Received: 27 October 2025 | Revised: 27 April 2026 | Accepted: 20 May 2026

DOI: 10.1002/jwmg.70242

THE JOURNAL OF WILDLIFE MANAGEMENT | THE WILDLIFE SOCIETY

RESEARCH ARTICLE

Seabird population responses after the removal of an introduced predator

Samuel B. Stark[1] | Daniel D. Roby[1] | David B. Irons[2] | Robert S. A. Kaler[2] | Erik E. Osnas[2]

[1]Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

[2]U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, M.S. 201, Anchorage, AK 99503, USA

Correspondence

David B. Irons, U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, M.S. 20, Anchorage, AK 99503, USA.
Email: dbironsak@gmail.com

Present address

Samuel B. Stark, Summit and Sound Collective LLC, 800 14th Street, Bellingham, WA 98225, USA.

Funding information

U.S. Fish and Wildlife Service; Exxon Valdez Oil Spill Trustee Council; National Fish and Wildlife Foundation; Oregon State University

Abstract

Removal of introduced predators is an effective tool for restoration of island-nesting birds; however, the effects of predator removal on target species recovery remain understudied. Pigeon guillemots (*Cepphus columba*), a crevice-nesting seabird in the family Alcidae, declined by 95% from 1979 to 2008 at the Naked Island Archipelago (NIA) in Prince William Sound, Alaska, USA, following the introduction of American mink (*Neogale vison*) and the 1989 *Exxon Valdez* oil spill. Following the initiation of mink removal from guillemot nesting areas in 2014, we studied guillemot breeding biology at the NIA from 2014 to 2023. By 2023 guillemot numbers detected on shoreline transects at the NIA had increased by 3.3 times. The number of active guillemot nests at the NIA increased by 4.7 times in the first 5 years following the initiation of mink removal. During 2014–2023, the numbers of guillemots at other nearby islands where mink were absent decreased 17% and the guillemot population trend throughout Prince William Sound was approximately stable. Following mink removal, we also observed an increase in the proportion of active guillemot nests in substrates accessible to mink and an increase in survival rates of nestling guillemots at the NIA. The immediate recruitment of guillemots to the NIA after the initiation of mink removal suggests that immigration occurred from nearby mink-free islands. Our results indicate that the removal of mink from guillemot nesting areas at the NIA was effective in initiating the

rapid recovery of a declining local breeding population of guillemots that was formerly the largest in the region. Our findings may be applicable to other insular bird populations subjected to predation from invasive species.

KEYWORDS
American mink, *Cepphus columba*, *Exxon Valdez* oil spill, invasive predator removal, *Neogale vison*, nest predation, pigeon guillemot, Prince William Sound, seabird restoration

In the infancy of modern-day seabird studies, Lack (1968) recognized that many seabird species nest colonially on isolated offshore islands where predation pressure from land-based predators is minimal or absent. At that time seabird population regulation was an important ecological question and was largely attributed to density-dependent factors such as food availability (Ashmole 1963). But in more recent decades, as seabirds around the world have declined (Croxall et al. 2012), questions about population regulation have turned to concerns about threats to seabirds. Non-native predators are one of the major drivers of declines in island bird populations worldwide and predator removal is one of the most common techniques used for restoring seabird populations (Towns et al. 2011, Whitworth et al. 2013). Previous studies of the response to removal of invasive mustelids, primarily introduced American mink (*Neogale vison*; Nordstrom et al. 2003, Banks et al. 2008, Lopez et al. 2023) and stoats (*Mustela ermina*; O'Donnell et al. 1996), found it effective in restoring ground-nesting birds, including seabirds (Nordstrom et al. 2003).

The 1976–1977 Climate Regime Shift (Agler et al. 1999, Anderson and Piatt 1999, Cushing et al. 2018, Litzow et al. 2020) and the 1989 *Exxon Valdez* oil spill (Piatt et al. 1990, Irons et al. 2000, Peterson et al. 2003, Esler et al. 2018) had negative effects on populations of several seabird species in Prince William Sound (PWS), Alaska, USA, including the pigeon guillemot (*Cepphus columba*; Irons et al. 2000, Golet et al. 2002). Both events have been implicated in long-term declines in the abundance of lipid-rich forage fishes in PWS (Carls et al. 2002). These fishes are an important food source for pigeon guillemots (hereafter guillemots) and other nearshore marine predators in PWS (Golet et al. 2000, Peterson et al. 2003).

The Naked Island Archipelago (NIA) in central PWS formerly supported the largest concentration of nesting guillemots in PWS, and studies of guillemot nesting ecology have been conducted at the NIA since 1978 (Oakley 1981, Kuletz 1983). By 2008 it was clear that the breeding population of guillemots at the NIA had crashed, but the cause of the 95% decline was unclear and controversial (Bixler 2010). Continued exposure to residual oil from the *Exxon Valdez* oil spill and reduced availability of preferred forage fishes were 2 favored hypotheses, but beginning in the early 1990s, elevated predation rates on guillemot nests at the NIA were noted (Hayes 1995, 1996; Oakley and Kuletz 1996; Golet et al. 2002). Also, by 2004 the impact of residual oil from the *Exxon Valdez* oil spill had diminished (Esler et al. 2018), and by 2008 forage fish stocks had somewhat rebounded (Bixler 2010). More recently, it was discovered that American mink had been slowly and intentionally introduced to the NIA during the 1970s and 1980s to establish a trappable population (D. B. Irons, U.S. Fish and Wildlife Service, unpublished data; Fleming and Cook 2010). Mink predation was identified as the primary cause of the steep decline in the local guillemot breeding population at the NIA during the 1990s and 2000s (Bixler et al. 2025). Bixler et al. (2025) reported high predation rates on guillemot nests, decreasing use of nest sites more vulnerable to mink predation, and disproportionate declines in the numbers of guillemots at the NIA compared to other nearby islands where mink were absent.

Based on studies by Bixler et al. (2025), the United States Fish and Wildlife Service (USFWS) and the Exxon Valdez Oil Spill Trustee Council decided to restore the guillemot breeding population at the NIA by removing introduced mink from guillemot nesting habitat on the NIA. Mink removal was initiated in late winter 2014. Long-term monitoring of guillemots nesting at the NIA provided a unique opportunity to evaluate the effects of predator removal (Oakley and Kuletz 1996, Golet et al. 2002, Bixler et al. 2025).

Our study objectives were to test 2 hypotheses based on knowledge obtained during the prior 35 years of intermittent data collection on guillemots in PWS. Our first *a priori* hypothesis was that predation by introduced mink was the primary limiting factor for the breeding population of guillemots at the NIA. We reasoned mink removal from guillemot nesting habitat at the NIA would result in the following 4 changes: 1) numbers of guillemots counted around the NIA during pre-nesting would increase, 2) numbers of guillemots nesting at the NIA would increase, 3) nest site substrates used by guillemots at the NIA would increasingly include sites accessible to mink, and 4) survival rates of nestling guillemots at the NIA would increase.

Our second *a priori* hypothesis was that the growth rate (λ) of the guillemot breeding population at nearby mink-free islands (Smith Islands, Seal Island, Fool Island), where guillemot breeding populations were not limited by mink predation, would differ from that at the NIA after the removal of mink. If this second hypothesis was true, we predicted that the annual rate of increase in the number of guillemots at the NIA would be greater in the years following mink removal than at nearby mink-free islands. Our study of the effects of mink removal on guillemot breeding biology at the NIA was initiated at the start of the 2014 nesting season, soon after the initiation of mink removal efforts.

STUDY AREA

The Naked Island Archipelago (NIA) consists of 3 major islands in central PWS (Figure 1). The 3 main islands, Naked (~3,970 ha), Peak (~630 ha), and Storey (~700 ha), are isolated large islands in PWS, separated from the nearest island by approximately 6 km of open water, greater than the maximum distance (4 km) that mink are known to have dispersed across open water (Gerell 1967). The archipelago is surrounded by shallow rocky shelves that extend up to 2 km offshore. This insularity combined with abundant foraging habitat provides ideal nesting habitat for nearshore-foraging marine birds such as guillemots (Drent 1965, Ewins 1993).

Nearby mink-free islands support high densities of nesting guillemots compared to the mainland, where mink were present. The Smith Island Group (Smith and Little Smith islands; ~340 ha and ~35 ha, respectively) and Seal Island (~45 ha) are similarly insular but are smaller islands than those of the NIA. Fool Island is close (2.7 km) to a large island (Perry Island) but too small (~11 ha) to support mink over winter (Figure 1). These islands supported similar densities of nesting guillemots compared to the NIA prior to the establishment of the introduced mink population (Oakley 1981, Kuletz 1983). While the number of guillemots at the NIA declined dramatically following the introduction of mink, the Smith Island Group, Seal Island, and Fool Island remained mink-free and experienced relatively small declines in guillemot numbers following the *Exxon Valdez* oil spill (Bixler 2010). We used these islands as controls to evaluate the effects of mink removal from guillemot nesting habitat at the NIA on numbers of nesting guillemots.

METHODS

Mink removal

Following the *Exxon Valdez* oil spill, efforts to restore the nesting guillemot population in PWS led the USFWS to determine that predation by introduced mink on guillemot eggs, nestlings, and adults in the NIA needed to be reduced (Irons and Roby 2007, Exxon Valdez Oil Spill Trustee Council 2014). To reduce mink predation on guillemots, professional trappers lethally trapped mink near historical and current guillemot nesting habitat throughout the archipelago annually during March and April 2014–2018.

Conibear traps, or body-grip traps (sizes #110 and #120), were set along the shoreline of the NIA by a crew of professional trappers employed by the United States Department of Agriculture - Animal and Plant Health

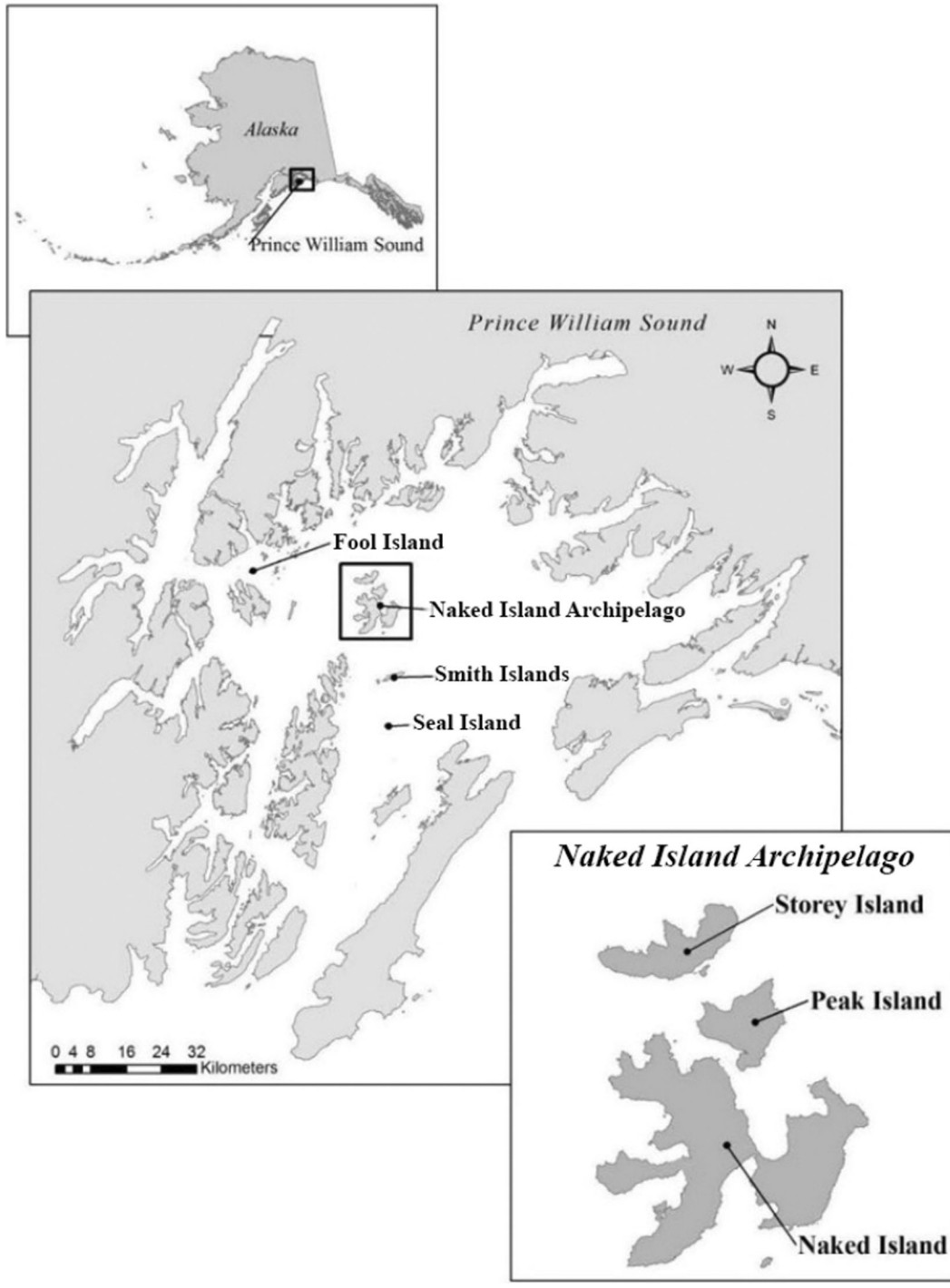

FIGURE 1 Map of the study area showing the location of Prince William Sound (PWS) in Alaska, USA (top left), the 4 island groups in central PWS where pigeon guillemots were monitored in 1978–2023 (middle), and the 3 main islands that comprise the Naked Island Archipelago (bottom right; after Bixler et al. 2025).

Inspection Service. Conibear traps are designed for the quick, humane dispatch of mammals, including mink. Annual trap deployments ranged from 3,234 to 17,274 trap-nights.

Guillemot abundance surveys

We surveyed the guillemot population at the NIA and nearby mink-free islands annually from 2012, 2 years before the initiation of mink removal in 2014, until 2023 following methods described by Ewins (1985, 1993) and used during previous surveys at the NIA (Oakley and Kuletz 1996, Golet et al. 2000, Bixler et al. 2025). We conducted boat-based surveys in late May, the pre-breeding period, during morning high tides beginning 2 hours before high tide and ending 2 hours after high tide (0600–1000), when guillemot attendance at colony sites is most consistent (Vermeer et al. 1993*a*). We conducted counts from skiffs moving parallel to the shoreline about 100 m offshore. Our analysis included historical guillemot pre-breeding surveys conducted at the NIA and the Smith Island Group in 1978–1979, 1990–1997, and 2007–2008, and at Seal and Fool islands in 2008, which followed the same survey protocols (Oakley 1981, Oakley and Kuletz 1996, Bixler et al. 2025). We did not correct counts from guillemot pre-breeding surveys for detection efficiency; therefore, they are minimum counts.

To test for effects of mink predation on local guillemot population trends, we separated annual pre-breeding guillemot surveys into 2 groups based on whether mink had been documented on the island. The NIA was in the mink-present group and nearby islands (the Smith Islands, Seal Island, and Fool Island) were in the mink-free group. We then separated the annual guillemot surveys at the NIA into 3 time periods, which included only years when monitoring was taking place at the NIA: 1) when mink were undetected at the NIA (1978–1979), 2) when mink were well-established and their presence was detected frequently at the NIA (1990–1997, 2007–2008, 2012–2013), and 3) after the initiation of mink removal from the NIA (2014–2023). The timing of growth in the introduced mink population at the NIA is uncertain and these 3 mink periods are based largely on anecdotal sightings of mink or their sign and observations of mink predation on guillemot nests, or lack thereof.

In addition to the guillemot surveys described above, we collected data on guillemot abundance during July surveys that recorded all seabird species along shoreline transects throughout PWS (Cushing et al. 2018, Kaler et al. 2024). These surveys, initiated in the aftermath of the *Exxon Valdez* oil spill in March 1989, were designed using a randomly selected sample of shoreline transects from throughout PWS. We conducted surveys 17 times between 1989 and 2023, and surveys included 6 transects from the NIA. We used the same protocols for these surveys as for the guillemot pre-breeding surveys except we conducted July PWS-wide surveys throughout the day and irrespective of tide stage. Guillemot count data from July PWS-wide surveys are also minimum counts because we did not correct for detection efficiency. We used the guillemot count data from the July PWS-wide seabird surveys to compare guillemot population trends at the NIA with trends in the rest of PWS. These data on guillemot abundance are not directly comparable with data collected during guillemot pre-breeding surveys at the NIA. But the July surveys provide insight into how guillemot population trends at the NIA, where mink predation on guillemot nests increased following mink introduction and then declined following mink removal, compared with trends in PWS as a whole, where mink were generally present. The sample of shoreline transects surveyed in the July surveys did not include any transects from the mink-free islands used as a control in the present study (Smith Islands, Seal Island, Fool Island).

Guillemot nesting

To test for the predicted increase in the number of active guillemot nests at the NIA following mink removal, we attempted to locate every active guillemot nest and provide a minimum estimate of the number of active guillemot nests during each year from 2014 through 2018. Replicating the protocols used in 1979 and 2008, we surveyed the

NIA for active guillemot nests from inflatable skiffs traveling parallel to the shoreline approximately 50 m from shore at least once per week throughout the breeding season (May–August; Ewins 1993, Bixler et al. 2025). When we sighted guillemots, we recorded their location, behavior, and group size, then observed them for up to one hour if they were performing activities associated with active nesting (e.g., resting on land in small groups [≥3 individuals], especially near historical nest sites, or carrying fish in their bills).

Guillemot nest site substrate selection and distribution are shaped by food availability and the local predator community (Emms and Verbeek 1989, Ewins 1993). We classified each active guillemot nest into 1 of 3 nest site substrate categories: cliff top, cliff face, and talus. Cliff top nests were partially or entirely in soil located at the top of a cliff, bluff, or bank. Cliff face nests were in rocky crevices on the face of a cliff. Talus nests were in rock rubble, typically at the base of cliffs. We pooled the 3 nest site categories into 2 groups based on relative accessibility to mink: more vulnerable, which included cliff top and talus nests, and less vulnerable, which included cliff face nests. Then we pooled available data on guillemot nest site substrate into years pre-mink detection (1979), years when mink were well-established (2008), and years after the initiation of mink removal (2015–2018).

To test our prediction that mink removal would increase guillemot nestling survival, we calculated nestling survival rate at the NIA during the 2017 nesting season (after mink removal) and compared it to nestling survival rate data collected at the NIA during the period before mink were detected (1978–1979; Oakley and Kuletz 1996) and to data collected when mink were well-established at the NIA (1990–2008; Golet et al. 2002, Bixler et al. 2025). To minimize disturbance and possible guillemot nest abandonment during the incubation period, we did not access active guillemot nests in 2017 until we confirmed hatching by observing the delivery of fish to the nest by an adult guillemot; adults visibly transport fish to feed nestlings in their bills. This precluded measuring hatching success rate. After hatching, we checked active guillemot nests to determine brood size (1 or 2 nestlings) and marked nestlings with temporary rolled plastic leg bands. To determine the fate of each nestling, we revisited nests at least once every 5 days until the nest failed or the young fledged. We calculated nestling survival rate (chicks fledged as a proportion of eggs hatched) for all guillemot nests monitored. We estimated guillemot hatch date as 1 day prior to the first observed meal delivery (Ewins 1993) and confirmed hatch date based on wing length measurements of nestlings during the linear phase of growth and using a regression of wing length versus age for a sample of known-age nestlings measured by Golet et al. (2000).

Statistical analyses

We used generalized additive models (GAMs) or generalized additive mixed models (GAMMs) fit using the R package mgcv (Wood 2017) to estimate trends in guillemot density (birds/km of transect) from the guillemot pre-breeding surveys and from the July PWS-wide seabird surveys. Exploratory model fitting showed that a negative binomial response fit well compared to Poisson or Tweedie distributions for these count data based on quantile-quantile plots and other residual diagnostics, so models for survey count data used a negative binomial response and a log link function. All models had an offset for transect length so that predictions accounted for transect length and were made in count density per unit of transect length (1 km). For the guillemot pre-breeding surveys, we used a GAM with a main effect of island and an island-specific smooth of year. We then used the predict function to estimate island-specific function values on the response scale over a range of years.

For the July PWS-wide seabird surveys, we fit 2 models. First, we fit a model that contained 1) a main effect indicating that the shoreline transect was in the NIA or elsewhere in PWS, 2) a random intercept effect for transect (in mgcv syntax, using the bs = re specification), and 3) a smooth function of year for each level of the main effect (i.e., an average smooth across all transects in the NIA and another smooth across the remainder of shoreline transects in PWS; in mgcv, using the by specification). Second, we fit a more complex model that contained all the terms in the first model plus a year-by-transect (interaction) smooth. This interaction smooth was specified as a deviation from lower-order effect (bs = sz in mgcv) and was constrained to share the smoothing penalty across all

transects. All smooth terms of year used the default thin-plate regression splines (Wood 2003) as the basis functions, and the number of knots was restricted to 10. For the PWS-wide seabird surveys, we used a GAM-specific version of Akaike's Information Criterion (AIC) to compare models (AIC.gam in mgcv; Wood et al. 2016). When predicting from the more complex PWS-wide survey model, we excluded the year-by-transect term so that predictions were made for the averages from the NIA shoreline transects and non-NIA shoreline transects.

We also used a GAM to estimate the number of active guillemot nests at the NIA during 2014–2018 as a function of year. For this model, we used a normal likelihood and a simple smooth of year using default options and a maximum knot number of 4 because we only had one count for each of 5 years.

To estimate the predicted increase in use of more vulnerable nest sites by guillemots nesting at the NIA post-mink removal, we counted guillemot use of each category of nest site for all active guillemot nests in each year. We then combined counts into more vulnerable (cliff top and talus) and less vulnerable (cliff face) nest sites and used a logistic regression with year as a random effect to estimate the proportion of nests in more vulnerable sites (using the gam function in mgcv with year as a random effect). We then used posterior simulation (see below for a description of posterior simulations) of the fitted model to compare the mean proportion of vulnerable sites used during the post-mink removal period (2015–2018) to the proportion used in a year prior to the detection of mink at the NIA (year = 1979) and when mink were present and numerous at the NIA (year = 2008).

For guillemot nestling survival, we used logistic regression with random effects for nest and year and fixed effects of mink period (i.e., pre-mink detection, mink established, post-mink removal) to estimate the probability of a hatched egg surviving to fledging age (fit using the mgcv function gam; Wood 2017). Because clutch size is small (1 or 2 eggs), there is little information for estimating nest random effects; nevertheless, nestlings in the same nest are not independent for a variety of reasons due to shared habitat, location, year, or other effects, so we felt it was important to include nest as a random effect. In addition, there is only one year (2017) of nestling survival data after mink removal, so we did not fit models with both a mink period and year effect. Therefore, we fit 4 models and compared them using the AIC function in mgcv: 1) a model with only a fixed effect of mink period, 2) a model with a random effect of year and fixed effect of mink period, 3) a random effect of year and random effect of nest, and 4) a random effect of year alone. Under the random effects model with little information to estimate nest effects, the variance of the nest effects will shrink to zero, making model 3 essentially identical to model 4 when there is no information for these effects. For models without a direct fixed effect of mink period, we used posterior simulations (see next paragraph) to compare averages of year effect across mink periods.

As implemented in mgcv, GAMs have a direct Bayesian interpretation (see Wood [2017], sections 4.2.4 and 6.10; also see Miller [2025] for an accessible discussion). Specifically, mgcv provides an empirical Bayes estimate with an implied multivariate normal prior for the smoothing parameters (parameters that are weights for a series of basis functions that add together to form a smooth function over the domain of the covariate). The prior is multivariate normal with a zero mean vector and a prior precision matrix proportional to the smoothing penalty parameter and a penalty matrix that depends on the squared derivatives of the smooth function being estimated (i.e., the wiggliness; Wood 2017, Miller 2025). As such, this prior expresses the belief that the estimated function is more likely to be smooth than to be very complex but does not assume any specific functional form (e.g., a quadratic polynomial). Posterior smoothing parameters are obtained using restricted maximum likelihood. In mgcv, Wood (2017) also provides an AIC that is appropriate for comparing GAM models and provides Bayesian posterior covariance matrixes that account for smoothing penalty uncertainty, which are used for credible interval construction, *P*-values, and posterior simulation.

We implemented posterior simulation of GAMs and mixed models as described in Wood (2017) and Simpson (2024) using the predict.gam function in mgcv and various wrapper functions in the R package gratia (Simpson 2024). Briefly, for any posterior quantity of interest (e.g., mink period-specific geometric mean change in expected density or a linear contrast between an effect in one year or average of years and another year or average of years), we sampled the posterior distribution of the model coefficients using a multivariate normal distribution a large number of times (1,000). A new data set was constructed with observations at each level of covariate where a

prediction was needed and used in the predict.gam function to return a design matrix (type = lpmatrix in predict.gam). The package then found posterior samples of the expected response by multiplying the design matrix by each posterior sample of the parameter vector and transforming from the link to the response scale. Derived quantities can then be calculated for each posterior sample (e.g., differences or geometric mean change between years) and the posterior summarized. We summarized the posterior using the mean and 2.5% and 97.5% percentiles. We calculated the geometric mean population change between year a and b as

$$\lambda_{ab} = \left(\frac{N_b}{N_a}\right)^{1/(b-a)},$$

where a is the starting time point and b is the end time point, and N_x is the expected (predicted) population size or density.

RESULTS

Mink removal

Trapping efforts reduced the population of introduced mink at the NIA to a level where no mink were detectable in guillemot nesting habitat following 5 seasons of trapping (2014–2018). Trappers removed 106 mink from guillemot nesting habitat on the NIA during the first 3 seasons of trapping (76 in 2014, 23 in 2015, and 7 in 2016). During the fourth trapping season, 2017, we detected a single set of mink tracks on a small island near Naked Island (Bass Harbor Island). In 2018, the final year of trapping, we did not detect mink or mink sign in guillemot nesting habitat at the NIA. During a 3-year follow-up effort to monitor for mink using trail cameras at 10 stations baited with mink scent and herring, we did not detect mink. We concluded that the 5-year trapping effort in guillemot nesting habitat at the NIA had removed all mink from the archipelago and that the NIA was mink-free by 2018.

Guillemot abundance in surveys

The GAM with separate smooth terms for each island or island group showed different trajectories on each (Figure 2) and explained about 95% of the variation in guillemot counts. All smooth terms, except for Seal Island, were significant ($P < 0.001$). Examining predictions from the model for specific time periods showed that guillemots declined from 1978 to 1995 at both the NIA and the Smith Islands (Figure 2). Then from 1996 to 2013, guillemots rapidly declined at the NIA (mean $\lambda = 0.874$ [95% CI = 0.858–0.890]), while at the nearby Smith Islands, guillemot numbers increased slightly (mean $\lambda = 1.023$ [95% CI = 1.008–1.037; Figure 2). The high rate of decline in guillemot numbers at the NIA compared to the mink-free Smith Islands during 1996–2013 is consistent with the conclusion by Bixler et al. (2025) that mink predation on guillemot nests and breeding adults drove the guillemot population at the NIA to very low levels by 2008, with no evidence of recovery by 2013. Mink removal began at the NIA in early 2014, and by 2023 guillemots had increased at the NIA by 326%, with a mean $\lambda = 1.139$ (95% CI = 1.096–1.183), while at the Smith Islands, guillemot numbers were stable or declined slowly during the same period (mean $\lambda = 0.989$ [95% CI = 0.956–1.022; Figure 2). Guillemot numbers at 2 other mink-free islands near the NIA, Fool Island and Seal Island, were either stable (Seal Island mean $\lambda = 1.00$ [95% CI = 0.999–1.00]) or declined (Fool Island mean $\lambda = 0.924$ [95% CI = 0.886–0.965]) during 2014–2023 (Figure 2).

To put these dramatic changes in the guillemot breeding population at the NIA in the context of guillemot population trends throughout PWS, we compared the densities of guillemots on shoreline transects at the NIA ($n = 6$) to those in the remainder of PWS ($n = 206$) based on July PWS-wide seabird surveys. The GAMs fit to these

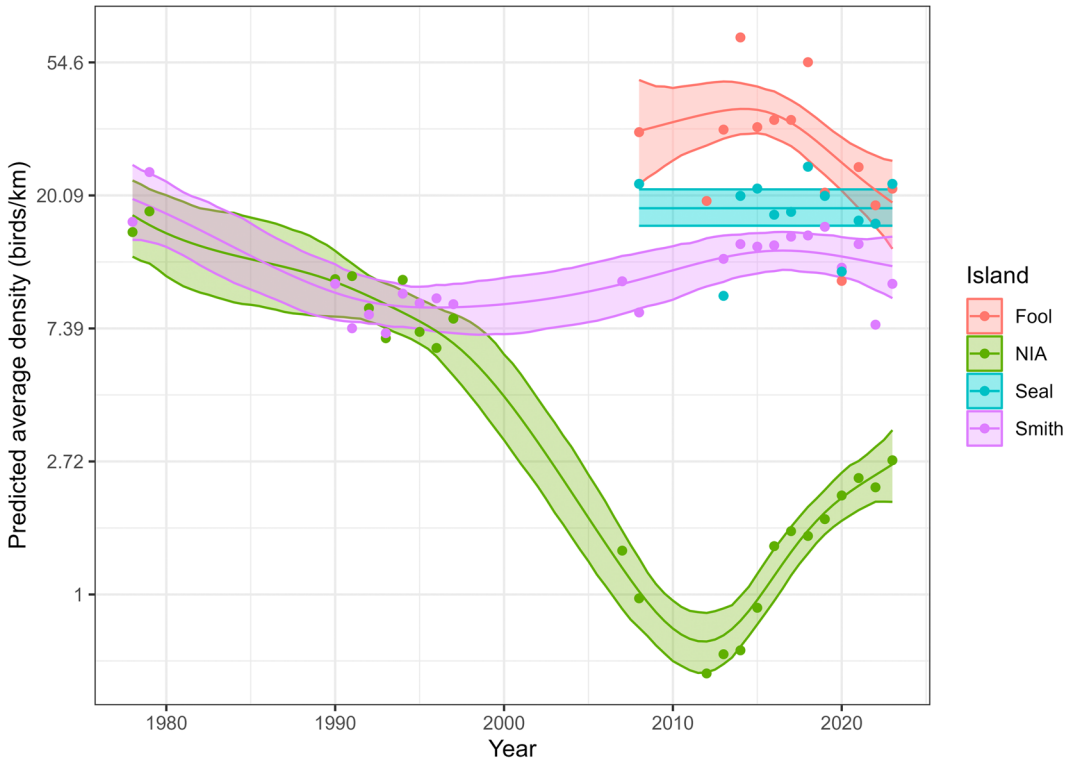

FIGURE 2 Predicted average density of pigeon guillemots (birds/km) on shoreline transects based on pre-breeding surveys (May) at islands in Prince William Sound, Alaska, USA. Surveys were conducted during 1978–2023 along the entire shoreline of the Naked Island Archipelago (NIA), where mink were introduced in the 1970s and 1980s and then removed starting in 2014, and the shorelines of 3 nearby mink-free islands or island groups: the Smith Islands (1978–2023), Fool Island (2008–2023), and Seal Island (2008–2023). We used generalized additive models (GAMs) to develop smoothing terms for trends at the NIA and at each of the 3 mink-free islands or island groups. Dots represent annual estimates of average density on transects and shaded areas represent the 95% credible interval for the smoothed trend line from the model.

data showed that the more complex model with a main effect for shoreline transects at the NIA, a random effect of transect, a separate average smooth of year for the NIA shoreline transects and for all other shoreline transects, and a separate transect-specific smooth of year for each transect (a transect-by-year interaction) fit better than a model without transect-specific smooths (ΔAIC = 72.3). In other words, trends differed among transects and there was an average difference between the trend for the NIA transects and the trend for the other PWS transects.

Using this best fitting model, posterior prediction of the average year smooth for the guillemot population density at the NIA versus the rest of PWS showed that in 1989 (before the major decline in guillemot numbers at the NIA), the NIA had a 46-fold higher density of guillemots (mean shoreline density = 8.99 birds/km [95% CI = 1.55–29.76]) compared to the rest of PWS (mean shoreline density = 0.192 birds/km [95% CI = 0.16–0.24]). Mink were (and are) present on the vast majority of the approximately 5,000 km of shoreline in PWS, exclusive of a few isolated islands like the Smith Islands, Fool Island, and Seal Island (Figure 1; Fleming and Cook 2010, E. Bilderback, Cordova, Alaska, personal communication). By 2014, when mink removal from the NIA was initiated, the shoreline density of guillemots at the NIA (0.371 birds/km [95% CI = 0.07–1.17]) had declined to just 3.6 times the shoreline density of guillemots in the rest of PWS (0.10 birds/km [95% CI = 0.08–0.13]; Figure 3). During 1989–2014 the average shoreline density of guillemots in PWS exclusive of the NIA was in decline (mean λ = 0.975

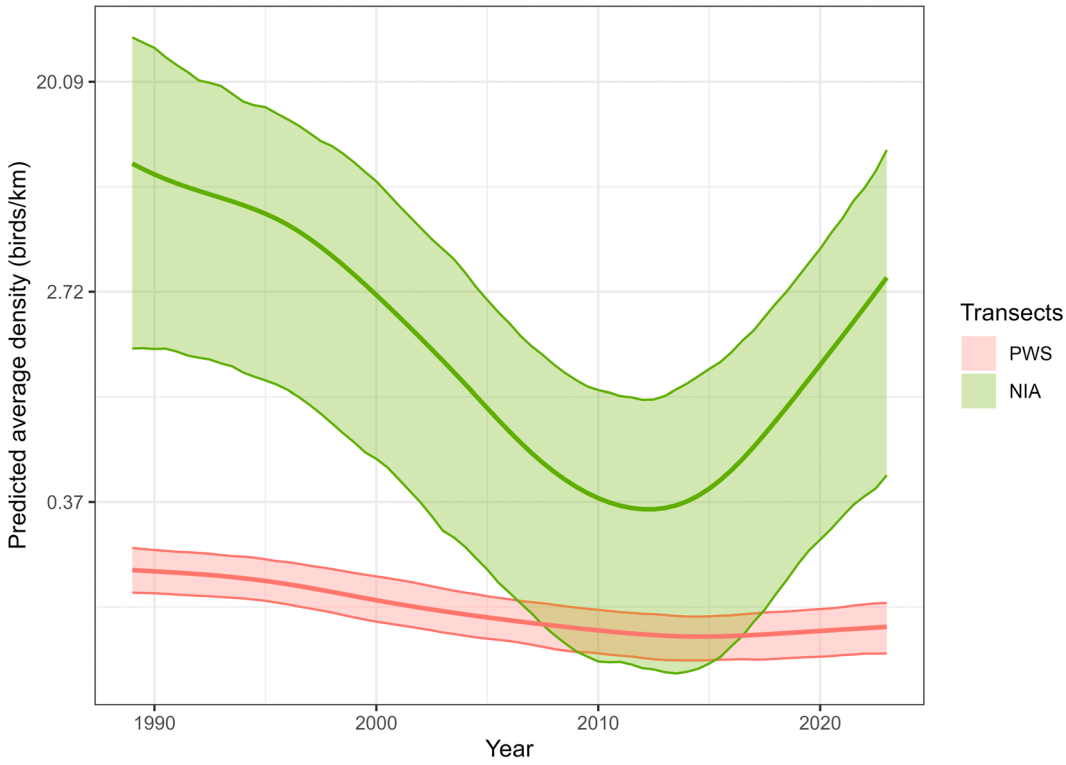

FIGURE 3 Predicted average density of pigeon guillemots (birds/km) on randomly-selected shoreline transects based on mid-nesting season (July) surveys throughout Prince William Sound (PWS), Alaska, USA, during 1989–2023. Average density of guillemots on shoreline transects ($n = 6$) in the Naked Island Archipelago (NIA), where mink were introduced and then removed, is shown separately from that of guillemots on shoreline transects elsewhere in PWS, where mink were generally naturally occurring ($n = 206$). We used generalized additive models (GAMs) to develop smoothing terms for trends at the NIA and in the remainder of PWS. Shaded areas represent the 95% credible interval of the smoothed trend line from the model.

[95% CI = 0.968–0.981]), but at a much lower rate than at the NIA (λ = 0.882 [95% CI = 0.847–0.918]; Figure 3). After the removal of mink from the NIA starting in 2014, the shoreline density of guillemots increased sharply and by 2023 had increased to 3.08 birds/km (95% CI = 0.47–9.95). In contrast, average shoreline density of guillemots in the rest of PWS stabilized during 2014–2023 at about 0.11 birds/km in 2023 (95% CI = 0.09–0.14), or about 3.5% of the shoreline density of guillemots at the NIA in 2023 (Figure 3).

Guillemot nesting

The number of active guillemot nests at the NIA increased from 11 nests in 2014 to 52 nests in 2018. The GAM explained >99% of the response variation in nest numbers among years, with an effective degrees of freedom for the smooth term of 2.63 (Figure 4), indicating a nearly quadratic response and an increase of 470% (95% CI = 385–588%) over the first 5 breeding seasons following the initiation of mink removal (Figure 4).

In 1979, before mink were well-established at the NIA, the random effects logistic regression estimated 64% (95% CI = 56–71%) of guillemot nests were in substrates that were more vulnerable to mink predation (i.e., cliff top or talus substrates). In 2008, after mink became well-established on the NIA, the model predicted 20%

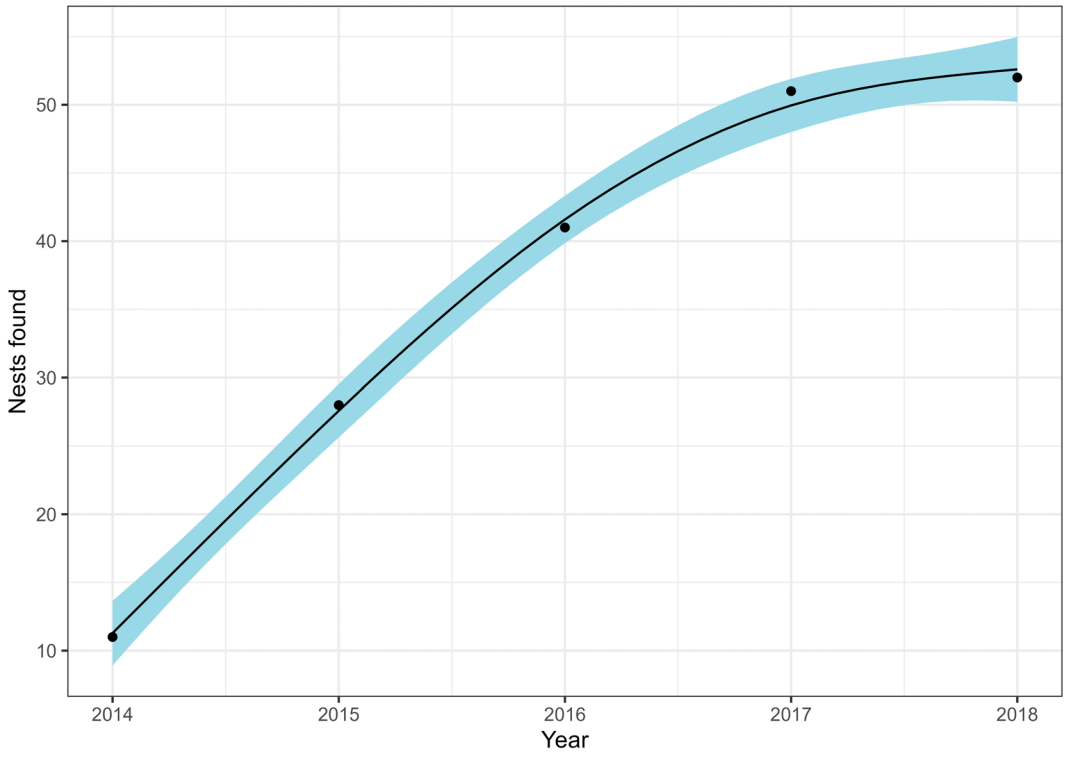

FIGURE 4 Predicted number of pigeon guillemot nests at the Naked Island Archipelago, Prince William Sound, Alaska, USA, in each breeding season during 2014–2018, following the initiation of mink removal. Dots represent the number of nests found, the line is the trend in predicted number of nests found from a generalized linear model (GAM), and the shaded area is ±2 standard errors from the predicted trend line.

(95% CI = 7–39%) of guillemot nests were in substrates more vulnerable to mink predation. Because of small sample size, the predicted percentage is greater than observed in that year (12%; Figure 5). During the period after the initiation of mink removal (2015–2018), we observed an increase in the percentage of more vulnerable nest site substrates used by guillemots at the NIA (posterior contrast in the mean of the 2015 to 2018 proportion minus the proportion in 2008 was 0.22 [95% CI = 0.02–0.37]; Figure 5). During the 2015 breeding season, the proportion of active guillemot nests that were in substrates more vulnerable to mink predation had increased to 36% (95% CI = 20–53%). In subsequent years the proportion increased to 39% (95% CI = 26–53%) in 2016, 45% (95% CI = 32–58%) in 2017, and 48% (95% CI = 35–60) in 2018, the last year when intensive nest search effort occurred (Figure 5).

During the 2017 nesting season, we checked active guillemot nests throughout the nestling period at 21 accessible nests containing a total of 36 nestlings (6 1-nestling broods and 15 2-nestling broods). Five of 36 guillemot chicks failed to fledge (13.9% mortality rate). Two nestlings (5.5%) were found dead in their nest crevice with a live sibling and no sign of nest predation; these 2 mortalities were considered non-predation events. Two other nestlings (5.5%) were apparently killed by predators. The first suffered injuries consistent with depredation by corvids (hole in the anterior cranium with emanating fracture lines, hole in the throat skin, and all breast and throat tissue missing); several common ravens (*Corvus corax*) were present near the nest when the nest was checked. The second nestling that was apparently killed by predators disappeared from the nest crevice prior to fledging (age ~19 days post-hatching) and was assumed to have been killed by a predator and removed. The final nestling mortality was a nestling that was apparently abandoned by its parents and died of starvation following the depredation of its brood mate, apparently by corvids.

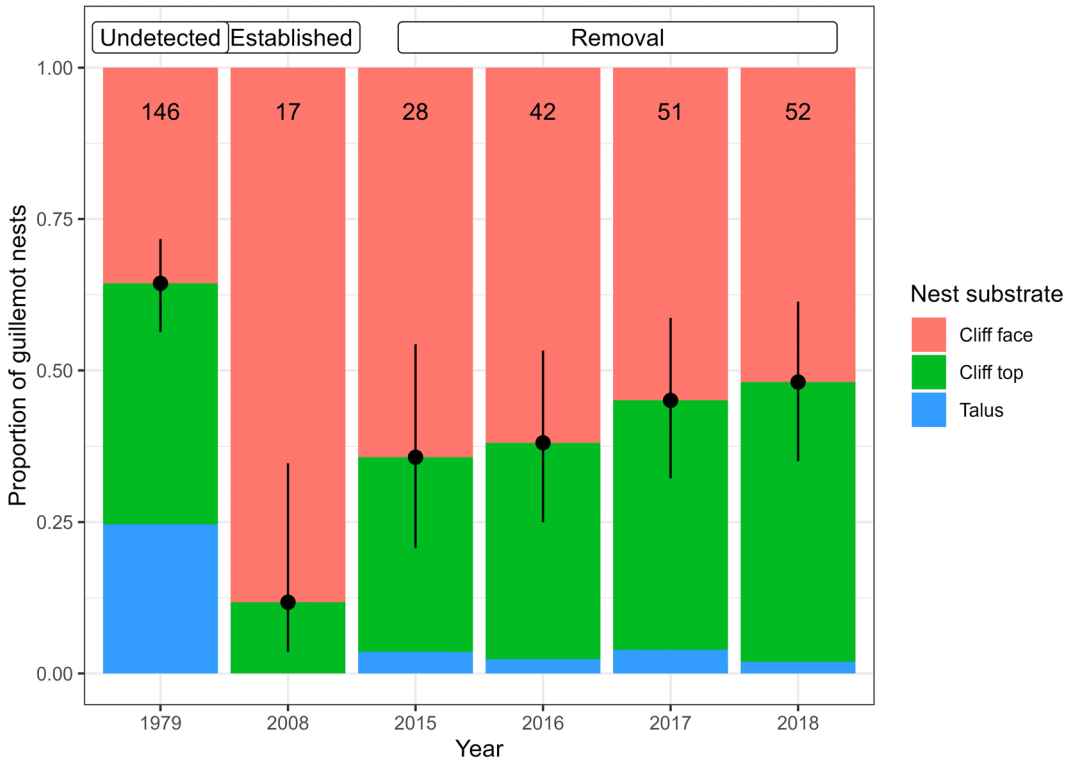

FIGURE 5 Proportion of pigeon guillemot nests in 3 types of nest site substrate (cliff face, cliff top, talus) at the Naked Island Archipelago, Prince William Sound, Alaska, USA, during 3 periods when mink abundance differed: undetected (1979), well-established (2008), and after removal (2015–2018). The proportions of nests in substrates more vulnerable to mink predation (cliff top, talus) were combined and compared to the proportion of nests in the substrate less vulnerable to mink predation (cliff face). Black points are the observed proportion of nests in cliff top and talus (more vulnerable) substrates, and error bars represent 95% credible intervals calculated using the observed frequencies within a year and a Beta (1, 1) prior.

A mixed model with nest and year random effects best explained nestling survival compared to the next best model that contained a random effect of nest and a fixed effect of mink removal period (ΔAIC = 50.3). The next best model only contained a random effect of year (ΔAIC = 52.5) and gave a similar result to the best model (not shown). Average nestling survival during 1978–1981, before mink were detected at the NIA, was 0.75 chicks/nest (95% CI = 0.62–0.86; Figure 6). During the period when higher numbers of mink were present on the NIA (1989–2008), nestling survival rates averaged 0.51 chicks/nest (95% CI = 0.44–0.59). The posterior difference between the average of nestling survival during 1979–1981 and 1989–2008 was 0.23 chicks/nest (95% CI = 0.09–0.37). In 2017, after mink removal, nestling survival rates rebounded to 0.88 chicks/nest (95% CI = 0.67–0.97; Figure 6), or an increase of 0.36 chicks/nest (95% CI = 0.15–0.50) between 2017 (after removal) and the average of 1989–2008 (when mink were present).

DISCUSSION

The dramatic increase in guillemot numbers at the NIA following mink removal and the absence of any increase in guillemot numbers at nearby mink-free islands support the hypothesis that mink removal from guillemot nesting areas at the NIA allowed the guillemot population to rebound once free from predation by mink. This provides

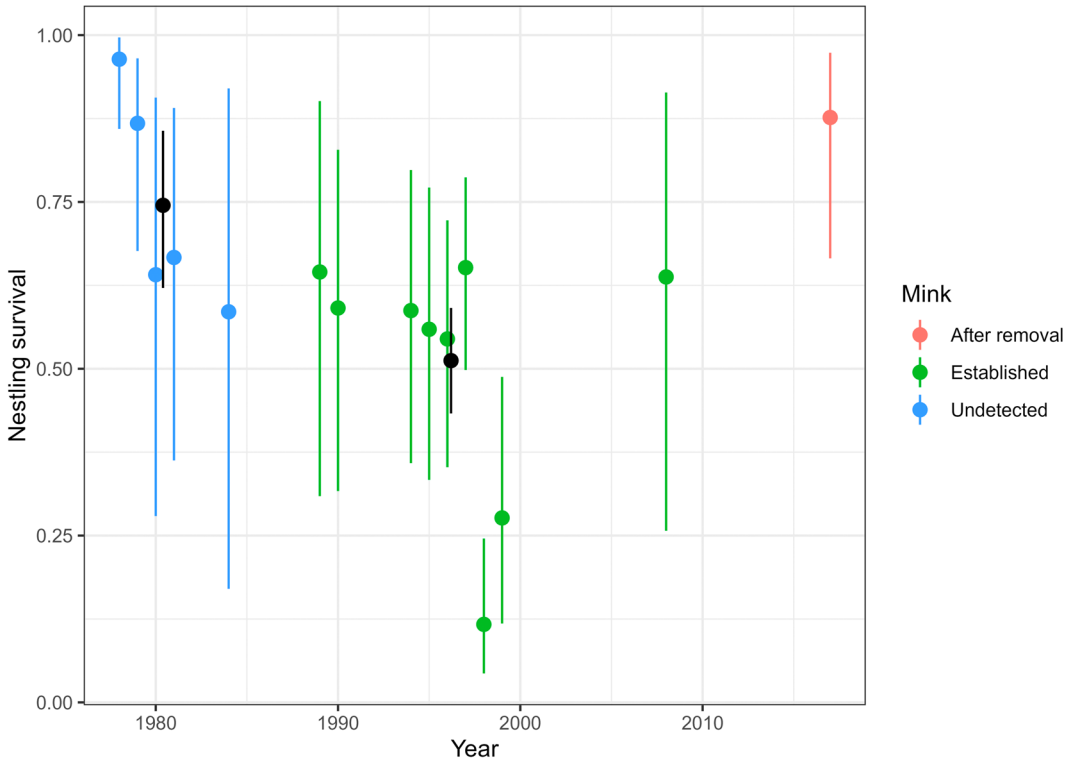

FIGURE 6 Pigeon guillemot nestling survival probability during 3 periods when mink abundance differed at the Naked Island Archipelago, Prince William Sound, Alaska, USA: undetected (1979–1984), well-established (1989–2008), and after removal (2017). Average nestling survival during the period when mink were undetected and when mink were well-established are indicated in black. Points are posterior means and error bars represent posterior 95% credible intervals.

further support for the conclusion by Bixler et al. (2025) that predation by introduced mink was the primary factor limiting the guillemot breeding population at the NIA during the 2000s.

To our knowledge, our study describes the first attempt to control an introduced population of American mink on a major island or archipelago in North America. The trapping of mink from 2014 to 2018 in guillemot nesting habitat at the NIA ultimately removed all mink from the islands. Apparently, all mink at the NIA were foraging or traveling in or near guillemot nesting habitat along the shoreline, and thus susceptible to the trapping effort. This presented us with a valuable opportunity to evaluate guillemot response to reduced predation pressure from mink during mink removal efforts and the elimination of mink predation afterwards.

The present study followed intermittent guillemot studies at the NIA in 12 different years over more than 3 decades, beginning in 1978 when the guillemot breeding population was very large compared to elsewhere in PWS. Information obtained from these previous studies allowed us to test our 2 hypotheses and the 5 predictions that followed from those hypotheses. Our first hypothesis was that predation by introduced mink was the primary limiting factor for the breeding population of guillemots at the NIA during 1990–2013. The data we collected during 2014–2023 confirmed our 4 predictions that mink removal would: 1) increase guillemot abundance, 2) increase the number of nesting guillemots, 3) increase the use of nest sites more accessible to mink, and 4) increase nestling survival rates compared to pre-mink removal. These results provided strong support for our first hypothesis. Our second hypothesis was that trends in guillemot numbers at nearby mink-free islands would differ from trends at the NIA after the removal of mink. We predicted that after mink removal, the annual rate of increase in the

number of guillemots at the NIA would be greater than at nearby mink-free islands (i.e., Seal Island, Fool Island, and the Smith Islands). The results of our study confirmed that guillemot population trends at the mink-free islands were stable or declining while the population at the NIA was sharply increasing (Figure 2), providing strong support for our second hypothesis.

The increase in the number of active guillemot nests during the first 5 years following the initiation of mink removal corresponded with the increase in guillemots counted at the NIA during pre-breeding surveys. During this period, the average annual recruitment rate of active guillemot nesting pairs to the NIA breeding population (λ) was 1.19 (19%/year). The rapid increase in nesting guillemots at the NIA after the initiation of mink removal demonstrates that nesting guillemots were recruited from outside the NIA, presumably from nearby mink-free islands where shoreline guillemot densities were highest (Figure 2). High rates of increase from intrinsic growth of the local guillemot breeding population at the NIA would not have occurred for several years after the initiation of mink removal efforts because the average age at first reproduction is 4 years (Ewins 1993, Russell 1999, Sæther and Bakke 2000).

The pre-breeding count of guillemots at the NIA increased substantially in 2015, immediately following the second year of mink trapping during late winter. Guillemots do not attend the colony until at least their third year, and many may not breed for the first time until their fifth or sixth year. Nevertheless, subadult guillemots are highly social and known to prospect for nest sites near active guillemot nests, particularly those containing nestlings (Nelson 1982, Ewins 1993, Vermeer et al. 1993*b*). The observed rapid increase in numbers of guillemots in pre-breeding surveys at the NIA supports the conclusion that immigration from nearby mink-free islands was the primary factor responsible for the large increase during the first 5 breeding seasons following the initiation of mink removal (Figure 4). A similar rapid increase in guillemot abundance was observed by Nordstrom et al. (2003) at some breeding islands following mink removal. Brooke et al. (2018) reviewed 69 studies of the effects of invasive predator removal on seabird populations nesting on islands and concluded that the initial increase following predator removal was wholly or mostly due to immigration.

In addition to the short time lag for the recruitment response, the magnitude of the initial response following mink removal was higher than expected. The average annual population growth rate (λ) observed at the NIA based on pre-breeding surveys during 2014–2023 was 1.14, similar to the increase in guillemot numbers at colonies in the Aleutian Archipelago, Alaska, following the removal of introduced arctic foxes (*Vulpes lagopus*), where the average λ was 1.13 over 6 years (Byrd 2001). Brooke et al. (2018) reported that in 8 studies involving seabird species in the family Alcidae, the average λ over a range of years after predator eradication was about 1.1, but they noted that λ was higher in the first several years following eradication and concluded that this initial surge was due to immigration.

Bixler et al. (2025) found that the local guillemot breeding population at the NIA declined during 1996–2008 at a rate greater than predicted based on the observed low nesting success and rate of adult mortality due to predation at the nest site. The higher-than-expected rate of decline was best accounted for by breeding guillemots emigrating from the NIA to other colonies. The reverse of this process may have driven the observed rapid rate of increase by guillemots in this study and suggests that suitable nest sites or forage fish resources were limited at mink-free islands near the NIA (Lewis et al. 2001, Litzow et al. 2002). Another possible source of these immigrating birds is from a cohort of floaters or birds unable to find suitable nest sites at other colonies (Kokko and Sutherland 1998). The NIA would have been an attractive area for floaters because of the removal of mink from guillemot nesting habitat and the high reproductive success of established breeders at the NIA (Danchin et al. 1998). As the number of floaters in central PWS declined, however, the rate of increase in guillemots counted during pre-breeding surveys and in numbers of active nests at the NIA would decline, and this was the pattern we observed (Figures 2 and 4).

Accessibility of nests to land-based predators has been associated with reduced nesting success and adult survival for guillemots (Emms and Verbeek 1989, Hayes 1995). Following the removal of mink from the NIA, we observed a rapid re-occupancy of nest sites that were readily accessible to mink. A similar change in nest site use

was observed following removal of black rats (*Rattus rattus*) from nesting colonies of Scripps's murrelet (*Synthliboramphus scrippsi*) on the Channel Islands of California, USA (Whitworth et al. 2013). In their study, nest sites that were accessible to rats had been vacant but were reoccupied following rat removal. The decrease in predation pressure in that study, as in the present study, allowed for successful nesting in these previously unoccupied nest site types.

The increase in guillemot nestling survival post-mink removal, concurrent with the increased use of nest sites readily accessible to mink, strongly supports the conclusion that the recent increase in numbers of guillemots nesting at the NIA was due to mink removal. Bixler et al. (2025) identified mortality of nestling guillemots as a factor limiting the growth of the guillemot breeding population at the NIA in 2008. Guillemot nestling survival at the NIA, which Golet et al. (2002) found was negatively correlated with predation rates on nestlings, returned to levels observed prior to the detection of mink at the NIA (1978–1981; Kuletz 1983) following mink removal. In 2017, we did not observe predation on adult guillemots at active nests, which was confirmed at 9% of monitored nests in 1998 (Golet et al. 2002) and at 10% of monitored nests in 2008 (Bixler 2010). The mortality rates of guillemots nesting at the NIA and their nest success rates have apparently returned to the levels observed before mink became well-established at the NIA (Kuletz 1983), levels expected at guillemot colonies that are free of mammalian predators (Ainley et al. 1990).

Having long-term monitoring data on our study species has allowed us to draw conclusions previously out of the reach of earlier studies of the effects of removing introduced mustelids. The robust design of our study allowed us to quantify the effect of predator removal through changes in demographic rates. Monitoring the number of active guillemot nests following control of introduced mammalian predators has not been conducted as part of previous studies (Byrd et al. 1997, Byrd 2001, Nordstrom et al. 2003). We agree with Brooke et al. (2018) that future predator removal studies should strive to collect post-removal data on both the predator and the prey.

MANAGEMENT IMPLICATIONS

We provide a case study of how the removal of an introduced predator resulted in a rapid, positive response in a seabird breeding population. Long-term monitoring of pigeon guillemots in our study area provided a rare opportunity to compare and contrast demography and nesting ecology of a seabird species 1) before an introduced predator became established, 2) once the predator was well-established, and 3) following predator removal. Future avian restoration efforts involving the removal of invasive predators may find comparable results when targeting insular bird populations in similar ecological settings. The results of our study provide further support for the efficacy of predator removal from islands to restore declining seabird breeding populations and the importance of monitoring following predator removal. The removal of mink from the NIA has the potential to restore a formerly large local breeding population of guillemots at the NIA that likely served as a source for the regional population in Prince William Sound, a population that has experienced long-term decline over the last half century.

ACKNOWLEDGMENTS

We thank M. Arias, G. Golet, B. Golet, B. Higgins, E. Labunski, T. Lawes, A. Peck-Richardson, A. Piggott, M. Reedy, and B. Underwood for their valuable field assistance. J. Dinkins and R. Suryan provided assistance with statistical analysis, and K. Bixler and K. Kuletz provided context and insight for this study as well as the study area figure. We are grateful to 2 anonymous referees and C. Rota for reviews and comments that improved an earlier draft. The USFWS, the *Exxon Valdez* Oil Spill Trustee Council, and the National Fish and Wildlife Foundation provided funding support for this study. Permission to conduct research on the NIA was granted by the United States Forest Service.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data, R code, R model objects, figures, and supplemental summary documents that support the findings of this study are available at https://doi.org/10.7944/m15x-3h89.

ETHICS STATEMENT

All protocols involving live mink were approved by the Institutional Animal Care and Use Committee (IACUC) of the USFWS, Region 1 (ACUP No. 2014-01). We captured and handled guillemots during this study following protocols approved by the IACUC of Oregon State University (ACUP 4919).

ORCID

Erik E. Osnas https://orcid.org/0000-0001-9528-0866

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Associate Editor: Christopher Rota.

How to cite this article: Stark, S. B., D. D. Roby, D. B. Irons, R. S. A. Kaler, and E. E. Osnas. 2026. Seabird population responses after the removal of an introduced predator. Journal of Wildlife Management e70242. https://doi.org/10.1002/jwmg.70242