Vulnerability of ground-nesting waterbirds to predation by invasive American mink in the Cape Horn Biosphere Reserve, Chile

Elke Schüttler [a,b,c,*], Reinhard Klenke [a,d], Steven McGehee [b,e], Ricardo Rozzi [b,f], Kurt Jax [a,b,c]

[a] Department of Conservation Biology, UFZ-Helmholtz Centre for Environmental Research, Permoserstr. 15, 04318 Leipzig, Germany
[b] Omora Ethnobotanical Park (IEB-Institute of Ecology and Biodiversity, University of Magallanes, and Omora Foundation), Puerto Williams, Antarctic Province, Chile
[c] Lehrstuhl für Landschaftsökologie, Technische Universität München-Weihenstephan, Am Hochanger 6, 85350 Freising, Germany
[d] Society for Nature Conservation and Landscape Ecology, Dorfstr. 31, 17237 Kratzeburg, Germany
[e] Department of Biology, University of Victoria, P.O. Box 3020, Victoria, B.C. V8W 3N5, Canada
[f] Department of Philosophy, University of North Texas, Denton, TX 76201, USA

ARTICLE INFO

ABSTRACT

Biological invasions constitute one of the most important threats to biodiversity. This is especially true for "naïve" birds that have evolved in the absence of terrestrial predators in island ecosystems. The American mink (Mustela vison) has recently established a feral population on Navarino Island (55°S), southern Chile, where it represents a new guild of terrestrial mammal predators. We investigated the impact of mink on ground-nesting coastal waterbirds with the aim of deriving a vulnerability profile for birds as a function of different breeding strategies, habitat, and nest characteristics. We compared rates of nest survival and mink predation on 102 nests of solitary nesting species (Chloephaga picta, Tachyeres pteneres), on 361 nests of colonial birds (Larus dominicanus, Larus scoresbii, Sterna hirundinacea), and on 558 artificial nests. We calculated relative mink and bird densities at all nest sites. Nests of colonial species showed the highest nest survival probabilities (67–84%) and no predation by mink. Nest survival rates for solitary nesting species were lower (5–20%) and mink predation rates higher (10–44%). Discriminant analyses revealed that mink preyed upon artificial nests mainly at shores with rocky outcroppings where mink were abundant. High nest concealment increased the probability for predation by mink. Conservation planning should consider that invasive mink might severely affect the reproduction success of bird species with the following characteristics: solitary nesting, nesting habitat at rocky outcrop shores, and concealed nests. We recommend that work starts immediately to control the mink population with a priority in the nesting habitats of vulnerable endemic waterbirds.

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1. Introduction

The earth's biota is greatly altered by invasive plant and animal species producing concern and discussion about their ecological consequences (Elton, 1958; Vitousek et al., 1997; Gobster, 2005; Vellend et al., 2007). Biodiversity on islands is particularly vulnerable to biotic exchange (Courchamp et al., 2003; Sax and Gaines, 2008). The survival of introduced species on islands and the significance of their ecological impacts are less a matter of low insular biodiversity (Levine and D'Antonio, 1999); rather it depends on the nature of those species that are present or those groups of species that are missing from the islands (Goodman, 1975; Simberloff, 1995). This is especially true for alien carnivore invasions on islands where terrestrial mammalian predators were absent before. Their impact on insular bird populations can cause extensive population reductions and even local extinctions (King, 1985; Atkinson, 1996; Macdonald and Thom, 2001).

Bird populations are regulated by natural limiting factors like predation, food supply, nest sites, parasites, pathogens, competition, and human-induced factors like hunting, pesticides or pollutants (Newton, 1998). The effects of predation depend on the extend to which it is additive to compensation by other losses. In some ground-nesting waterbirds, however, predation can not only reduce egg and chick stages (Opermanis et al., 2001; Kauhala, 2004; Nordström and Korpimäki, 2004), but actually also their breeding numbers (Côté and Sutherland, 1997; Newton, 1998). Hence, bird species are assumed to develop their own strategies to minimize predation (Martin, 1993). It is widely accepted that prey naïvety plays a significant role in the confrontation with the threat of an introduced predator, because native fauna often lack those strategies to minimize predation as behavioral or evolutionary

adaptations (Berger et al., 2001; Short et al., 2002; Nordström et al., 2004). Critical factors among those adaptations are (i) social factors like coloniality (Inman and Krebs, 1987; Siegel-Causey and Kharitonov, 1990), (ii) area-specific factors like habitat (Willson et al., 2001; Whittingham and Evans, 2004) or nest density (Ackerman et al., 2004), and (iii) site-specific factors like nest height (Martin, 1995) or nest concealment (Butler and Rotella, 1998; Rangen et al., 2000). Those factors have been investigated separately or in combination, with artificial and/or natural nests, often with contradictory results (Major and Kendal, 1996). Finally, nest predation processes cannot fully be understood without knowledge of the predator community, i.e., abundance and searching behavior of predators (Angelstam, 1986; Miller and Knight, 1993).

The American mink (*Mustela vison*) is a carnivorous species from North America that has recently established its southernmost reproducing population in the world on Navarino Island, Cape Horn Biosphere Reserve (southern Chile, 54–56°S). It was first registered on the island in 2001 (Jaksic et al., 2002; Rozzi and Sherriffs, 2003), but arrived earlier in Tierra del Fuego on the other side of the Beagle Channel in the 1940s and 1950s (Lizarralde and Escobar, 2000). Therefore, it is most probable that some individuals crossed the Beagle Channel after escaping from fur farms in Tierra del Fuego (Rozzi and Sherriffs, 2003). On Navarino Island, mink represent a new guild (Root, 1967) because the island lacks native terrestrial mammalian predators. In this pristine ecoregion the most diverse and abundant group of vertebrates are birds (Rozzi et al., 2006). Many of them are ground-nesting, including two songbird species (*Turdus falcklandii*, *Zonotrichia capensis*) that use ground nests in the Cape Horn region (S. McGehee, unpublished data), while in other parts of Chile the same species nest in trees. Therefore, scientists and public agencies have expressed strong concerns about the impact of mink on the island's avifauna, especially ground-nesting birds (Rozzi and Sherriffs, 2003; Anderson et al., 2006; Soto and Cabello, 2007).

American mink are semi-aquatic mustelids inhabiting marine coasts, flowing waters, and banks with a generalist diet including prey from both aquatic and terrestrial sources (Dunstone, 1993). Birds are most exposed to the risks of opportunistic predation by mink during their reproductive period due to the birds' limited mobility (Arnold and Fritzell, 1987; Bartoszewicz and Zalewski,

2003) in combination with the higher energy requirement of the breeding mink (Dunstone, 1993). In Europe, introduced mink have successfully established feral populations (reviews in Macdonald and Harrington, 2003; Bonesi and Palazon, 2007), which prey significantly upon ground-nesting wetland birds (Ferreras and Macdonald, 1999) and seabirds (Collis, 2004; Nordström and Korpimäki, 2004). Also some cases of surplus-killing of chicks and adults within a colony have been reported (e.g., Craik, 1997). In South America, wild mink populations in the southern part of Chile and Argentina also include birds in their diets (Medina, 1997; Previtali et al., 1998; Fasola et al., 2008; Schüttler et al., 2008; Ibarra et al., 2009). However, studies on the impact of mink on waterbirds in the southern hemisphere are scarce.

The main purpose of our study was to understand the impact of the American mink as a recently introduced terrestrial predator on the nest survival of naïve ground-nesting waterbirds on Navarino Island. We aim to draw an overall vulnerability profile of bird species to predation by mink as a function of their breeding strategy (colonial vs. solitary nesting), as well as area-specific (habitat), and site-specific (nest concealment) factors. Based on this profile, we discuss high priority species of ground-nesting waterbirds for conservation and implications for the management of mink populations in the southernmost tip of the Americas.

2. Methods

2.1. Study area

The study was carried out on Navarino Island (2528 km^2), Chile, located at the extreme southern tip of South America (Fig. 1). The island forms part of the Cape Horn Biosphere Reserve (Rozzi et al., 2006) and belongs to the Magellanic Sub-Antarctic forest ecoregion, recently identified as one of the 24 most pristine wilderness areas of the world Forest Biome (Mittermeier et al., 2003). The main habitats include (i) evergreen rainforests dominated by *Nothofagus betuloides* and *Drimys winteri*, (ii) Magellanic deciduous forests of *Nothofagus pumilio*, (iii) peatlands, moorlands, and bogs (*Sphagnum* spp.), (iv) high-Andean communities dominated by
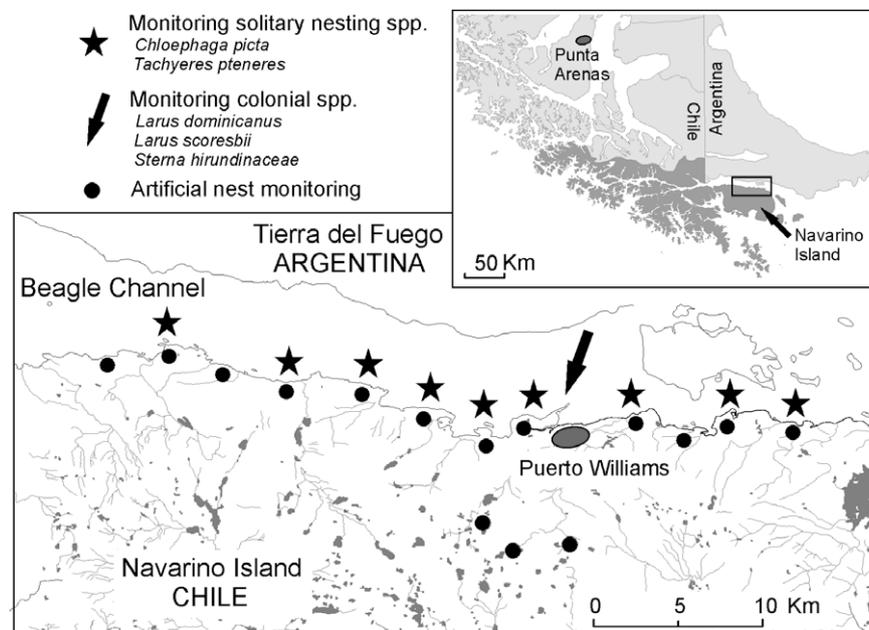

Fig. 1. Map of the nest monitoring study sites. Navarino Island is located within the Cape Horn Biosphere Reserve (54°–56°S, shaded in dark grey, top right) in southern South America.

cushion plants and lichens, and (v) thickets or scrublands in naturally or anthropogenically disturbed areas (Pisano, 1977; Rozzi et al., 2006). The climate type is oceanic, with a low annual thermic fluctuation (<5 °C), a mean annual temperature of 6 °C, and an annual precipitation of 467.3 mm (Pisano, 1977). During winter, streams and lakes are ice-bound. Human population is concentrated in the town of Puerto Williams (ca 2200 inhabitants), the capital city of the Chilean Antarctic Province, on the northern coast of Navarino. Due to the extremely limited infrastructure on Navarino Island – only one dirt road connects the northern coast – our research was mainly restricted to this accessible coast of the island. The interior of the island must be reached by the three existing trekking trails, and western, southern and eastern coasts rely on water transport.

Our study sites comprised twelve 4 km long transects of marine shoreline and three lakes at a distance of 5.3–7.7 km from the coast and an altitude of 387–510 m. All study sites were separated by more than 3 km in order to cover distinct territories of mink, which occupy on average linear territories of 3 km (Dunstone, 1993). We conducted natural and artificial nest monitoring, bird counts, and mink surveys in the same coastal study sites and during the same breeding seasons. At lakes, we only focused on artificial nest monitoring and mink surveys.

2.2. Species studied

We concentrated our study on solitary nesting and colonial species that are resident, common, or endemic in the region. The solitary nesting species studied were the upland goose (*Chloephaga picta*) and the flightless steamer duck (*Tachyeres pteneres*). The upland goose occurs as a resident on coasts and in wet grasslands of Patagonia and the Falkland Islands (Couve and Vidal, 2003). It usually breeds close to water (up to 200 m), along the coast, river valleys, and around ponds (Summers and McAdam, 1993). On Navarino Island, upland geese were found breeding close to water mainly in scrublands dominated by *Berberis buxifolia*, *Pernettya mucronata* and *Chiliotrichum diffusum* (Moore, 1983), and less frequently in forested habitats or meadow communities. The flightless steamer duck is a strictly coastal species endemic to western Patagonia and Tierra del Fuego (Couve and Vidal, 2003). The flightless species nests on rocky outcrops, but access to uplands and to the sea must be easy (Weller, 1976). This pattern was observed on Navarino Island, too. Among colonial seabirds, we focused on kelp gulls (*Larus dominicanus*), dolphin gulls (*Larus scoresbii*), and South American terns (*Sterna hirundinacea*). Only the dolphin gull is endemic to Patagonia and the Falkland Islands (Couve and Vidal, 2003). Kelp gulls nest in a wide variety of environments along the sea coast and at continental wetlands (Yorio et al., 1999; Yorio and Borboroglu, 2002), whereas dolphin gulls and South American terns are more restricted to breeding habitats on bare rocks close to the water's edge or on small offshore islands (Scolaro et al., 1996; Yorio et al., 1996). On Navarino Island, these three species nested in close vicinity (<20 m) to each other on an exposed marine peninsula composed of bare gravels with marine deposits and meadow patches, the latter were used for nesting by the terns (Fig. 1). Potential autochthonous predators of eggs include the southern crested caracara (*Caracara plancus*), chimango caracara (*Milvago chimango*), Chilean skua (*Catharacta chilensis*), and kelp gull (Johnson, 1965). Among the mammal species introduced to the Cape Horn Biosphere Reserve, the American mink and feral domestic dog (*Canis familiaris*) prey upon bird eggs. Predation by Norway rats (*Rattus norvegicus*) and feral pigs (*Sus scrofa*) was assumed to be uncommon as rats are only associated with the one town on the island, Puerto Williams (Anderson et al., 2006), and tracks of pigs were absent along our transect walks. Humans occasionally take eggs from the nests of upland geese and gulls.

2.3. Natural nests

Breeding activity of solitary nesting and colonial bird species was monitored along the northern coast of Navarino Island during 74 days of the nesting season of 2005/2006 and during 88 days of the nesting season of 2006/2007 starting on 1st November on each year. We monitored 463 nests: upland goose ($n = 79$), flightless steamer duck ($n = 23$), kelp gull ($n = 204$), dolphin gull ($n = 83$), and South American tern ($n = 74$). Study sites comprised seven (2005/2006) and nine transects (2006/2007) of 4 km shoreline. In order to detect nests of solitary nesting species, we walked the transects and recorded territorial behavior or presence of a guarding male. Dolphin gulls and South American terns were only found breeding in 2006/2007 and in close vicinity to the kelp gull colony. Typically, eight days (8.16 d, SD = 1.91 d) elapsed between successive visits to the same nest. At each visit we recorded the number of eggs until hatching, abandonment, or predation occurred. In order to minimize positive or negative observer effects on nest survival as a result of human tracks, nest attendance, or behavior (Götmark, 1992), we chose a moderate frequency of nest visits, flagged shrubs decently with short orange and yellow tapes at a distance of 5 m from the nest and reduced nest visit time to the minimum (<1 min). We use the term nest survival to refer to the probability that a nest will hatch at least one young over the entire nesting period (Dinsmore et al., 2002; Jehle et al., 2004). This definition does not take into account predation events affecting only some eggs of a surviving nest; therefore, it overestimates offspring's survival. However, in our nest data, predation or unknown loss of some eggs in successful nests only happened in 9% of all successful nests ($n = 318$). These nests concerned 7 nests of upland geese, 16 nests of kelp gulls, 2 nests of dolphin gulls, and 3 nests of South American terns. We guess that possible predators for upland geese were autochthonous bird predators or humans rather than the mink, since it destroys many or all eggs at once (Ferreras and Macdonald, 1999). In the colonies the gulls themselves were probably responsible for scavenging or removing eggs.

2.4. Artificial nests

Although artificial nests are widely used in avian field studies (Moore and Robinson, 2004), they have been criticized as not reliably reflecting predators and predation rates of natural nests (e.g., Faaborg, 2003). This is because artificial nests differ from real nests in a number of important ways such as nest type, egg type, concealment, nest spacing, odor, missing adults etc. (Major and Kendal, 1996). In order to maximize the external validity of experimental design, authors recommend using artificial nests primarily in conjunction with active nests and identifying the predators at both types of nest (Mezquida and Marone, 2003; Moore and Robinson, 2004). So far, a direct comparable context (same data taken at the same time and location, and with the same methods) has been achieved in only a few studies (review in Moore and Robinson, 2004). Here, we combined natural nest monitoring with artificial nests in a comparable context as a way to effectively investigate the influence of habitat and nest characteristics on the predator type. Yet, we are aware that the interpretation of our data derived from artificial nests has to be treated with caution.

Artificial nests were constructed to imitate geese nests and were baited with one domestic chicken egg and one clay egg. Artificial ground nests were of approximately 20 cm in diameter, lined with dry plant material and upland goose down. In order to reduce olfactory cues that might influence predators, we washed the chicken eggs and used gloves when handling eggs and nests. The nests were marked with flagging tape in the same manner as for the natural nests.

Five hundred and seventy-five artificial nests were installed at twelve study sites in marine coastal habitats ($n = 500$) and at three sites along lakes ($n = 75$). These sites included two different types of shore: (1) "rocky outcrop" ($n = 225$ nests), and (2) "beaches" ($n = 350$ nests). These two shore types were assigned as follows: within each study site, each 200 m we measured the percentage of cliff, rock, pebbles, sand, mud, and vegetation (leaf litter, grasses, mosses) within 10×1 m of the shoreline, as well as the incline of the shore within 10 m from the water shed (flat: 0–1 m, medium: 1–2 m, steep: <2 m). The first shore type, rocky outcrop, was assigned when over the half of these measurements were predominated by cliffs, rocks, and steep shores, whereas beaches were characterized by over 50% pebbles, sand, mud, vegetation, and flat shores. The adjacent vegetation in the twelve study sites were majorly shrubs of *B. buxifolia* and *C. diffusum*, but also forested habitats (*Nothofagus* spp.) and meadows (Pisano, 1977; Moore, 1983; Rozzi et al., 2006). In coastal habitats, 200 nests were placed in a 71 day nesting season starting on 29th December 2005, and 300 nests were placed in a 69 day nesting season starting on 4th December 2006. At the lakes, 75 nests were installed starting on 6th January 2007 in order to survey for mink predation in the interior of the island where upland geese use wetlands for breeding (Summers and McAdam, 1993; S. McGehee, unpublished data).

Each of the 12 artificial nest sites comprised a stretch of 1.25 km, where 25 nests were distributed with a distance of 50 m in between each nest. Nests were placed up to 30 m from the water's edge in different vegetation types, cover and different degrees of nest concealment defined by the vegetation found at each 50 m mark. We monitored nests at 5 day intervals (5.12 d, SD = 0.41 d) for 29–30 days, which is the incubation period of upland geese after completing the clutch (Summers and McAdam, 1993). We considered a nest to have been preyed upon when at least one egg was found preyed on or marked with bills or teeth. Humans destroyed 17 nests in the marine coastal habitat. These nests were excluded from our analysis (total $n = 558$).

2.5. Predator identification

We categorized predators into five groups: American mink, domestic dogs, humans, birds, and "unknown" for uncertain cases caused by multi-predator visits or the lack of clues. The identification of predators was based on a detailed examination of eggshells and their location, nest material dislocation, and other signs, such as the presence of hairs or scats. Although some authors preclude the identification of nest predators from nest remains (e.g., Larivière, 1999), we believe that we classified predators in an unbiased manner. The predator community on Navarino Island is remarkably small and overlaps in predator patterns are rare. However, for the three species nesting in colonies, it was difficult to identify predators, mostly due to the disappearance of egg shells, which were exposed to strong winds and bird activity in the colony. To diagnose mink predation, we followed Craik (1995) and Opermanis et al. (2001) Mink predation signs were: canine marks, typically 1–2 mm wide and, if paired, ca 10 mm apart, eggshells often hidden under vegetation, eggs might be untouched, and nests little damaged. Bird predation signs were: small egg fragments, eggshells in nest or vicinity, eggs missing, nest material lifted or spread to the nearby surroundings. Dog predation signs were: egg punctures 4–5 mm wide and, if paired, >3 cm apart, egg fragments >½ egg, widespread, and nest remains spread out. If all eggs disappeared without signs of fragments, and downy feathers still covered the nest, this pattern was attributed to humans (but only for solitary nesting species). Employing comparison with beak imprints in the clay eggs taken from specimens, 42.3% of artificial clay eggs preyed upon by birds could further be classified into species. A small number of imprints of rodent incisors on artificial clay eggs

(2.5%, $n = 14$ nests) were attributed to mice (either *Abrothrix xanthorhinus* or *Oligoryzomys longicaudatus*).

2.6. Area and nest site characteristics

We examined the effect of area and site characteristics of nests on the type of predator (mink vs. birds) they attracted. We chose variables that were important for different search tactics (e.g., Butler and Rotella, 1998) (Appendix A). We took measurements at all nest sites of solitary nesting species ($n = 102$) and at all artificial nests set in the nesting period 2006/2007 ($n = 375$). Area-specific variables were taken for all artificial nests ($n = 558$). Measurements were conducted on the day a nest was found or constructed.

2.7. Bird and mink abundance

We censused bird populations 2–4 times during each breeding season at seven (2005/2006) and nine (2006/2007) coastal study sites. We counted the target species and avian predators (together eight species) using binoculars (8×25) while walking 4 km transects along the shorelines during the morning. We recorded all observations of adult and juvenile animals on both sides of the transect, up to 50 m away (1 transect = 40 ha). Line transects are favored over point counts if targeted species are relatively easy to identify, but mobile, and occurring at low densities (Bibby et al., 2000). Gulls and terns occupying large colonies were counted from a larger distance to prevent flushing and were cross-checked by a second observer. However, we are aware that our estimations of colonial birds are approximate. For our analysis we pooled data over study sites, although the abundance of solitary nesting species and predatory birds (colonies excluded) differed significantly between sites (Kruskal-Wallis-Test: $\chi^2 = 224.7$, $df = 6$, $p < 0.001$). However, further investigation of the causes of these differences is beyond the scope of this paper.

We systematically surveyed for mink signs (scats, tracks, sightings) twice each breeding season (spring and summer) at seven (2005/2006) to twelve (2006/2007) marine coastal study sites and at three lakes (2006/2007). At three marine sites and at lakes, we relied on data from one survey only (summer 2007). The 4 km transects and lake perimeters (1 km) were divided into 500 m contiguous sections and the proportion of positive sections (with signs) for each transect was calculated (e.g., Bonesi and Macdonald, 2004).

2.8. Statistical analysis

For estimates of nest survival of natural and artificial nests, we used the Mayfield estimator (Mayfield, 1961) with the standard error developed by Johnson (1979). The Mayfield method estimates the daily survival rate (*DSR*) as $DSR = 1 - DPR$ (daily predation rate). *DPR* is calculated as the number of failed nests divided by the number of exposure days. For the calculation of the number of exposure days of failed nests, we assumed that failure occurred at the midpoint between the final nest checks. The nest survival rate over the nesting period t (days) is calculated as $(DSR)^t$, which can be expressed as a percentage. The durations of egg-laying and incubation periods were taken from the literature (see caption Fig. 2). As we lacked literature for flightless steamer ducks, we used the periods described for upland geese. Data for both breeding periods were pooled. As data from the egg-laying period was sparse, we could not stratify by stages (as recommended by Jehle et al., 2004) and thus had to assume constant nest survival.

We used principal component analysis (PCA) and linear discriminant analysis (DA) in order to check for the compatibility of artificial nests with natural nests, and to check for differences in site-specific nest variables (six variables, Appendix A) between
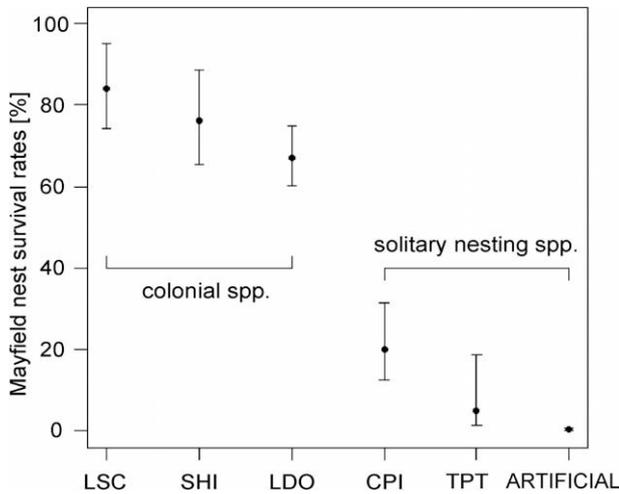
Fig. 2. Nest survival estimates for colonial and solitary nesting species. Survival probabilities followed Mayfield (1961) with 95% confidence intervals (Johnson, 1979). Breeding periods were pooled. LSC = *Larus scoresbii*[a], SHI = *Sterna hirundinacea*[b], LDO = *Larus dominicanus*[c], CPI = *Chloephaga picta*[d], TPT = *Tachyeres pteneres*[e], ARTIFICIAL = Artificial nests[f]. Egg-laying and incubation periods (*t*) applied in *DSR*^*t*. [a]26 days (Yorio et al., 1996), [b]26 (Scolaro et al., 1996), [c]28.5 (Yorio and Borboroglu, 2002), [d]36 (Summers and McAdam, 1993), [e]36 (as *C. picta*), [f]30.

nests of the solitary nesting species (classes = species). This first data set (DA 1) combined artificial and natural nests (*n* = 475). In a second data set (DA 2), we investigated the combination of area-specific and site-specific nest variables (eleven variables, Appendix A), which best separates the type of predator (classes = predators) using artificial nests (*n* = 375, 2006/2007). We performed a DA based on the results of the PCA using the ade4 package rewritten for the R environment (R Development Core Team, 2008) of the ADE-4 software (Thioulouse et al., 1997). The implementation of the ade4 package follows the "French way" (Holmes, 2008) and is based on the use of a unifying mathematical tool: the duality diagram (for details see Dray and Dufour, 2007). For DA 2, we applied a reduced set of variables based on the PCA results in order to prevent redundancy of information. The significance of the DA was tested by a Monte-Carlo permutation test. Continuous variables that were not normally distributed were transformed. We log transformed distance and height, and arcsine square-root transformed mink density. The PCA routine of the ade4 library applies variables standardized to zero mean and unit variance.

We used non-parametric statistics for comparing proportions (2-sample tests for equality of proportions), sample medians (Wilcoxon's rank sum test), and for testing for independence in contingency tables (Fisher's exact and chi-square tests) with Yates'

continuity and Bonferroni corrections, all two-sided. The statistical analyses conducted in R version 2.7.1. (R Development Core Team, 2008) were considered significant when *p*-values were < 0.05. The discriminant analysis DA 2 was documented in R source code and submitted as Supplementary material.

3. Results

3.1. Nest survival probabilities

Mayfield constant nest survival rates were comparatively high for species nesting in colonies: 84.2% for dolphin gulls, 76.3% for South American terns, and 67.2% for kelp gulls. In contrast, nest survival rates were low for the solitary nesting upland goose (20.0%), and very low for the solitary nesting flightless steamer duck (5.2%) (Fig. 2). Artificial nests had the lowest survival rates with only 0.4% surviving. As the 95% confidence intervals of Mayfield nest survival probabilities of species nesting in colonies did not overlap with those of solitary nesting species, differences in the nest survival of these two breeding strategies were significant.

3.2. Identified predators

We found different patterns of predation for solitary nesting species, colonial species, and the artificial nests (Table 1). Minks were the most important predators of nests of flightless steamer ducks accounting for 52.6% of preyed nests (successful and abandoned nests excluded). On the contrary, the mink was responsible for only 18.2% of the preyed nests of upland geese, the difference being significant between the two solitary nesting species (2-sample test for equality of proportions: χ^2 = 6.1, *p* = 0.01). The predation rate of mink on artificial nests (pooled over breeding periods as there were no significant differences) was 17.3% and thus comparable with values of predation by mink on upland geese nests. Predation on artificial nests in rocky outcroppings, however, yielded a significantly higher predation rate (36.4% of total predators) than along beaches (6.2%, 2-sample tests for equality of proportions: χ^2 = 77.9, *p* < 0.001). The same trend was detected for upland geese, whose nests were preyed upon by mink to a higher proportion at rocky outcrop shorelines (27.3% or 3 out of 11 preyed nests) than at beaches (15.2% or 5 out of 33 preyed nests). This was not true for flightless steamer ducks, though (46.7% or 7 out of 15 at rocky outcrops versus 75.0% or 3 out of 4 at beaches). We did not find any predation by mink in the three colonial species, but they had a quite high rate of unknown nest failure of 84.6–100% (9.6–24.0% of total nests found). Thus predation by introduced mink coincided with those species characterized by rather low Mayfield nest survival probabilities.

Birds as autochthonous predators were greatly responsible for lowering the nest survival of artificial nests (68.6%). We identified

Table 1
Nest fate of natural and artificial nests. Numbers indicate the percentage of total nests found and, in parenthesis, the percentage of total preyed nests (successful and abandoned nests excluded).

Nest fate	*Chloephaga picta*	*Tachyeres pteneres*	*Larus dominicanus*	*Larus scoresbii*	*Sterna hirundinacea*	Artificial nests
Successful[*]	36.7	8.7	74.0	90.4	82.4	0.0
Abandoned	7.6	8.7	0.0	0.0	0.0	–
Mink	**10.1 (18.2)**	**43.5 (52.6)**	**0.0 (0.0)**	**0.0 (0.0)**	**0.0 (0.0)**	**17.3 (17.3)**
Bird	17.7 (31.8)	21.7 (26.3)	2.0 (7.5)	0.0 (0.0)	0.0 (0.0)	68.6 (68.6)
Human	13.9 (25.0)	4.4 (5.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Dog	1.3 (2.3)	8.7 (10.5)	0.0 (0.0)	0.0 (0.0)	2.7 (15.4)	0.0 (0.0)
Mouse	–	–	–	–	–	2.6 (2.6)
Unknown	12.7 (22.7)	4.3 (5.3)	24.0 (92.5)	9.6 (100.0)	14.9 (84.6)	11.5 (11.5)
Total nests	79	23	204	83	74	558

[*] No. of successful nests/no. of total nests found yields into the naïve nest survival estimator which is positively biased (Jehle et al., 2004).

bird predators of 236 clay eggs: the southern crested caracara was the most common avian predator with 62.7% predation on 236 clay eggs, followed by the chimango caracara (31.3%). *Larus* spp. (5.1%) and the Chilean skua (0.9%) did not play a major role in the predation of artificial nests. For the natural nests, birds accounted for 31.8% of preyed nests in upland geese, 26.3% in flightless steamer ducks, and only 7.5% in colonial species. Finally, humans were identified as an important predator for upland geese, causing 25.0% of failed nests.

3.3. Factors influencing mink predation

Using discriminant analysis on PCA results, we tested the representativeness of artificial nests ("artificial"), and the explanatory nest site variables which best separated the species classes of upland goose ("CPI") and flightless steamer duck ("TPT") (n = 475, DA 1). The first principal component explained 37% of the variance, the second component 19%. Variables with high loadings (>|0.7|) on the first component was height of shrubs around the nest (0.82). Two discriminant functions (the axes) were generated (in general $n - 1$, n = number of classes), and the first axis accounted for 85% of total inertia. The Monte-Carlo permutation test showed that the discrimination of these two axes was significant ($p < 0.001$, based on 1000 permutations). The centroid of artificial nests strongly overlapped with the centroids of solitary nesting species (Fig. 3). However, the chosen set of variables discriminated very well between the nests of both "real" species. The first (horizontal) axis was mainly determined by distance to the shore (cosines = −0.77) and top nest cover (0.58, all other cosines <|0.46|) (Fig. 3 circle). Along the second axis (15% of total inertia), side nest cover (0.54, all other cosines <|0.47|) contributed to the separation of classes. Thus upland geese built their nests at a greater distance from the shore, whereas nests of flightless steamer ducks were characterized by a high overhead and lateral concealment (see Table 2 for empirical values).

The same multivariate analysis was performed on 375 artificial nests with four predator classes "mink", "bird", "mouse", "unknown", and a fifth class containing "successful" nests (DA 2). The first principal component explained 27% of the variance, the second 23%. High loading variables (>|0.7|) for the first component were lakes (1.3), top nest cover (−0.75), and height of shrubs around the nest (−0.71). This time, we out sorted redundant variables such as relative abundance of mink signs as it highly correlated with the type of shore (Spearman's rho = 0.86). Other redundant variables were temperature, cover, and side. We then performed the discriminant analysis with seven main variables. Accordingly, the predator classes were significantly separated ($p < 0.001$, Monte-Carlo test based on 1000 permutations) along four discriminant functions. The first function accounted for 50% of total inertia, the second for 38%, and the following axes for 10% and 2%, respectively. The centroid of successful nests was very well separated from the centroids of preyed nests (Fig. 4). Of the
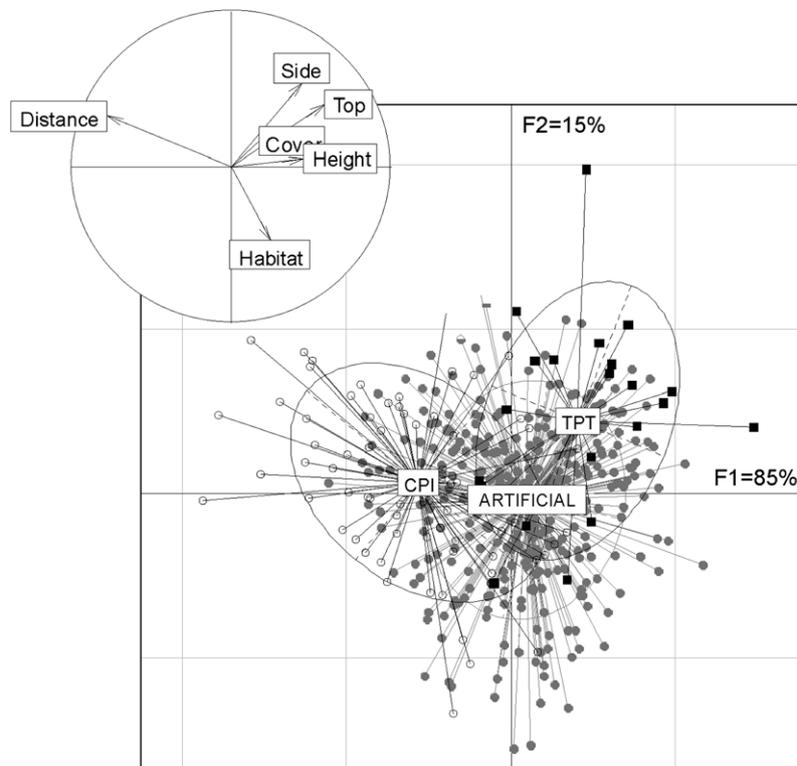
Table 2
Empirical values for variables with discriminatory power in discriminant analysis 1.

Discriminant variables DA 1	*Chloephaga picta*	*Tachyeres pteneres*	Artificial nests
Distance [m] (mean, SD, median, range)	35.8 ± 47.6 6 (1–236)	8.5 ± 6.5 17 (1–24)	9.1 ± 6.1 7 (2–32)
Top (median, range)	1 (1–4)	4 (1–4)	2 (1–4)
Side (median, range)	2 (1–4)	4 (1–4)	3 (1–4)
Total nests	77	23	375

The variables are described in the Appendix A.

Fig. 3. Results of the discriminant analysis 1. DA 1 was based on PCA results of six site-specific nest variables classified by artificial nests and natural nests of solitary nesting species (n = 475). ARTIFICIAL = Artificial nests, CPI = *Chloephaga picta*, TPT = *Tachyeres pteneres*. Eigen values F1: 0.26 (85% total inertia), F2: 0.05 (15% total inertia). The circle represents the cosines between the variables and the canonical scores. Direction and length of the arrows are a metric of the discriminatory power of the variables.

four predator classes, mink formed the most distinct class, although overlapping with the three remaining classes, which were located close together. Nests with unknown reasons for failure were more probably preyed upon by birds and mice rather than by mink, although multi-predator visits cannot be excluded. Along the first axis, the type of shore (cosines = 0.94 for rocky outcrop, and −0.94 for beaches, all other cosines <|0.32|) was the variable contributing most to separating the predator classes (Fig. 4 circle). Along the second axis, nest age (−0.70), height of vegetation at the nest (−0.54), and top nest cover (−0.50, all other cosines <|0.36|) were the three variables contributing most discriminatory power. Thus mink mainly preyed on nests at coastal habitats with

rocky outcroppings where relative mink abundance was also higher than along beaches (Wilcoxon rank sum test: $W = 114$, $p < 0.001$, $n = 22$ sites). At rocky outcrops 68.8% 500 m sections contained signs (median, range 25–100%, $n = 9$), whereas at beaches only 12.5% of the sections were positive (0–43.8%, $n = 13$). Nests built towards the end of the breeding season were apparently more successful (see Table 3 for empirical values).

3.4. Navarino Island's bird community

As the abundance patterns are different for colonial species, which occur clumped, individual numbers per colony were used,
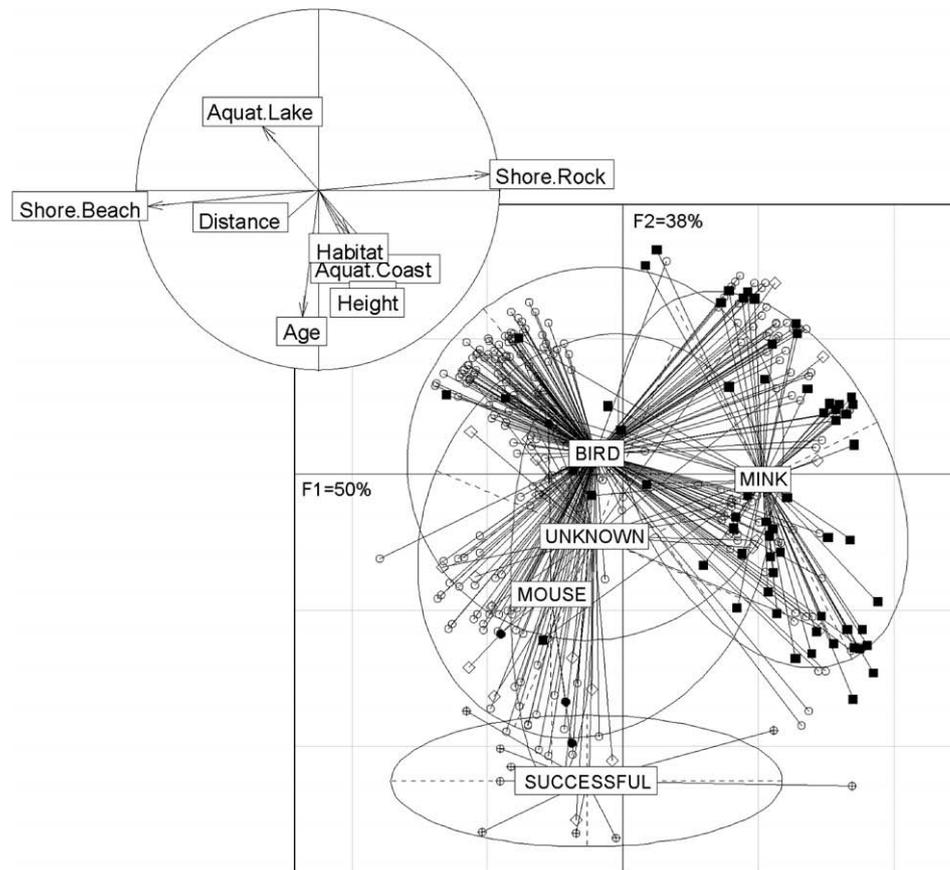

Fig. 4. Results of the discriminant analysis 2. DA 2 was based on PCA results of seven area-specific and site-specific nest variables of artificial nests ($n = 375$), classified by nest fate ("successful", "mink", "bird", "mouse", "unknown"). Mice can either refer to *Abrothrix xanthorhinus* or *Oligoryzomys longicaudatus*. The variable Top is covered by Height. Eigenvalues F1: 0.22 (50% total inertia), F2: 0.17 (38% total inertia). The circle represents the cosines between the variables and the canonical scores. Direction and length of the arrows are a metric of the discriminatory power of the variables.

Table 3
Empirical values for variables with discriminatory power in discriminant analysis 2.

Discriminant variables DA 2	Mink	Bird	Mouse	Unknown	Successful
Shore, rocky outcrop (# nests)	55	85	0	8	2
Shore, beaches (# nests)	8	183	5	22	7
Age [days] (mean, SD, range)	28.1 ± 20.8 (5–57)	28.5 ± 18.8 (5–58)	31.4 ± 23.2 (6–49)	31.7 ± 20.4 (5–59)	68.4 ± 0.73 (67–69)
Height [m] (mean, SD, range)	0.47 ± 0.44 (0–2)	0.38 ± 0.31 (0–2)	0.38 ± 0.08 (0.3–0.5)	0.39 ± 0.39 (0.1–1.7)	0.28 ± 0.08 (0.2–0.4)
Top (median, range)	2 (1–4)	1 (1–4)	4 (2–4)	3 (1–4)	3 (1–4)
Total nests	63	268	5	30	9

The variables are described in the Appendix A. The main focus of DA 2 was to assess differences between predation patterns of invasive mink and autochthonous birds. Sample sizes for artificial nests preyed on by mice and for successful nests were small, but included into the analysis for reasons of integrity.
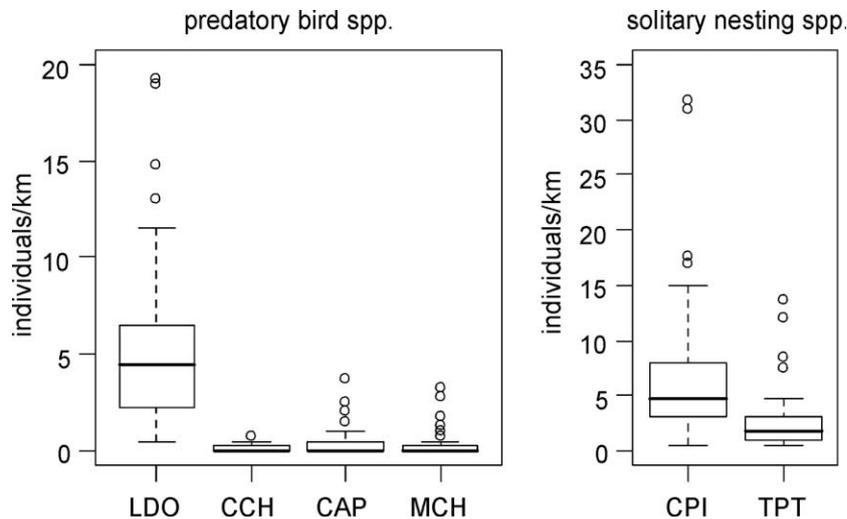
Fig. 5. Bird counts of predatory birds and solitary nesting species. Predatory birds refer to kelp gulls on search flights and raptors. Counts were made along the northern coast of Navarino Island and cover all study sites and breeding periods (2005–2007). LDO = *Larus dominicanus*, CCH = *Catharacta chilensis*, CAP = *Caracara plancus*, MCH = *Milvago chimango*, CPI = *Chloephaga picta*, TPT = *Tachyeres pteneres*.

whereas for the other species studied individuals/km was employed. Kelp gulls as a predatory species on search flights were also counted along our transects. The kelp gull colony had a size of 315 individuals (range 168–433, both breeding seasons pooled), dolphin gulls of 150 individuals (132–200) and South American terns of 90 individuals (64–320). Among the predatory birds, kelp gulls had a relative abundance of 4.5 individuals/km (median, range 0.5–19.3) per transect, a significantly higher abundance than estimated for the three raptor species (all Wilcoxon-tests: $W = 820$, $p < 0.001$) (Fig. 5). Abundances for raptors ranged from 0 to 0.75 individuals/km for crested caracara, 0 to 3.75 for the Chilean skua, and 0 to 3.25 for chimango caracara. Among solitary nesting species, we estimated 4.75 individuals/km (0.5–31.75) for the upland goose and 1.75 individuals/km (0.5–13.75) for flightless steamer ducks. Although we made our counts in the same sites where nests were monitored, these counts refer to resting and feeding birds as well as guarding males (cryptic incubating females could not be included) (Fig. 5).

4. Discussion

4.1. Vulnerability profile

With a combined approach of natural and artificial nests a vulnerability profile was drawn for ground-nesting waterbirds under mink invasion on Navarino Island. We found patterns of nest predation by mink among social nesting strategies, habitat, and nest characteristics. Thus the ground-nesting waterbirds that are especially vulnerable to predation by mink are those that are (i) solitary nesting, (ii) breeding in coastal habitats with rocky outcrop shores, and (iii) concealing their nests. This profile is best illustrated by a high predation rate of mink (44%) on flightless steamer ducks, a species with very low densities (1.75 individuals/km), which perfectly match all the characteristics of our vulnerability profile. Other ground-nesting species to which most of these characteristics apply are: flying steamer duck (*Tachyeres patachonicus*), crested duck (*Lophonetta specularioides*), and kelp goose (*Chloephaga hybrida*). In consequence, these represent bird species vulnerable to mink predation, and might require special conservation efforts.

How can these patterns characteristic for predation by mink be explained? We start with the first pattern, solitary nesting (i).

Depending on group size, nest densities, predator type, and predator size, colonial breeding can lead to a decrease in predation risk due to earlier predator detection and/or higher nest defense efficiency (reviews in Wittenberger and Hunt, 1985; Siegel-Causey and Kharitonov, 1990). For example, gull colonies successfully show aggressive behavior towards predators (Kruuk, 1964), a reason why some bird species are found associated with gull colonies during nesting, e.g., tufted ducks (Opermanis et al., 2001). The second pattern, the association with rocky outcrop marine shore habitats (ii), apparently is a function of habitat requirements of mink. Dunstone (1993) stated that in coastal habitats sheltered rocky shores are ideal for mink. Our results agree with this. Mink abundance was significantly higher along steep and rocky coastal shores than along beaches. Our results also revealed the importance of concealed nests (iii) as predictors for predation by mink. Many researchers agree about the differences between avian and mammalian predators with respect to the importance of nest concealment (e.g., Butler and Rotella, 1998; Opermanis et al., 2001). Thus, avian predators appear to visualize nests, whereas mammalian predators primarily depend on olfactory cues and therefore prey upon nests irrespective of concealment (Guyn and Clark, 1997). This explains why mink were preying upon both types of nests; open nests (predominantly upland geese) and concealed nests (flightless steamer ducks). However, our results on natural and artificial nests indicate that concealed nests in surroundings with dense vegetation were more vulnerable to predation by mink. We suggest two reasons. First, concealing nests requires a minimum amount of dense vegetation, which is a habitat preference of mink (e.g., Yamaguchi et al., 2003), and second, concealment is limiting the view of the surroundings of the nest and thus might prevent appropriate response if predators are not detected in time (trade-off hypothesis by Götmark et al., 1995).

4.2. Vulnerability and "naïvety"

Behavioral decisions under the risk of predation include escaping from predators, inspecting predators, and mobbing predators depending on the encounter situation and type of prey, i.e., adults or offspring (Lima and Dill, 1990). Defense strategies against potential avian predators on their clutches have been described for upland geese (Quillfeldt et al., 2005) and flightless steamer ducks (Livezey and Humphrey, 1985). However, assuming that a mam-

malian predator will induce different encounter situations than avian predators, this requires different behavioral decisions than those for avian predators. On Navarino Island, bird species were not confronted with a terrestrial mammalian predator until the arrival of mink during the mid-1990s (Rozzi and Sherriffs, 2003). There is no evidence for evolutionary isolation from native terrestrial predators as Navarino Island does not harbor endemic bird species (Couve and Vidal, 2003). Bird species endemic for Patagonia have been evolved together with native predators like the Fuegian red fox (*Pseudalopex culpaeus lycoides*) in Tierra del Fuego. Although bird species on Navarino Island should have developed evolutionary adaptations to terrestrial predators, we believe that they might lack behavioral adaptations to the recently arrived mink. Animals have the ability to behaviorally influence their risk of being preyed upon in ecological time, i.e., during their lifetime (reviewed in Lima and Dill, 1990). Missing confrontation with a terrestrial predator therefore should result in behavioral naïvety for resident bird species as shown for arctic terns in mink removal areas (Nordström et al., 2004).

4.3. Validity of predicting vulnerability

Concerns about the validity of inferences made about nest survival of natural nests from artificial nests basically originate from the differences in parental presence, odor, egg characteristics, and location of these two nest types (Butler and Rotella, 1998). In our study, artificial nests had significantly lower survival rates than natural nests. We assume that the main draw-back of artificial nests, "no cryptic female sitting on the eggs" (Angelstam, 1986, p. 370), could have attracted more avian predators to the more visible nests. A possible solution for this draw-back could be to cover the eggs of artificial nests with down, just like geese and ducks in our study area do when leaving their nests. Despite these difficulties and possibilities to improve our study design, we think that our data is sufficiently reliable, for three reasons. First, as we were primarily interested in predation by mink, we think that our artificial nests provided sufficient olfactory cues (downy feathers) to attract mammalian predators irrespective of concealment (see the comparable predation rates of mink between artificial nests and upland geese). Second, the internal validity of our artificial nest design was maintained carefully in order to accurately measure predator behavior (see Moore and Robinson, 2004); and third, an extrapolation of our results to real nests might be justified to a certain degree as we maximized comparability, for example nest characteristics of artificial nests matched well with those of natural nests (results of DA 1) indicating that they were quite "truly" built.

We have been investigating predation of mink in its early colonization stage at the beginning of the 2000s. Since then, mink sightings have been increasing, suggesting a rapid increase in the mink population (Rozzi and Sherriffs, 2003). However, trapping and sign surveys in different semi-aquatic habitats of Navarino Island (Anderson et al., 2006, E. Schüttler, unpublished data) have shown that the density of mink is still below densities measured in other invaded regions (e.g., Previtali et al., 1998; Bartoszewicz and Zalewski, 2003). Although we lack knowledge of the carrying capacity for mink on Navarino Island, we assume that the population of mink will grow further. The consequences this might have for bird populations have to be investigated by long-term research and cannot be extrapolated from our short-term results. One possible divergence from our suggested vulnerability profile could be that species nesting in colonies will also be affected by a future increasing population of mink. The higher defense behavior of colonies does not always protect them from predation by mink as various studies have demonstrated (e.g., Kilpi, 1995; Clode and Macdonald, 2002; Collis, 2004; Craik, 1997; Nordström et al., 2004). Mink predation on bird populations seems to be further influenced by a variety of factors as several studies in Europe (most are mentioned in Bonesi and Palazon, 2007) have shown. Among those factors (majorly assessed through mink removal) figure: the body size of waterbirds (smaller sized waterbirds increased in breeding densities after mink removal, e.g., Nordström et al., 2002); the timing of breeding (later breeders seem to be stronger affected than earlier ones, because of the increasing food requirements of growing mink kits, Banks et al., 2008); the predator community (compensatory predation may occur, e.g., Opermanis et al., 2005); the activity of the predator (mink are described as nocturnal predators, and seabird colonies can hardly defend against nocturnal predators, Hunter and Morris, 1976 in Banks et al., 2008).

4.4. Management implications

The observed vulnerability patterns are valuable for decision-making and priority setting in the management of invasive mink on Navarino Island. We identified ground-nesting waterbirds under risk from a conservationist point of view. Control programs should focus on preventing mink from establishing territories near breeding areas of vulnerable ground-nesting species and bird colonies. The assessment of coastal breeding habitats can be facilitated by using Geographical information systems (GIS) and existing digital data archives (Rönkä et al., 2008). Predator removal programs have been shown to have a positive effect on hatching success and post-breeding population size of target bird species (reviews in Newton, 1994; Côté and Sutherland, 1997). Targeted removal of mink from particular areas, particularly rocky outcrop coasts, during the breeding season (e.g., Clode and Macdonald, 2002; Banks et al., 2008; Ratcliffe et al., 2008) could therefore represent a first task of conservationists. The design of a long-term management plan should include clear objectives, participation of local stakeholders, careful consideration of costs vs. benefits, possible negative effects of target and non-target species, and prevention efforts (e.g., Moore et al., 2003; Nordström et al., 2003; Baxter et al., 2008). However, mink control should not overshadow vigilance against other human-induced factors contributing to mortality in ground-nesting waterbirds, such as dog predation or egg-stealing by humans.

Acknowledgments

Appendix A

Area and nest site variables measured at artificial nests and natural nests of solitary nesting species.

	Definition	Measurement/ categories
Area variables		
Age	Age of the nest at hatching/failure counted from the first day of the breeding season	Continuous [days]
Aquatic	Type of aquatic habitat defined for each site	Coast and lakes
Mink	Relative abundance of mink signs measured as percentage of positive 500 m sections	Continuous [%]
Shore	Type of shore defined for each site (slope and composition of shore)	Rocky outcrop and beaches
Temperature	Median temperature with 4 daily measurements across survival period of each nest	Continuous [°C]
Site variables		
Cover	Area covered by vegetation in a 5×5 m^2 square around nest	1. 0–20% 2. 20–40% 3. >40%
Distance	Shortest distance of nest to shore, measured with GPS	Continuous [m]
Habitat	Predominant habitat type in a 10×10 m^2 square around nest	Bare: earth/rock Uniform: pasture, peatland, wetland Simple: shrubs, grasses, but no mature trees Complex: evergreen, mixed, deciduous forest
Height	Height of shrubs and bushes at nest, estimated by hand palm	Continuous [m]
Side	Percentage lateral coverage of nest, taken adjacent to the nest from the 4 cardinal directions	1. 0–25% 2. 25–50% 3. 50–75% 4. >75%
Top	Percentage overhead nest concealment, quantified looking from above down to nest	1. 0–25% 2. 25–50% 3. 50–75% 4. >75%

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.02.013.

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