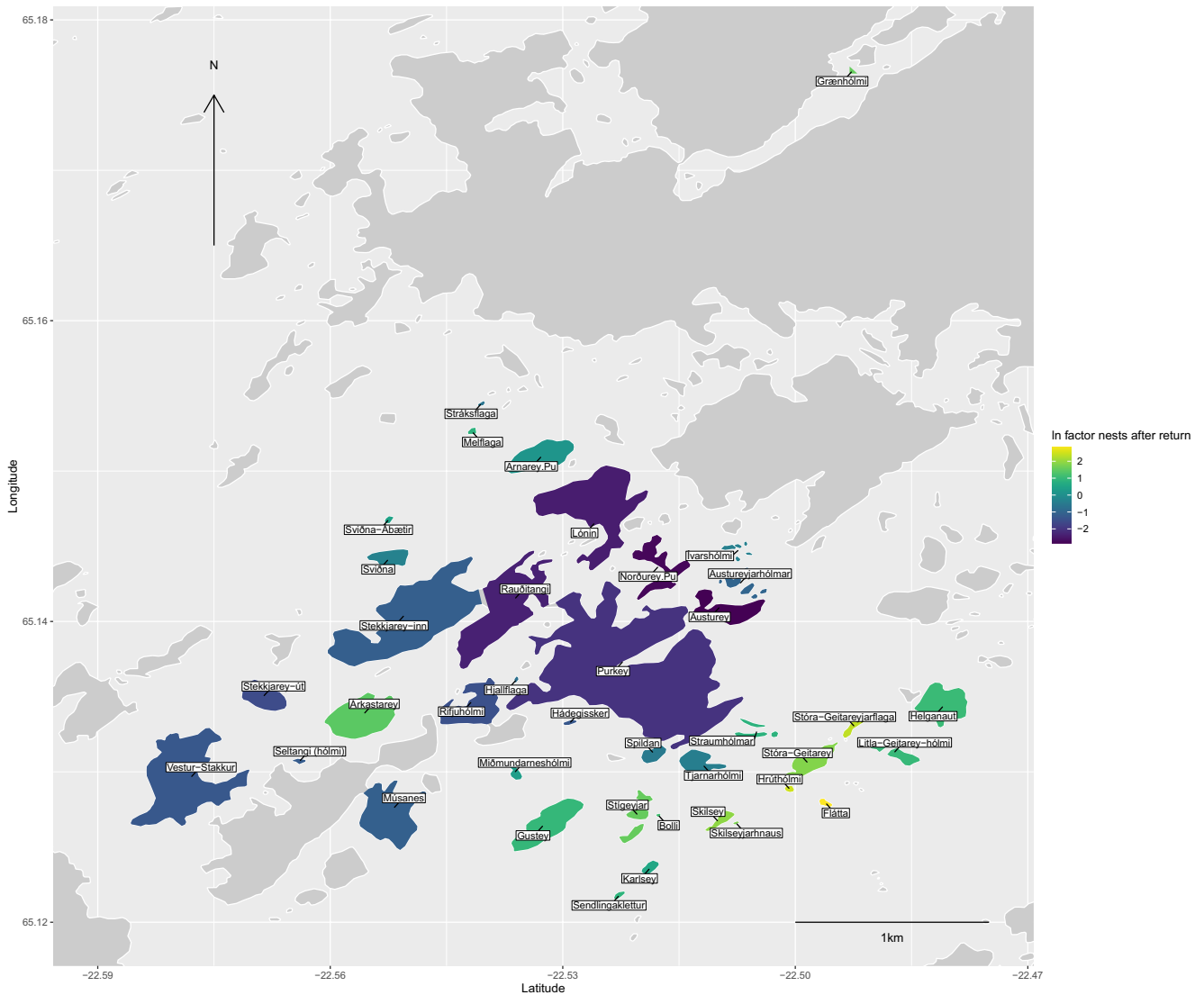


FIGURE 4 The \ln (natural logarithm) of the change in yearly nest numbers in the Purkey archipelago after the return of the arctic fox, indicated for each of the 39 islands. Dark blue shades indicate losses, green shades stable populations and yellow shades show increasing numbers.

TABLE 2 The results of model comparisons among all combinations for the Purkey archipelago (*model 2*). Shown are models with an accumulated AIC weight of >0.95.

Model (fixed effects)	AICc	Δ-AIC	AIC weight	Deviance	logLik
foxPresent +foxAccessible +asRatio -foxPresent:foxAccessible -foxPresent:asRatio	7181.7	0.0	0.628	7165.7	-3582.8
foxPresent +foxAccessible +asRatio (-distanceFromMainland) -foxPresent:foxAccessible -foxPresent:asRatio	7183.7	2.03	0.227	7165.7	-3582.8
foxPresent +foxAccessible +asRatio (-distanceFromMainland) -foxPresent:foxAccessible -foxPresent:asRatio (-foxPresent:distanceFromMainland)	7185.6	3.96	0.087	7165.6	-3582.8
foxPresent +foxAccessible +asRatio -foxPresent:foxAccessible	7187.3	5.55	0.04	7173.3	-3586.6

of the invasive and semi-aquatic mink in the Brokey archipelago heavily reduced eider numbers. As a good swimmer, this opportunistic predator can reach remote breeding grounds. We discuss how the discrepancy in impact between the fox and the mink on eiders may be related to environmental conditions, predator traits—which often render invasive predators more dangerous than native ones (Salo et al., 2007)—or differences in shared evolutionary history between predators and prey. The discrepancy remains after correcting for bottom-up effects on eider population dynamics using the AMO.

Long-term nest number fluctuations in Brokey

The AMO is used to capture cyclic changes that can have profound effects on ecosystems (Trenberth & Zhang, 2021), and we found evidence for the Bottom-up control hypothesis of eiders, as climate-driven resource availability partly drives eider nest dynamics in Brokey over the 123 years of study. While there are effects on algal blooms, zooplankton and fish abundance (Drinkwater & Kristiansen, 2018), the population effects on bird species need to be better understood (Nye et al., 2014). The increased oceanic productivity in warm AMO regimes could be projected to translate into higher bird numbers, but this has, for example, not been found in great cormorant (*Phalacrocorax carbo*) abundance in Iceland (Gardarsson & Jónsson, 2019). However, for the Atlantic puffin population of the Westman Islands in Iceland, the correlation of puffin numbers and AMO was shown to be an important driver from 1880 to 2000—a study period comparable to ours (Hansen et al., 2021). We detected one similar shift: eider nests were negatively correlated to AMO from 1892 until the late 1940s, followed by a positive correlation until the end of our observation period in 2014. So, in order to understand the role of AMO for the eider, it is necessary to look at extreme weather events and dynamics of other species in the ecosystem, both of which we discuss below.

Effects of AMO on eider nest numbers can be classified into three types. First, the direct effect of extreme weather events as seen in the low AMO period in the beginning of the 20th century. In 1918, the coldest January and June in Iceland to date were measured

(Anonymous, 1918), and mass deaths of live-stock and wildlife were reported, including of eiders, oystercatchers (*Haematopus ostralegus*) and whooper swans (*Cygnus cygnus*; Arnþórsson, 1979; Ásgeirsson & Jónsson, 2017; Guðmundsson, 1918).

Second, the bottom-up effect of AMO on eider populations through prey availability. Blue mussels (*Mytilus edulis*), for example, are the eiders' preferred prey item throughout their range (Waltho & Coulson, 2015) and attain a greater soft body mass in colder years (Waldeck & Larsson, 2013). Also the southward migration of cold-water species such as the capelin (*Mallotus villosus*) into Icelandic waters in low AMO years can provide resources for the eider, as was the case in the 1980s when capelin fisheries were at a record high in Iceland (Jónsson, 2017).

Third, eider nest numbers may be influenced indirectly by AMO via top-down predator numbers. Nest numbers decreased significantly in Brokey, from occasionally surpassing 2500 nests per year to consistently staying below 1500 nests per year after the mink's arrival (Figure 1). Even the relationship of long-term climate fluctuations (in the form of the AMO) and eider nest numbers changed from negative to positive. At this stage, we cannot formulate a clear hypothesis for this sign change, but a possible explanation would be the relationship of alternative prey of mink with AMO, indirectly increasing predation pressure on eiders in low AMO years. Presence of humans on the Breiðafjörður islands provided some protection to the colonies, but farms were abandoned in the middle of the 20th century with the numbers of farms in operation decreasing over the years 1942, 1960 and 1972 to 26, 8 and 3 farms, respectively (Anonymous, 1960; Anonymous, 1975; Björnsson et al., 1989). These years fall within the period of most severe eider nest losses, potentially exacerbated by a delay in eiders changing their nest site in response to this novel invasive predator.

Nest-site changes in response to an invasive and a native predator

What makes the mink a novel and dangerous predator is primarily its swimming capabilities, but also that it

is a generalist evolutionarily adapted to predate ducks and other ground-nesting birds within its native range. It is difficult for ground-nesting birds to defend against such a predator, especially in an archipelago like Brokey where islands are easily accessible from the sea, there are few cliffs that would offer protection, and no tidal currents within the archipelago like the ones in Purkey. We believe that this is how overall nest numbers declined with the arrival of the mink (Top-down control hypothesis). Our study shows how the invasive mink versus native fox affected eider nest numbers and locations, potentially triggered in part by different behavioural responses in the nesting behaviour of the eider. We discuss which factors limited the eider's range of options and if its low eco-evolutionary experience (sensu Saul & Jeschke, 2015) with mink played a role.

In line with our Novel predator rapid response hypothesis, eider nests disappeared from mink-prone islands and nest numbers rose on islands that provide relative safety (Figure 2). We believe this was caused by two factors, the direct predation of eider nests and the associated disturbance, and the resulting relocation of nest sites by conspecifics, much like what is observed in shags responding to mink invasion (Barros et al., 2016). Björnsson and Hersteinsson (1991) reported that fewer mink were found on islands further from the shore, and we were able to show how this translates into relatively lower predation and higher nest numbers on such islands. Similarly, the path a mink takes, circling an island in the intertidal zone to forage for marine and terrestrial prey, drives eiders to choose islands with a larger area-shoreline ratio instead of islands with easier sea access, which they usually prefer. Again, this change in nest locations only slightly reduces predation risk, as mink sometimes do cross large islands. Predation on small islands and subsequent recruitment of young on large and remote islands alone cannot explain the initial decrease and subsequent rise of nest numbers from 1953 to 1960. Many ecological factors changed since the beginning of the observation period in the end of the 19th century, including prey abundance and human activities. We provide evidence for our Top-down control hypothesis, that despite those factors, the arrival of the mink has had a particularly strong impact on eiders, decreasing their colony densities to well below levels prior to mink settlement.

The concept of prey naïveté to invasive predators further helps us to understand the eider-mink interaction (Banks & Dickman, 2007). Level-1 naïveté means that the native prey does not recognize the invasive predator as a threat. Level-2 naïveté triggers an inappropriate antipredator response and level-3 naïveté an appropriate response that is, however, outperformed by the predator (e.g. prey that is outrun by a faster predator). In our case, we can see the limited success that eiders have with relocating their nests as either level-2 or level-3 naïveté

with different implications. Either relocation of nest sites is not an effective strategy against the swimming mink, in which case we would describe eiders as being level-2 naïve. Or it is a case of level-3 naïveté, where relocation is the appropriate response, but eiders would have to relocate their nest sites even further to be safe from mink predation.

The naïveté of the eider in interacting with the mink can be framed within the concept of eco-evolutionary experience (Saul & Jeschke, 2015). If the invasive predator species possesses a novel trait, like in the mink's case its apt swimming skills, the native prey species has low eco-evolutionary experience and is more risk prone: The invasive predators that native prey are interacting with are often generalists with respect to the prey they hunt, and thus changes in prey choice or predation strategy by invasive predators are often fast; at the same time, changes in defence mechanisms of native prey typically need much more time to emerge, frequently many generations (Ruland & Jeschke, 2020). The mink even has an evolutionary history with ducks, even with some of the eider's North American populations in sub-arctic or temperate regions, whereas the Icelandic eiders of the subspecies *Somateria mollissima borealis* have not come into contact with the mink before its arrival (Baldassarre, 2014). Our focal predator-prey system is thus an example of a high-risk novel interaction (sensu Saul & Jeschke, 2015) in which the native species (the eider) has a low eco-evolutionary experience with the invasive species (the mink), whereas the invasive species has a high eco-evolutionary experience with the native species. The decline in eider nest numbers may therefore be explained by a combination of: (1) the insufficient eider defence behaviour, as nests in Brokey were not completely safe against mink predation; and (2) the mink having immediately recognized eiders as prey and feeding on them upon its arrival in Iceland, while eiders were only slowly adapting to this novel predator.

In contrast to the mink, the arctic fox is a predator known to the eider throughout their joint circumpolar range. In Purkey, most islands are accessible to the fox, but 11 islands are fox-inaccessible. These latter islands are not separated by linear distance from the mainland, but two deep channels with strong tidal currents (Stangarstraumur and Knarrbrjótur, Figure 4). In line with hypothesis 4, eider nest density increased on these inaccessible islands after the fox returned to the archipelago, while overall nest numbers in Purkey did not decrease. We observed losses in nest numbers in Brokey after the arrival of the mink, but not in Purkey after the return of the fox. While nest locations changed in both archipelagos, there was an increase in the proportion of nests on large islands in Brokey since the arrival of the mink, whereas such an increase was observed for Purkey on fox-inaccessible islands since the return of the fox.

Eiders are typically consistent in their nest choice, but the capacity to relocate the nest site between breeding seasons certainly exists (Öst et al., 2011). We therefore believe that the shift in nest numbers from fox-exposed to safe islands is caused by a combination of nests disappearing due to predation and associated disturbance on fox-accessible islands, and conspecifics migrating their nests as a consequence to fox-inaccessible islands. Eiders often breed gregariously as a defence against predation (dilution effect and early warning against predators; Öst et al., 2002). These very dense colonies are more prone to parasitism, but cooperative breeding—as observed in Rif, also part of Breiðafjörður—can leave females more breeding recesses and therefore time to preen their feathers (Kristjánsson & Jónsson, 2015). This means that eiders tend to copy the nest-site choice of conspecifics. The fox was absent for ca. 20 years, which is around the lifespan of most female common eiders and below their maximum lifespan (Fransson, 2010). After the fox's return, fox-accessible islands were deserted within ca. 5 years. During this period, young eider females could have copied the nest-site choice of older females that knew the fox hunting range from before. Alternatively, these changes could have been due to: (i) eiders shifting islands based on trial and error until they found a fox-inaccessible island to breed on undisturbed for several years or (ii) increasing hunting pressure on fox-accessible islands by a growing fox population in Purkey. In either case, eider nests will still be observed even on fox-accessible islands, as the fox does not completely wipe out colonies. Conversely, it also took several years for eiders to return to islands after the fox disappeared (Páll Hjaltalín, pers. comm.). To ultimately answer these questions, detailed capture-recapture studies are needed, which were not conducted in Purkey or Brokey during the study period.

Conclusions

Our findings suggest that eiders and other native bird species in Iceland will not be able to protect themselves against mink predation by nest-site choice and colonial breeding. The novelty of the invasive mink—primarily its swimming capability—puts pressure on eider populations that is not ameliorated by evolutionarily acquired antipredator defences. This has implications for conservation management and suggests continuing control measures against the mink, which have proven to be effective in other locations (Jaatinen et al., 2022). Further, our results highlight an imbalance in predator–prey dynamics in biological invasions and how thereby threatened species can be evolutionarily constrained to adjust to their novel interaction partners in time, or simply not able to cope with the new predator's abilities except in a narrow set of geographical conditions. Finally, this study is an example of how exceptional datasets provided by

citizen scientists can improve our understanding of long-term population dynamics in the Anthropocene.

AUTHOR CONTRIBUTIONS

JEJ: Conceptualization, Data Curation, Funding Acquisition, Investigation, Resources, Supervision, Writing—Original Draft Preparation, Writing—Review & Editing; FSR: Data Curation, Formal Analysis, Investigation, Methodology, Visualization, Writing—Review & Editing; FR: Formal Analysis, Investigation, Methodology, Visualization, Writing—Original Draft Preparation, Writing—Review & Editing; ÁÁ: Investigation, Writing—Review & Editing; MJM: Conceptualization, Funding Acquisition, Resources, Supervision, Writing—Review & Editing.

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DATA AVAILABILITY STATEMENT

Underlying data and code are available from the Dryad Digital Repository at <https://doi.org/10.5061/dryad.7m0cfxpzh>.

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REFERENCES

- Alheit, J., Licandro, P., Coombs, S., Garcia, A., Giráldez, A., Santamaria, M.T. et al. (2014) Reprint of “Atlantic multidecadal oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern north and Central Atlantic”. *Journal of Marine Systems*, 133, 88–102.
- Alvarez-Fernandez, S., Lindeboom, H. & Meesters, E. (2012) Temporal changes in plankton of the North Sea: community shifts and environmental drivers. *Marine Ecology Progress Series*, 462, 21–38.
- Anonymous. (1918) Óáran við Breiðafjörð [A bad year for Breiðafjörður]. Morgunblaðið. Icelandic. Available at: http://timarit.is/view_page_init.jsp?issId=98451&pageId=1203195&lang=is&q=Kafb%Eltsminnismarki%20%ED%20Kiel
- Anonymous. (1960) Eggjatekja góð á Breiðafjarðareyjum. [Good egg harvest in Breiðafjörður islands]. *Morgunblaðið*. Icelandic. Available at: http://timarit.is/view_page_init.jsp?issId=111253&pageId=1328710&lang=is&q=%E1%20Brei%F0afjar%F0areyjum%20g%F3%F0
- Anonymous. (1975) Hvallátur í eyði—aðeins þrjár Breiðafjarðareyjar eftir í byggð. [farm in Hvallátur abandoned—only three Breiðafjörður Islands remain inhabited] *Tíminn*. Icelandic. Available at: http://timarit.is/view_page_init.jsp?issId=27089

- 6&pageId=3864840&lang=is&q=%ED%20Hva11%Eltur%20%ED%20ey%F0i%20%ED
- Arnþórsson, G. (1979) 40–100 minkar drepnir á ári í Brokey á Breiðafirði [interview with eider farmer Jón Hjaltalín of Brokey]. Alþýðublaðið, Icelandic. Available at: http://timarit.is/view_page_init.jsp?issId=236380&pageId=3223150&lang=is&q=40--100%20minkar%20drepnir
- Ásgeirsson, Á. (2011) Breytingar og faersla lunda á sudursvaedi Breidafjardar. *Fuglar*, 8, 44–46.
- Ásgeirsson, Á. & Jónsson, J.E. (2017) Heyskapur, dúntekja og kofnar í Rifgirðingum í byrjun 20. Aldar [haying, down collection and puffin harvest in Rifgirðingar in the early 20th century]. *Breiðfirðingur*, 65, 60–64.
- Baldassarre, G. (2014) *Ducks, geese, and swans of North America*. Baltimore, MD: JHU Press.
- Banks, P.B. & Dickman, C.R. (2007) Alien predation and the effects of multiple levels of prey naiveté. *Trends in Ecology & Evolution*, 22(5), 229–230.
- Barros, Á., Romero, R., Munilla, I., Pérez, C. & Velando, A. (2016) Behavioural plasticity in nest-site selection of a colonial seabird in response to an invasive carnivore. *Biological Invasions*, 18(11), 3149–3161.
- Barton, K. (2009) Mu-MIn: Multi-model inference. *R Package Version 0.12.2/r18*. Available at: [<http://R-Forge.R-project.org/projects/mumin/>]
- Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 24–25.
- BirdLife International. (2019) Species factsheet: Somateria mollissima. Available at: [<http://www.birdlife.org>]
- Björnsson, Á., Gíslason, E.G. & Petersen, Æ. (1989) Breiðafjarðareyjar [Islands of Breiðafjörður]. In: *Árbók Ferðafélags Íslands [yearbook of the Iceland touring association]*. Reykjavík: Ferðafélag Íslands. Icelandic.
- Björnsson, T. & Hersteinsson, P. (1991) Minkar við sunnanverdan Breidafjord [Mink in southern Breidafjordur Bay, W-Iceland]. *Wildlife Management News*, 7, 3–12.
- Blumstein, D.T. & Daniel, J.C. (2005) The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B: Biological Sciences*, 272, 1663–1668.
- Carpenter, J.K., Innes, J.G., Wood, J.R. & Lyver, P.O.B. (2021) Good predators: the roles of weka (*Gallirallus australis*) in New Zealand's past and present ecosystems. *New Zealand Journal of Ecology*, 45(1), 1–14.
- Chen, G. (2016) Ethnoecology of eider farmers in Iceland: typology of a multiform experience [master thesis]. Joint program with the French National Museum of Natural History and the Paris-Sorbonne University. French with an English summary. Available at: http://rannsoknasetur.hi.is/sites/rannsoknasetur.hi.is/files/pdfs_snaefellsnes/report_english_gilles_25_april.pdf
- Dall, W.H. (1875) Notes on the avifauna of the Aleutian Islands, especially those west of Unalaska. *Proceedings of the California Academy of Sciences*, 5, 270–281.
- Drinkwater, K.F. & Kristiansen, T. (2018) A synthesis of the ecosystem responses to the late 20th century cold period in the northern North Atlantic. *ICES Journal of Marine Science*, 75(7), 2325–2341.
- Dueñas, M.A., Hemming, D.J., Roberts, A. & Diaz-Soltero, H. (2021) The threat of invasive species to IUCN-listed critically endangered species: a systematic review. *Global Ecology and Conservation*, 26, e01476.
- Fransson, T. (2010) EURING list of longevity records for European birds. Available at: [http://www.euring.org/data_and_codes/longevity-voous.html]
- Gardarsson, A. & Jónsson, J.E. (2019) Numbers and distribution of the great cormorant in Iceland: limitation at the regional and metapopulation level. *Ecology and Evolution*, 9(7), 3984–4000.
- Gerell, R. (1985) Habitat selection and nest predation in a common eider population in southern Sweden. *Ornis Scandinavica*, 1, 129–139.
- Greig, K. & Rawlence, N.J. (2021) The contribution of kurī (*Polynesian dog*) to the ecological impacts of the human settlement of Aotearoa New Zealand. *Frontiers in Ecology and Evolution*, 9, 757988.
- Guðmundsson, G. (1918) Af Barðaströnd. *Fréttir*. Icelandic. Available at: [http://timarit.is/view_page_init.jsp?pubId=179&lang=is]
- Hansen, E.S., Sandvik, H., Erikstad, K.E., Yoccoz, N.G., Anker-Nilssen, T., Bader, J. et al. (2021) Centennial relationships between ocean temperature and Atlantic puffin production reveal shifting decennial trends. *Global Change Biology*, 27(16), 3753–3764.
- Hátún, H., Lohmann, K., Matei, D., Jungclaus, J.H., Pacariz, S., Bersch, M. et al. (2016) An inflated subpolar gyre blows life toward the northeastern Atlantic. *Progress in Oceanography*, 147, 49–66.
- Hersteinsson, P. (Ed.). (2004) *Spendýr [mammals of Iceland]*. Reykjavík: Vaka-Helgafell. Icelandic.
- IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services). (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Available at: [<https://ipbes.net/global-assessment>]
- Ireland, M.C. (1990) The behaviour and ecology of the American mink *Mustela vison* (Schreber) in a coastal habitat. (Doctoral dissertation, Durham University).
- Jaatinen, K., Hermansson, I., Mohring, B., Steele, B.B. & Öst, M. (2022) Mitigating impacts of invasive alien predators on an endangered sea duck amidst high native predation pressure. *Oecologia*, 198(2), 543–552.
- Johannesson, J.H. & Guðjónsdóttir, B. (2007) The effect of mink-predation on six monitored black guillemot colonies in Strandasysla, NW-Iceland. *Naturufraeðingurinn*, 76, 29–36.
- Jónsson, J. (2001) Æðarfugl og æðarrækt. [Eider and eider husbandry in Iceland]. Reykjavík: *Skrúdda*. Icelandic.
- Jónsson, J.E. (2017) Eru tengsl milli æðarvarps og loðnugengdar? *Náttúrufræðingurinn*, 87, 45–51 Icelandic with an English summary.
- Jónsson, J.E., Gardarsson, A., Gill, J.A., Pétursdóttir, U.K., Petersen, A. & Gunnarsson, T.G. (2013) Relationships between long-term demography and weather in a sub-arctic population of common eider. *PLoS One*, 8(6), e67093.
- Kristjánsson, T.Ö. & Jónsson, J.E. (2011) Effects of down collection on incubation temperature, nesting behaviour and hatching success of common eiders (*Somateria mollissima*) in West Iceland. *Polar Biology*, 34(7), 985–994.
- Kristjánsson, T.O. & Jónsson, J.E. (2015) Cooperative incubation behaviour in a super dense common eider *Somateria mollissima* colony. *Bird Study*, 62(1), 146–149.
- Macinnis-Ng, C., Mcintosh, A.R., Monks, J.M., Waipara, N., White, R.S.A., Boudjelas, S. et al. (2021) Climate-change impacts exacerbate conservation threats in Island systems: New Zealand as a case study. *Frontiers in Ecology and the Environment*, 19(4), 216–224.
- map.is. (2022) Loftmyndir ehf. Available at: [<https://map.is/>] Last accessed 26 January 2022
- Murphy, E.J., Trathan, P.N., Watkins, J.L., Reid, K., Meredith, M.P., Forcada, J. et al. (2007) Climatically driven fluctuations in Southern Ocean ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 274(1629), 3057–3067.
- Nordström, M. & Korpimäki, E. (2004) Effects of Island isolation and feral mink removal on bird communities on small islands in the Baltic Sea. *Journal of Animal Ecology*, 73(3), 424–433.
- Nye, J.A., Baker, M.R., Bell, R., Kenny, A., Kilbourne, K.H., Friedland, K.D. et al. (2014) Ecosystem effects of the Atlantic multidecadal oscillation. *Journal of Marine Systems*, 133, 103–116.
- Öst, M., Lehtikoinen, A., Jaatinen, K. & Kilpi, M. (2011) Causes and consequences of fine-scale breeding dispersal in a female-philopatric species. *Oecologia*, 166, 327–336.

- Öst, M., Mantila, L. & Kilpi, M. (2002) Shared care provides time-budgeting advantages for female eiders. *Animal Behaviour*, 64(2), 223–231.
- Pergl, J., Pyšek, P., Essl, F., Jeschke, J.M., Courchamp, F., Geist, J. et al. (2020) Need for routine tracking of biological invasions. *Conservation Biology*, 34, 1311–1314.
- Petersen, M.R., Byrd, G.V., Sonsthagen, S.A. & Sexson, M.G. (2015) Re-colonization by common eiders *Somateria mollissima* in the Aleutian archipelago following removal of introduced arctic foxes *Vulpes lagopus*. *Journal of Avian Biology*, 46(5), 538–549.
- Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T. et al. (2020) Scientists' warning on invasive alien species. *Biological Reviews*, 95, 1511–1534.
- Robertson, H.A., Baird, K.A., Elliott, G., Hitchmough, R., McArthur, N., Mekan, T. et al. (2021) *Conservation status of birds in Aotearoa New Zealand, 2021*. Wellington, New Zealand: Department of Conservation, Te Papa Atawhai.
- Ruland, F. & Jeschke, J.M. (2020) How biological invasions affect animal behaviour: a global, cross-taxonomic analysis. *Journal of Animal Ecology*, 89(11), 2531–2541.
- Salo, P., Korpimäki, E., Banks, P.B., Nordström, M. & Dickman, C.R. (2007) Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B: Biological Sciences*, 274(1615), 1237–1243.
- Saul, W.-C. & Jeschke, J.M. (2015) Eco-evolutionary experience in novel species interactions. *Ecology Letters*, 18(3), 236–245.
- Sayers, D.L. (1935) *Gaudy night: a Lord Peter Wimsey mystery with Harriet vane*. Glasgow, UK: Olive Editions.
- Schamel, D. (1977) Breeding of the common eider (*Somateria mollissima*) on the Beaufort Sea coast of Alaska. *The Condor*, 79(4), 478–485.
- Stefánsson, R.A., von Schmalensee, M. & Skorupski, J. (2016) A tale of conquest and crisis: invasion history and status of the American mink (*Neovison vison*) in Iceland. *Acta Biologica*, 23, 87–100.
- Strayer, D.L., Eviner, V.T., Jeschke, J.M. & Pace, M.L. (2006) Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, 21(11), 645–651.
- Trenberth, K. & Zhang, R. (2021) The Climate Data Guide: Atlantic Multi-decadal Oscillation (AMO). Retrieved from: <https://climatedataguide.ucar.edu/climate-data/atlantic-multi-decadal-oscillation-amo>. Last accessed 05 Jun 2021.
- Venables, W.N. & Ripley, B.D. (2002) *Modern applied statistics with S*, Fourth edition. New York, NY: Springer.
- Waldeck, P. & Larsson, K. (2013) Effects of winter water temperature on mass loss in Baltic blue mussels: implications for foraging sea ducks. *Journal of Experimental Marine Biology and Ecology*, 444, 24–30.
- Waltho, C. & Coulson, J. (2015) *The common eider*. London, UK: Bloomsbury Publishing.
- Zeileis, A., Kleiber, C., Krämer, W. & Hornik, K. (2003) Testing and dating of structural changes in practice. *Computational Statistics & Data Analysis*, 44(1–2), 109–123.

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