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CONSERVATION ECOLOGY – ORIGINAL RESEARCH

Mitigating impacts of invasive alien predators on an endangered sea duck amidst high native predation pressure

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Abstract

Anthropogenically introduced invasive species represent a major threat to global biodiversity by causing population declines and extinctions of native species. The negative impacts of introduced predators are well documented, yet a fundamental knowledge gap exists regarding the efficiency of potential mitigation methods to restore the ecosystem. Other understudied aspects concern prey behavioural antipredator responses and the historical context of native predator–prey interactions, which may moderate invasion impacts on native prey. Invasion impacts of American mink (*Neovison vison*) and raccoon dog (*Nyctereutes procyonoides*) into the Baltic Sea archipelago are poorly understood, and the efficiency of removal efforts as a means to alleviate depredation pressure on native prey is debated. Here, we examine the effectiveness of invasive predator removal on ground-nesting female common eider (*Somateria mollissima*) mortality, breeding success and breeding propensity over a 9-year period, while controlling for predation risk imposed by the main native predator, the white-tailed eagle (*Haliaeetus albicilla*). Our results clearly show that intensified removal of American minks and raccoon dogs decreased the number of female eiders killed during nesting, while improving both nesting success and breeding propensity. Such obvious positive effects of invasive predator removal are particularly noteworthy against the backdrop of a soaring eagle population, indicating that the impacts of invasives may become accentuated when native predators differ taxonomically and by hunting mode. This study shows that invasive alien predator removal is an effective conservation measure clearly aiding native fauna even under severe native predation pressure. Such cost-effective conservation actions call for governmental deployment across large areas.

Keywords Avian conservation · Invasive species · Predator control · Ecosystem restoration · Common eider

Introduction

Anthropogenically introduced invasive species are one of the major threats to biodiversity on Earth (Tilman et al. 2017). Once invasive species succeed in establishing viable populations, they may become extremely abundant causing a dramatic increase in predation or competition, leading to population declines and extinctions (Allendorf et al. 2003; Doherty et al. 2016). Although negative impacts of introduced predators have been well documented, we understand little about why some native prey species can, and others cannot, cope with alien predators (Ehlman et al. 2019). A significant knowledge gap also relates to the efficiency of potential mitigation methods to restore the ecosystem (McGeoch and Jetz 2019), either through eradication of the invasive species, or through persistent suppression of their negative effects.

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Although understudied, the impact of non-native predators on their prey critically depends on prey behaviour (Sih et al. 2010). The effects of exotic predators are predicted to be more severe when the local prey species are naïve to the novel predators in their environment (Cox and Lima 2006; Salo et al. 2007). Insular ecosystems are characterized by smaller and less diverse predator communities than their mainland counterparts (Cox and Lima 2006). This relaxed selection on insular prey can result in a rapid loss of anti-predator behaviour (Beauchamp 2004; Blumstein and Daniel 2005), often with dire consequences for population persistence when faced with exotic predators (Cox and Lima 2006; Doherty et al. 2016).

Predicting the outcome of invasive alien predator (IAP) introductions on fauna is also complicated by the degree of similarity between the novel and native predators and the prevalence of predators in a prey's past (Ehlman et al. 2019). For example, native and non-native predators may exert synergistic negative effects on prey (Sih et al. 1998). Furthermore, while it is well documented that increased threat of depredation may lead to increased mortality (e.g. Preisser et al. 2005) and/or decreased reproductive output (e.g. Zanette et al. 2011), it is less clear how the antipredator behaviours employed by the native prey species affect its population dynamics (Sih et al. 2010). One such anti-predator strategy in long-lived animals is reduced breeding propensity due to the high risk associated with breeding in a predator-riddled environment (Lee et al. 2017), since they have the potential to postpone breeding to a safer time (Shaw and Levin 2013; Öst et al 2018). Successful human interventions to control or eradicate invasive predators may therefore increase breeding propensity, although this latter effect has not been previously examined.

Fennoscandia has been invaded by two mammalian predators with potentially dire consequences on ground-nesting birds (e.g. Nordström et al. 2003); the American mink (*Neovison vison*) and the raccoon dog (*Nyctereutes procyonoides*). The American mink was brought to Finland for fur farming in 1920 and after escaping, the first minks living in the wild were observed in 1932 (Kauhala 1996). Raccoon dogs were intentionally introduced as a quarry species for fur hunting into current day Russia in the 1920s and the first raccoon dog was observed in Finland in 1935 (Helle and Kauhala 1987). These invasive predators, now having a solid foothold in Finnish nature, prefer habitats close to water and impact various water bird populations breeding in wetlands and in the Baltic Sea archipelago (e.g. Dahl and Åhlén 2019). One such emblematic species is the common eider (*Somateria mollissima*; hereafter, eider), currently classified as endangered in the EU (BirdLife International 2015).

Long-lived, cryptic, ground-nesting eiders exhibit extreme nest-site fidelity (Öst et al. 2011; Ekroos et al. 2012). American minks and raccoon dogs readily kill breeding eiders (Öst et al. 2018), and depredate nests (Holopainen et al. 2020). The high breeding site fidelity of eider females, coupled with their insular breeding habits, makes them especially vulnerable to the presence of mammalian predators. Thus, female eiders keep breeding on the same island (Öst et al. 2011; Ekroos et al. 2012), relying on an intermittent breeding strategy in response to elevated predation risk (Öst et al. 2018). These traits, combined with the high responsiveness of eiders to variation in predation pressure (Jaatinen and Öst 2013; Öst et al. 2015; Jaatinen et al. 2014, 2016), make eiders a well-suited case study for assessing the impacts and efficiency of invasive predator control schemes in the Baltic Sea archipelago.

The main native predator of eiders, the white-tailed eagle (*Haliaeetus albicilla*), has made an astonishingly rapid recovery, after nearly a century of absence as a breeding bird, setting up interesting dynamics between native and non-native predators in this study system. The white-tailed eagle was on the brink of extinction in the 1970s due to the widespread use of pesticides and persecution (Helander et al. 2008). The species was saved from extinction thanks to considerable conservation efforts and its population has been rising ever since in the Baltic Sea region (Treinys et al. 2016). In the 2019 Finnish assessment of threatened species, the white-tailed eagle was taken off the red list and its populations are currently deemed "Least concern" (Hyvärinen et al. 2019). This unique 'natural experiment' involving large-scale temporal variation in native predation pressure led us to expect vulnerability of eiders to non-native predators, either because of the long absence of significant native predation pressure (see Ferrari et al. 2015), and/or because antipredator responses targeted at a native avian predator may be inappropriate or ineffective against invasive mammals (see Carthey and Blumstein 2018).

Here, we capitalize on a long-term eider study (1990-present) carried out in the Tvärminne archipelago in Hanko, SW Finland. This individually marked eider population has recently experienced a sharp increase in predation by white-tailed eagles, American minks and raccoon dogs (Öst et al. 2018). In 2011, an invasive predator control scheme was launched to curb the increasing predation pressure and aid the dwindling eider population. We examine the effects and effectiveness of predator removal on eider breeding behaviour and mortality over a 9-year period. We elucidate the associations between invasive predator removal intensity and the annual number of killed incubating females, nest success and breeding propensity, while controlling for the effects of a general increase in predation pressure experienced by the study population.

Methods

This study was conducted in Tvärminne (59° 50′N, 23° 15′E), western Gulf of Finland, in 2011–2019. The study area of ca 15 km^2 includes 38 islands (size range 0.13–10.2 ha). Fourteen out of these 38 islands were only subjected to a standard population monitoring scheme conducted once annually since 1990, during which females are trapped and ringed with a standard metal ring and the numbers of active nests (incubating female present) and depredated nests recorded. On the remaining 24 study islands, a more in-depth study of the population has been conducted since 2003. This in-depth study involves unique colour ringing of females for individual identification at distance (up to ca 600 m using a spotting scope), additionally equipping them with unique temporary wing flags allowing identification of swimming individuals. Furthermore, final nest fate (see below) has been recorded by revisiting the nests upon and/or after the estimated hatch date.

Female eiders were captured predominantly during the later phase of incubation using hand nets. For each of the 24 intensive study islands, we also calculated the year-specific proportion of active nests from which we succeeded in trapping the female (range of annual means for 24 islands over 9 years = 0.55–0.71), for use as a covariate in the analysis regarding breeding propensity (see below and Öst et al. 2018). This proportion is solely based on active nests and excluded nests encountered as depredated upon the first monitoring visit, since re-nesting, although unlikely, may still be possible after nest failure at an early stage. Female handling procedures were approved by the Animal Experiment Board at the State Provincial Office of Southern Finland (permit number ESAVI/4053/2018). Female trapping procedures also complied with the specific regulations of the Tvärminne Zoological Station.

We recorded the number of nests that were depredated at first encounter, to quantify the ratio of active and depredated nests. This ratio, although not encompassing depredation exposure for the entire breeding period, is a robust proxy for the likelihood of nest depredation on each island and is available from both single-survey monitoring islands and from intensive study islands. For nests on the intensively studied islands, hatching success (hatched or depredated) was determined by returning to the nest at the end of incubation and documenting the presence of ducklings. If no ducklings were found in the nest, they had either already hatched and left the nest, or the nest had been depredated. Determining nest fate was usually straightforward also in these cases. This is because hatched eggs have an intact leathery membrane, while depredated eggs, typically eaten in the immediate nest surroundings, leave shattered shells with the membrane, usually bloody, still attached to the shells (Öst and Steele 2010; Jaatinen and Öst 2013). A nest was considered as hatched if at least one duckling or one hatched egg membrane was found. In this way, we were able to determine the fate of the great majority of nests (2200 out of 2457 nests; mean annual determination success (± SD) = 90.4 ± 5.7%, range 81–99.5%). This second metric is a reliable proxy for the level of predation pressure experienced by nesting females during the entire nesting phase.

To identify colour-ringed females and collect data on breeding status (breeder versus non-breeder) of females not captured during the focal year, two to five observers equipped with spotting scopes daily located all individually identifiable females in late May–late June, from the first appearance of broods at sea until young were close to independence (Jaatinen and Öst 2013). We recorded the identity of each individually marked female, whether she was attending a brood, the number of ducklings in the brood, and, if present, the number of other females in the brood. Each focal female was followed long enough to ensure correct assessment of her brood-rearing status (see Öst et al. 2003). Based on all annual observations of a focal untrapped female at sea, we categorized each individual as either a solitary female never seen associated with young (i.e. as a non-breeder) or a brood-tending female associated with young at least once during the season (i.e. as a breeder) (Öst et al 2018). For each individually identifiable female observed at sea in a focal year, we assigned a status as breeder if trapped on the nest while incubating in that year (unless trapped for the first time and ringed, see below) and/or identified at sea associated with young at least once (Öst et al. 2018). We removed first-time breeders (i.e. females trapped for the first time and ringed in the focal year of examination) from the analysis of breeding propensity. This was done to reduce bias, as females are ringed when caught breeding for the first time, hence no first-time breeder could be classed as a non-breeder (Öst et al. 2018). First-time breeders were excluded from the analysis also because of the risk of analysing annual variation in recruitment, ultimately reflecting population productivity, rather than mere variation in breeding propensity. Furthermore, exclusion of first-time females in the breeding propensity analysis guards it against false positives, i.e. type I error.

We quantified the annual number of killed incubating females (mean ± SD = 42.89 ± 17.46, N = 386 killed females) (Jaatinen et al. 2011). Active predation is the primary cause of mortality of females in our population (Öst et al 2018). Post-mortem examination of carcasses in the field often revealed typical signs of predation (e.g. subcutaneous haemorrhaging of the head, neck, or breast regions). Often the killer could be identified based on the wounds and the predators handling of the carcass (e.g. plucking, dragging or decapitating). However, in almost half of the cases examined (164 out of 386, 42.5%), the killer could not unambiguously be determined.

To obtain a measure of the depredation pressure imposed by white-tailed eagles that is independent of our data on killed eider females, we calculated an index measuring the annual abundance of white-tailed sea eagles at Hanko Bird Observatory (HALIAS, 59° 49′ N, 22° 54′ E), situated ca 18 km west of the Tvärminne study area (Jaatinen et al. 2011). This eagle index was calculated by dividing the total sum of daily numbers of resident white-tailed sea eagles observed during 1 April–15 June in 2011–2019 (corresponding to the breeding season of eiders) by the number of annual observation days during the same period (eagle abundance index mean ± SD = 6.43 ± 1.46, $N = 9$ years). The eagle abundance index showed a notable increase over time (log-linear regression: 6.4% annual increase, $CI_{95\%} = 2.2–10.8\%$, $N = 9$ years).

American minks have been present in the study area since the 1970s, whereas the raccoon dog became common in the area during the 1990s. On all of the 38 study islands, surrounding islands ($n = 9$) and on the nearby coastline, invasive predators have been controlled since 2011. This study, and the predator control programme implemented in it, was not originally set up as a before–after–controlled-impact 'BACI' experimental design (Christie et al. 2020). We rather intend to analyse the data yielded from a predator control programme aimed at reducing the severe depredation eider females were subject to. In hindsight, the BACI design would have given a more rigorous framework within which to test our hypotheses. In such a setup, a random subset of the 38 islands would have been set aside as controls with no predator removal, and the results compared between the impacted (predator control) islands and the control islands to evaluate the effectiveness of predator control on the eider population. Nonetheless, our current approach makes the best possible use of existing data and using rigorous statistical modelling yields sound and robust estimates of the impact of non-native predators on eider reproduction and survival.

Predator removal was conducted by using both traps and dog patrols and resulted in an average (± SD, range) of ten (± 8.97, 1–30) IAPs removed annually from the predator control area. For this value to be of biological significance for nesting eiders, it was recorded as the number of IAPs removed between the previous eider breeding season and the current one, i.e. from 1 August in the previous year to 1 May in the current year. While the low sample size of culled IAPs per study island precluded us from analysing data on predator removal on an island-wise basis, this is not a critical limitation. This is because both individual minks and raccoon dogs are able to easily roam across most of the study area, consisting of islands in close proximity to each other. For example, the mean home range of male and female American minks in the nearby Archipelago Sea is ca 34 and 9 ha, respectively (Salo et al. 2008). The traps used for capturing minks were Conibear 120 traps located inside wooden boxes with an aperture diameter of 70–75 mm at one end of the box. The traps were baited with feathers, fish oil and a paraffin oil-based female American mink anal gland extract. The number of traps started at 20 traps in 2011 and was elevated to 35 in 2017. Traps were open and baited between August and April, during which time they were controlled and re-baited ca. once a month, during the sea ice-free season. However, in 2015 and 2016 the traps were only checked once due to an unforeseen shortage of trapping personnel. No traps were used in the removal of raccoon dogs.

During 2011–2019, dog patrols were conducted in spring and autumn using one to three specially trained dogs, which seek out invasive predators and indicate their location by means of barking and/or digging the ground. Both larger dogs that venture out far from the handler(s) when seeking their quarry (long-range dogs) and smaller dogs with shorter range were used. Raccoon dogs were most often located on the ground, under thick vegetation or in crevices between rocks, whereas American mink were most often found under rocks, in rock piles or underground tunnels. IAPs were mainly dispatched using small calibre firearms. However, when American minks were found under rocks, in rock piles or underground, a leaf blower was used to flush them out and subsequently they were shot using a shotgun.

Detailed IAP removal effort was only available for dog patrols from 2018 onward; however, the number of working days used for predator removal on the entire predator removal area during the study years of 2011–2019 serves as a crude proxy for effort, being on average (± SD) 2.67 (± 4.09) days/year. For the traps, the IAP removal effort is impossible to measure accurately, due to challenges of recording the timing of trap triggering (either when catching an American mink or due to empty triggering by waves during storms). Our IAP removal efforts aimed at maximizing the number of IAPs removed given the available time, and the nature of the efforts was opportunistic (traps moved to likely or proven mink sites, etc.). Although removal effort was unknown, this is not a significant limitation, as this tends to weaken the correlation between removed IAPs and our response variables, hence making our statistical analysis more conservative in detecting effects of IAP removal.

Statistical methods

To test the impact of predator removal on the annual number of killed females, using year as the sampling unit, we constructed a generalized linear model (GLM) with a negative binomial error distribution, where the annual number of killed females was explained by the total number of removed IAPs between the previous and the current breeding season. The annual eagle index was added as a covariate to account for the increasing eagle numbers, which may lead to increased numbers of killed females, and to a smaller number of females available for IAPs to prey upon (Öst et al. 2018). We used the negative binomial model to account for the observed overdispersion. The response variable included all killed females regardless of the identity of the killer to also include those not identified (see 'Methods' above), as most of them are likely to also have been killed by the most common predators, i.e. white-tailed eagle, American mink and raccoon dog (Öst et al. 2018).

Next, we studied the effect of IAP removal on nesting success using individual islands as the sampling unit. To this end, we constructed a generalized linear mixed model (GLMM) with a binomial error distribution and Laplace parameter estimation, where the ratio of active and depredated nests at first encounter (combined using the 'cbind' function in the software R) on each island in each year was explained by the number of removed IAPs between the previous breeding season and the current one. We added the annual eagle index as a covariate to control for the effect of a constantly rising number of eagles. To control for the intragroup correlation between observations within islands, we added island identity as a random effect in the model.

To test the effect of predator removal on female eider breeding propensity, we constructed a GLMM with binomial error distribution and Laplace parameter estimation, where the likelihood of breeding was explained by the number of removed IAPs between the previous breeding season and the current one. The sampling unit here was individual females, and we added covariates known to affect female breeding propensity, i.e. island-specific nest depredation pressure as measured by the total proportion of successfully hatched and depredated nests at the end of the nesting period in each year, and annual white-tailed eagle abundance (Öst et al. 2018). We also added the annual island-specific proportion of trapped females to control for the potential bias arising from variation in eider trapping efficiency (Öst et al. 2018). Female identity was added as a random effect to account for repeated measurements of the same individuals.

We scaled the explanatory variables in all three analyses to a mean of zero and an SD of 1 to allow a direct comparison of effect sizes. All models were tested for multicollinearity between variables, finding none (all VIFs < 10). All statistical analyses were conducted using the software R 3.6.0. (R Core Team 2019). Conditional coefficients of determination (R^2c) values were calculated for the GLMMs using the 'MuMIn' package in R.

Results

The GLM explaining the annual number of killed females ($R^2c = 0.10$) exhibited a significant negative relationship between the number of killed females and the number of IAPs removed (estimate (± SE) = -0.66 (± 0.21), z = − 3.23, $p = 0.001$; Fig. 1). Consequently, it seems evident that IAP removal impacted the numbers of American minks and raccoon dogs roaming the area and thus reduced the number of killed females. Expectedly, the eagle index exhibited a significant positive relationship with the number of annually killed females (estimate (± SE) = 0.61 (± 0.21), z = 2.88, $p = 0.004$).

The GLMM explaining the probability of nest depredation ($R^2c = 0.61$) exhibited a significant negative relationship between the number of removed IAPs and this probability (estimate (± SE) = -0.33 (± 0.08), z = − 3.93, $p < 0.0001$; Fig. 2). The model also showed that the eagle index was positively associated with the probability of nest depredation (estimate (± SE) = 0.40 (± 0.08), z = 4.71, $p < 0.0001$). Thus, IAP removal decreases the overall likelihood of nest depredation, while increasing numbers of white-tailed eagles are associated with more nest depredation.

The GLMM describing female eider breeding propensity ($R^2c = 0.19$) showed a significant positive relationship between the number of removed IAPs and the probability of breeding (estimate (± SE) = 0.38 (± 0.16),

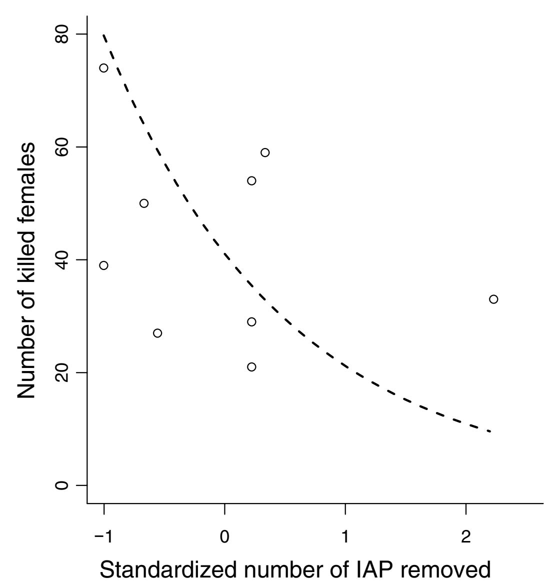

Fig. 1 The number of breeding common eider females killed annually by predators was found to decrease with an increasing number of invasive alien predators (IAPs) removed between the previous and the current breeding seasons (standardized values presented). The dashed line represents the fitted values of killed females from a GLM with binomial error distribution (see Methods for details)

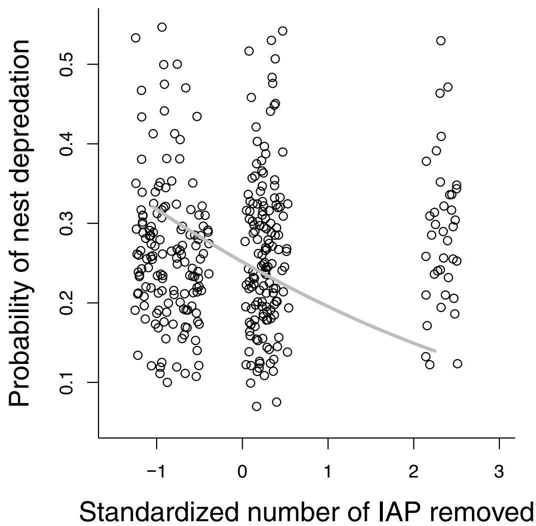

Fig. 2 The probability of common eider nest depredation decreased with an increasing number of invasive alien predators (IAPs) removed between the previous and the current breeding seasons (standardized values presented). Each data point in the graph describes the probability of nest depredation on one island during 1 year. For visual clarity, a small amount of random jitter along the x-axis has been added to the data points. The grey line represents the fitted values of nest depredation from a GLMM with a binomial error distribution (see Methods for details)

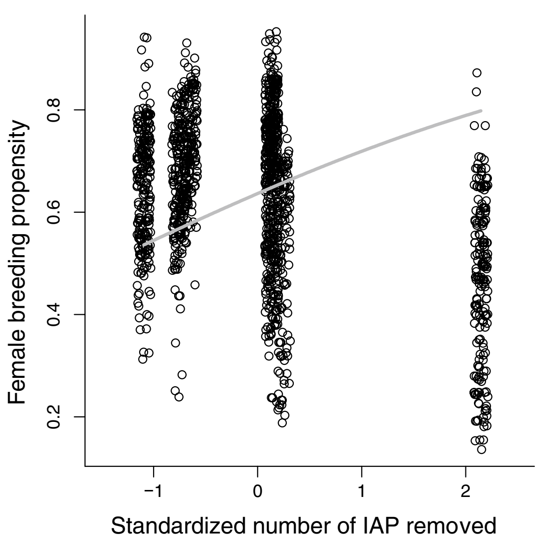

Fig. 3 Breeding propensity of female common eiders (for definition, see text) increased as a result of increasing numbers of invasive alien predators (IAPs) removed between the previous and the current breeding seasons (standardized values presented). The data analysis was based on recording the annual breeding decisions (breeding or not; for definition, see text) of individual females. For visual clarity, a small amount of random jitter along the x-axis has been added to the data points. The grey line represents the fitted values of breeding propensity from a GLMM with a binomial error distribution (see Methods for details)

$z = 2.43$, $p = 0.01$; Fig. 3). Also the eagle index (estimate (± SE) = − 0.72 (± 0.16), $z = -4.54$, $p < 0.0001$) and annual nest depredation risk (estimate (± SE) = − 0.56 (± 0.07), $z = -7.98$, $p < 0.0001$) showed negative associations with eider breeding propensity. The island-specific proportion of trapped females exhibited a significant positive association with breeding propensity (estimate (± SE) = 0.25 (± 0.07), $z = 3.67$, $p = 0.0002$).

Discussion

Our modelling suggested that removal of American minks and raccoon dogs decreased the number of eider females killed during nesting, while improving both nesting success and breeding propensity. The consistently positive effect of IAP removal on eider survival and reproduction is encouraging, especially since the Baltic/Wadden Sea flyway population is set in a precipitous decline (BirdLife International 2015), the main driver of which is depredation of adults and young in the northern parts (Öst et al. 2016; Tjørnløv et al. 2020). Although intuitively appealing, these findings are by no means self-evident. For example, an American mink eradication programme in the nearby Archipelago Sea (SW Finland) showed no effects on subsequent breeding densities of early-breeding and large-bodied waterfowl such as eiders (Nordström et al. 2003). Although the exact reason for this discrepancy is unknown, our study may have benefitted from greater statistical power. Thus, we used islands (nest success analysis) or individuals (breeding propensity analysis), rather than whole archipelago areas (cf. Nordström et al. 2003), as the sampling unit, and we also controlled for the abundance of white-tailed eagles, the main native predator. It should be added that both our current study and that conducted by Nordström et al (2003) would have largely benefitted from a BACI design (Christie et al. 2020); however, in the numerous cases where introduced alien predator species invade islands and decimate native flora and fauna, there is typically not an opportunity for a non-culled control island or area. This is especially true in the Finnish archipelago, where land predators readily move between islands. Perhaps the most striking, if inadvertent, demonstration of the impact of the predator control programme is the fact that our removal efforts declined to a minimum due to unforeseen changes in the available predator control personnel in 2015–2016. This drop in culling activity, which amounted to an experimental before–after treatment, translated into a concurrent, very sharp, spike in the number of killed females (Fig. 4). The novelty of our study is that IAP control not only affected prey survival and fecundity, but also the decision of whether or not to breed. Although poorly understood, such behavioural responses may moderate the impact of non-native predators (Sih et al. 2010).

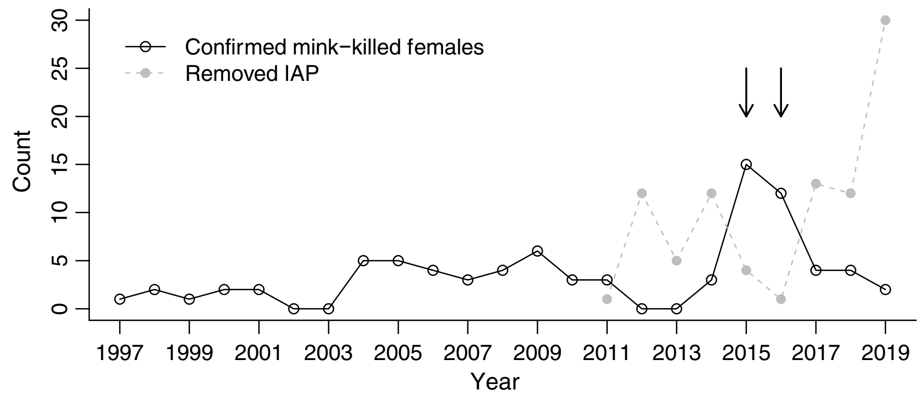

Fig. 4 The number of common eider females confirmedly killed by American minks during the period 1997–2019. After initiation of the invasive alien predator (IAP) removal scheme in 2011, the numbers of mink-killed females declined. When the IAP removal efforts temporarily declined to a minimum in 2015 and 2016 (indicated by two vertical arrows), minks killed more female eiders than before the IAP removal scheme was initiated. Intensified IAP removal (2017 and onward) led to a clear decrease in the number of mink-killed eider females

Globally, there are many examples of invasive predators wreaking havoc among native insular species not adapted to depredation (e.g. Rayner et al. 2007; Jones et al. 2008), these effects sometimes cascading through the island ecosystem (e.g. Rogers et al. 2017). While the Finnish archipelago is not fully comparable to the relatively large and isolated oceanic islands, they are widely inhabited by ground-nesting waterbirds. Many of these species are vulnerable or endangered in Europe, such as the eider and the common pochard (*Aythya ferina*) (BirdLife International 2015). The invasions of American mink and raccoon dog into the Finnish archipelago are relatively poorly documented, and IAP removal as a means to alleviate depredation pressure on prey is debated (Nordström et al. 2003; Kauhala 2004). Here, we show that when deployed with sufficient intensity, IAP control measures can indeed benefit ground-nesting birds, including large-bodied eiders, previously believed to be relatively immune to predation by particularly the American mink (Nordström et al. 2003).

The removal of one predator species may be of little benefit to nesting birds due to compensatory numeric and functional responses of other predators (Kauhala 2004). Another hypothesis that has gained momentum recently is that of mesopredator control by apex predators (e.g. Ritchie and Johnson 2009). Thus, Salo et al. (2008) argued that the American mink suffers negative effects when co-occurring with white-tailed eagles in the Baltic Sea, as evidenced by the reduced movements of female American mink in response to increased eagle-induced predation risk. Viewed against this backdrop, it is particularly noteworthy that our study was conducted amidst an unprecedented increase in the white-tailed eagle population (Högmander et al. 2020) and eagle depredation on eiders (Öst et al 2018). Our robust findings that the more American minks and raccoon dogs are removed, the more this facilitates both adult female and nest survival (Figs. 1, 2) suggests that functional and/or numerical responses by other local predators (e.g. white-tailed eagles) are insufficient to outweigh the positive effects of IAP removal. It is also pertinent that the effect sizes of IAP removal and the eagle index on both female and nest survival are remarkably similar, indicating that the positive effect of IAP removal on survival and nest success is of comparable magnitude as the negative impact imposed by the main natural predator of eiders. We therefore highlight the importance of implementing efforts to mitigate the impacts of IAPs despite the currently high levels of natural depredation.

The here demonstrated susceptibility of eiders to the two non-native predators may be associated with both the historical context of native predator–prey interactions, and the difference in hunting strategies between native and non-native predators. It should be acknowledged that the current period of high danger has been short and preceded by a much longer period of ‘unnaturally’ low predation rates, due to the absence of eagles and non-native mammalian predators. The effects of non-native predators on prey are likely to become accentuated under conditions in which the prey have historically lacked predators (Sih et al. 2010). Furthermore, prey are expected to fare poorly when exposed to alien predators that do not closely resemble familiar predators (Ehlman et al. 2019). Consequently, antipredator responses that are effective against visually oriented eagles may be ineffective, or even maladaptive, as a defence against olfactory-oriented invasive mammalian predators. A compelling case in point is that the proportion of female eiders nesting on forested islands has gradually increased over time in our study area, mainly due to selection imposed by eagle predation (Ekroos et al.

2012). While forested islands offer more opportunities for nest concealment, and hence should reduce detection by hunting eagles, this benefit may not apply when predators primarily hunt by scent. In fact, increased concealment of eider nests may interfere with female escape performance once detected by a predator (Öst and Steele 2010). Consequently, the net fitness effects of nesting under more closed canopy may be negative where IAPs abound.

Intermittent breeding may be an adaptive reproductive strategy in long-lived species if breeding conditions fall short of certain requirements (Shaw and Levin 2013; Jean-Gagnon et al. 2018). Although adaptive for the individual, increased intermittent breeding due to excess environmental forcing may compromise population-level productivity and cause population declines and/or extinction (Lee et al. 2017). Our study population may currently be approaching a critical tipping point where productivity is permanently depressed to a low level, as indicated by the strong negative correlation between the progressively increasing annual incidence of intermittent breeding and offspring productivity (Öst et al. 2018). IAP removal efforts may be an effective way of increasing the breeding propensity of females (Fig. 3), thus mitigating the negative impacts on population growth potential. Given this mounting predation pressure from white-tailed eagles on nesting eiders, it is ever more important to maximize the population growth potential. Given the relatively modest time–investment required when using efficient and professionally trained hunting dogs to locate IAPs, we suggest that IAP removal is one of the most cost-effective actions that can be taken towards this end.

Due to potential compensatory reproductive responses, it is important to deploy sufficiently intense and long-term culling efforts to control invasive predators. For example, a culling programme that reduced the population density of American mink led to increased conception probabilities and litter sizes (Melero et al. 2015). This compensatory increase in fecundity became amplified by the immigration of younger, more fecund mink females, replacing the resident, senescent females removed during the culling effort (Melero et al. 2015). Our observation that the number of eider females confirmedly killed by minks during 2015 and 2016 was the highest ever recorded, even higher than before launching our IAP removal scheme (i.e. 1997–2010 in Fig. 4), is consistent with the findings by Melero et al. (2015). Thus, if a culling or eradication programme is abandoned or relaxed too early, the outcome may even be worse than the starting situation. This is by no means a reason not to start control measures or eradication programmes, but rather highlights the importance of intense, long-term control and culling efforts when aiming to mitigate the ecological impacts of invasive alien predators. The marked drop in the number of females killed by American minks, following the high numbers of American mink removed in 2017–2019 (Fig. 4), highlights the efficacy of reinstating an intense culling effort.

The effort required to eradicate or control invasive alien predators depends on the degree of geographical isolation affecting the rate of predator immigration (Zalewski et al. 2009). The Finnish archipelago, containing numerous variable-sized islands close to one another, makes for a relatively continuous landscape, especially for the raccoon dogs and American minks, both of which are strong swimmers. Due to the high connectivity between islands, and between islands and the mainland, large areas of this archipelago are likely to receive immigrant American minks and raccoon dogs. Thus, eradication of IAPs is challenging in the Baltic Sea archipelago. The negative impact inflicted by invasive alien predators may here best be controlled by deploying a continuous and sufficiently intense culling effort, instead of aiming towards total eradication. Our predator control scheme serves as an example of how IAPs can be cost-efficiently controlled to the benefit of native fauna, despite frequent immigration events thwarting complete eradication. Reduced female mortality, increased nest success and increased breeding propensity all underline the benefits of continuous IAP removal on ground-nesting archipelago birds. Such cost-effective actions call for governmental deployment across large areas, not only in the Finnish archipelago, but also at the scale of the entire Baltic Sea.

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Author contribution statement KJ and MÖ conceived the idea for this study; KJ conducted and coordinated the IAP removal scheme; KJ, IH, BM, MÖ and BS conducted field work regarding eider breeding; KJ conducted the statistical analyses; KJ, IH, BM, MÖ and BS wrote and commented upon previous versions of the paper.

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Availability of data and material The data is available upon request from the lead author.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that there is no conflict of interest or competing interests regarding this paper.

Ethics approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. Eider female handling procedures were approved by the Animal Experiment Board at the State Provincial Office of Southern Finland (permit number ESAVI/4053/2018). Female trapping procedures and IAP removal also complied with the specific regulations of the Tvärminne Zoological Station.

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