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Behavioural plasticity in nest-site selection of a colonial seabird in response to an invasive carnivore

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Abstract Non-native invasive species are one of the most serious threats to biodiversity and are considered the leading cause of extinction of several bird taxa, including seabirds. Introduced American mink (*Neovison vison*) have caused devastating effects on island populations of several colonial seabird species. In this study, we investigated the direct and indirect effects of mink on population dynamics and reproductive success of European shags (*Phalacrocorax aristotelis*) breeding at Illas Cíes, one of the most important colonies of the species in Southern Europe. A severe episode of mink predation on adult shags occurred in the year when mink arrived in the breeding colonies, though the number of shags killed dropped abruptly in subsequent years. We found that, after the arrival of mink, shags moved to nest-sites that afforded greater protection from carnivores. This shift caused a substantial reduction in mortality by predation, but probably entailed a cost in terms of their reproductive success because sites with lower levels of predation risk showed a higher risk of egg loss by nest flooding due to poorer drainage. Our study highlights that behavioural plasticity may allow shags to cope with invasive predators.

Keywords American mink · European shag · Non-native predator · Mink predation · Habitat change · Reproduction

Introduction

The impact of invasive non-native species on native biotas and its ecological consequences is a worldwide issue of great concern in conservation biology (Mooney and Hobbs 2000; Gobster 2005). By breaking down natural biogeographic barriers and providing new habitats suitable for invasive species establishment, human activity has historically facilitated their expansion (Vitousek et al. 1997; McNeely 2005; Hulme 2009). Invasive species are considered one of the most serious threats to biodiversity, and the leading cause of extinction of several bird taxa,

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including seabirds (BirdLife International 2000). On islands, the impact of introduced invasive predators can be particularly severe, and commonly entails the extirpation of entire bird populations (Blackburn et al. 2004).

Seabirds have evolved mainly in predator-free habitats and thus they are virtually defenceless against introduced predators (Furness and Monaghan 1987; Bennett and Owens 1997; Saether and Bakke 2000; Short et al. 2002). In seabirds, adult survival has a high impact in population growth rates (Croxall and Rothery 1991; Saether and Bakke 2000). In some cases, invasive predators and seabirds may coexist (Quillfeldt et al. 2008), but most often they lead to the extirpation of entire seabird local populations and the abandonment of breeding areas, especially when adult individuals are preyed upon (Croxall and Rothery 1991; Russell 1999). In addition to such harmful direct effects, non-native predators may affect seabird populations indirectly. For example, predator disturbance may induce juvenile dispersal with effects on local and metapopulation dynamics (Oro et al. 1999). Moreover, seabirds under risk of predation will tend to reduce nest attendance in order to enhance their own survival (Harfenist and Ydenberg 1995; Velando and Marquez 2002). On the other hand, birds may change the location in which nests are built in order to reduce the risk of predation (Forstmeier and Weiss 2004; Fontaine and Martin 2006; see review in Mainwaring et al. 2014). For example, terrestrial birds place their nests in higher trees in response to predator presence (Martin 1993), and some waterfowl species may use artificial habitats near human settlements to reduce predation (Brzeziński et al. 2012); these changes may allow avian populations to coexist with invasive predators. However, in seabirds, changes in nest-site preferences immediately after the introduction of predators are poorly documented (but see Bixler 2010).

The American mink (*Neovison vison*, hereafter “mink”), a semi-aquatic carnivorous mammal that is naturally distributed throughout North America, has successfully colonised large areas of East Asia, South America and Europe. Escapes from fur farms gave rise to feral populations, with relevant effects on native biota (Dunstone 1993; Bonesi and Palazón 2007). Mink are able to swim relatively long distances (Fleming and Cook 2010) and they can reach offshore islands by island hopping (Björsson and Heirstensson 1991). Accidental and deliberate introductions have also facilitated the colonisation of some remote islands (Ratcliffe et al. 2008; Bixler 2010). Severe effects on the island populations of colonial seabirds, including whole-colony breeding failures and abandonment of breeding areas due to mink presence have been documented throughout Northern Europe and the British Isles (Craik 1997; Nordström et al. 2003). In the Iberian Peninsula, the first free-living mink populations were detected in the early 1980s in three separated areas, including southwest Galicia (Vidal-Figueroa and Delibes 1987; Melero and Palazón 2011); however, the large islands of Galicia remained free of mink until the early 2000s (Pereira 2006).

Here, we study the effect of introduced mink on the breeding ecology of a coastal colonial seabird, the European shag (*Phalacrocorax aristotelis*) in the archipelago of Illas Cíes, southwest Galicia, one of the main breeding grounds of the species in the Iberian Peninsula (Velando and Álvarez 2004). In the last 10–15 years this population has been declining at an annual rate of about 12 % due to continued low adult survival and poor reproductive success, attributed to the effects of the *Prestige* oil spill (that happened in November 2002) and mortality in fishing gear (Velando and Freire 2002; Velando et al. 2005a, b; Martínez-Abraín et al. 2006; Velando and Munilla 2008; Barros et al. 2014).

In this study, we first summarize records of mink predation on European shags at Illas Cíes since 2009 (the year when mink were suspected to arrive in the breeding colonies), and study the association between mink abundance and the population dynamics of European shags. Secondly, we study whether shags changed their nest-site preferences after mink arrival. The long-term (1994–2013) monitoring of this population has allowed us to test the effects of the introduction of mink on adult mortality and reproductive success associated with nest-site characteristics.

Methods

Study area and species

This study was carried out at Illas Cíes, a three island archipelago (433 ha) that is part of the National Park of the Atlantic Islands of Galicia, in Northwestern

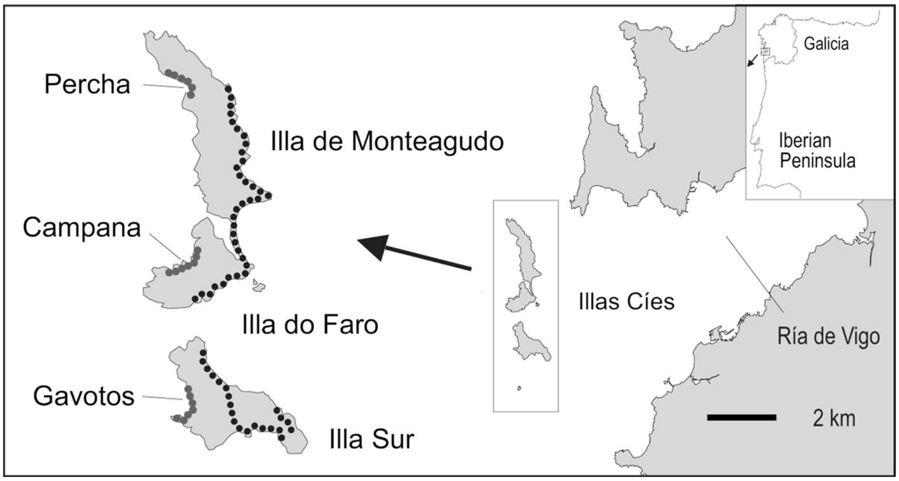

Fig. 1 Map of the study area showing the main islands of the Illas Cíes archipelago. The European shag subcolonies sampled are shown by *grey dots*. *Black dots* indicate line transects made to estimate American mink density. Transects in Illa de Montegudo-Illa do Faro (6 km long) were made in 2009 (1; June), 2010 (1; February), 2011 (2; January and June), 2012 (2; February) and 2013 (3; January, February and March). Transects at Illa Sur (3 km long) were made in 2010 (2; March and May), 2011 (4; January, March and 2 in April), 2012 (1; March) and 2013 (2; April)

Iberia (Fig. 1). At each of the main islands, from north to south, Monteagudo, Faro and Sur, we selected a sampling study colony (respectively, Percha, Campana and Gavotos; Fig. 1). The climate is temperate oceanic, mild and wet, and protection against adverse weather conditions (heavy rain, gales) and from insolation explains the nest-site attributes selected by shags in this population (Velando and Freire 2003). Nests were located in the steep cliffs of the western side of the islands, mostly in cavities under detached granite rocks and boulders, well above the sea level. In 2008 the breeding population was estimated at 385 pairs.

The first records of mink at Illas Cíes were reported by the Park wardens in 2003. However, the first signs of mink activity in shag breeding areas (e.g. preyed carcases, scats, footprints) were recorded during the 2009 (see results) survey of our long-term (1994–2013) monitoring program of the shag population. Annual surveys include the inspection of a large number of nests repeatedly during the breeding season (see above); therefore it is unlikely that mink were active in the colonies before 2009. We cannot discard the possibility of an occasional presence of mink in the Illas Cíes shag breeding colonies before that year, albeit the consequences on shags (if any) were not evident.

In the winter of 2009, a control program that consisted on the installation of several baited cage-traps in areas with mink presence was initialized in Illas Cíes. Traps were revised periodically by the Park wardens and all the mink trapped were removed from the islands. The only native carnivore in our study area is the Eurasian otter (*Lutra lutra*), that sporadically visits intertidal and rocky shore areas along the eastern coastline. Apart from mink, another non-native predator, the feral cat (*Felis catus*) is present in two of the main islands, Monteagudo and Faro (Fig. 1). Although cats have often been reported from shag breeding areas since at least 1994, no adult or chick losses related to cat predation have ever been recorded there (Velando and Munilla 2008). Thus, before the spread of mink in the western cliffs (this study), the reproductive success of shags in these colonies was mainly regulated by hatching failure and chick mortality due to food limitation and bad weather conditions (Velando et al. 1999, 2005a, b), but not by predation of chicks or adults, by either native nor non-native mammals (Velando and Munilla 2008).

Mink abundance and predation

During 2009–2013, a series of fixed line transects (6 km in Monteagudo-Faro and 3 km in Sur, see Fig. 1) were used to estimate changes in the abundance of mink. Transects were surveyed between the end of January (the start of the mink mating period) and the first half of June (when most mink cubs are still at the den; see Dunstone 1993; García-Díaz and Lizana 2013), therefore overlapping with the breeding period of shags from courtship to fledgling. To help minimize the potential biases associated with scat detectability survey transects were conducted on non-vegetated areas (paths and beaches) under good weather conditions. Relative mink abundance was estimated annually as the average number of scats per lineal km. Mink scats are easily distinguishable from that of feral cats by size, shape and odour (Dunstone 1993; Bonesi et al. 2004). Scat counts have been commonly used as an index of mink abundance (Bonesi and Macdonald 2004; Shüttler et al. 2009).

The mortality of shags due to predation by mink was estimated directly during the annual counts (2009–2013) of the breeding population (early May) and during the monitoring of its reproductive success (see below). We recorded the location of all the shag carcasses with signs of carnivore predation (i.e. cut feathers and canine marks on bones) (Craik 1995; Opermanis et al. 2001). All the scats found near predated shags were recognizable as mink scats (see discussion).

Changes in shag breeding numbers

During the period 2007–2013, the breeding population was censused as the number of apparently occupied nests (nests in advanced stage of construction and with reproduction signs) in April–May. The mean annual breeding population growth rate (λ, thereafter population growth) was estimated as $\lambda = e^r$, where $r = \ln N_{t+1} - \ln N_t$, N_t is the population size at year t and N_{t+1} the population size in the following year. We also compared changes in the size of the breeding population at our study site with two nearby mink-free colonies (see details in Electronic Supplementary Material, hereafter ESM).

Nest-site characteristics and reproductive success

The study of nest-site selection was based on the characterization of 225 sites used by shags at least once between 1994 and 2013 in any of the three sampled subcolonies: Percha, Campana and Gavotos (Fig. 1). At the study site, adult shags are characterized by a high site fidelity (all marked birds re-nested within 100 m of their previous year nest-site; Velando and Freire 2002). Thus, since nest-sites were often occupied in more than 1 year, our analyses included many reused nest-sites. The number of monitored nest-sites varied across subcolonies and years (see Table 1). Note that in some years we have no data on reproductive success (1998, 1999, 2002, 2010 and 2011).

Previous studies conducted in Campana subcolony suggested that shags prefer nest-sites with overhead and lateral covers, and with good drainage and visibility (Velando and Freire 2001, 2003). These attributes correlated positively with the probability of occupation of a nest-site as well as with the reproductive success of the breeding pairs (Velando and Freire 2003), thus they are likely good proxies of nest-site quality. Accordingly, for each nest-site we scored the following three variables: (1) *cover*, as the number of surfaces (lateral walls and overhead) surrounding the nest chamber (from 0, no walls, to 5, four walls and a roof); (2) *drainage*, as the number of side walls sloped towards the nest, which increases the risk of nest flooding by rain water (from 1, four walls sloped towards the nest and meaning the worst drainage, to 4, no walls sloped towards the nest); (3) *visibility,* as the ability of shags sitting on the nest to watch nearby shags or, eventually, predators approaching (1 no visibility, 2 medium visibility and 3 full visibility). We have assumed that the location of nest-sites, whether they are located in vertical, steep, gradual or flat areas, is related to their accessibility to terrestrial predators and to the probability of escape from predators. On one extreme, nests located in vertical cliff ledges are inaccessible to terrestrial predators, and allow a rapid escape by flight. On the other hand, concealed nests (i.e., in cavities between or under rocks and boulders) in flat ground areas pose no difficulties to predator access and, since shags cannot take-off swiftly, adults may have more difficulties to escape. Thus, additionally, we recorded the *steepness* of nest-sites as a proxy of its predation risk, according to a scale that ranged from 0 (level access to the nest-site), to 3 (nest-sites located in vertical cliffs).

During monitoring years (see above), nest-sites were marked and visited three to five times from March to June. As described above, a site was considered occupied if a nest was built or if any evidence of reproduction (eggs or chicks) was recorded. The reproductive success of each occupied site was estimated as the number of chicks surviving to

Table 1 Sample size (number of nests-sites) used for the occupancy analysis in each of the three study subcolonies during 1994–2013

	1994	1995	1996	1997	2000	2001	2003	2004	2005	2006	2007	2008	2009	2012	2013
Subcolony															
Percha								39	39		39	39	39	39	39
Campana	131	131	131	86	86	86	86	131	131	131	131	131	131	131	131
Gavotos											55	55	55	55	55
Total	131	131	131	86	86	86	86	170	170	131	170	225	225	225	225

full growth, >35 days of age (Barros et al. 2013). We also compared the reproductive success in our study area with the reproductive success in two nearby free-mink islands (see ESM).

Effect of mink presence and nest-site characteristics on occupation and reproductive success

In order to analyse the effect of mink presence on nest-site selection by shags, we considered that mink were absent from breeding areas before 2009, when the first evidence of mink predation was recorded at colonies. Thus, 1994–2008 were considered mink-free years and 2009–2013 mink-affected years. The probability of nest-site occupation was analysed using a Generalised Linear Mixed Model (GLMM) with a binary distribution of the response variable (occupied vs. unoccupied), and a logit link function. Sub-colonies (Percha, Campana and Gavotos), the four variables describing site characteristics (cover, drainage, visibility and steepness), mink presence period (absent vs. present) and the interaction between mink presence and site characteristics were included as fixed effects. Year (nested within mink period) was included as a random factor. Since nest-sites were repeatedly sampled over several years, we modelled a mixed model (Little et al. 2006), with year and nest-site identity as random factors. Similarly, observed reproductive success (number of full-grown chicks) was analysed by means of a GLMM with Poisson errors, a log link function and similar structure as described above. In both models, the Laplace method for likelihood approximation was used (see Little et al. 2006; Bolker et al. 2009). Since the study periods of the three subcolonies differed in length, we re-ran the models considering only the Campana data set (the more complete data set, from 1994 to 2013), to be confident that our results on mink presence were not due to differences among sub-colonies. Similar results were also achieved when analyses were restricted to breeding events after the *Prestige* oil spill (2004–2013). We used the Akaike information criterion (Burnham and Anderson 2002) for selecting model and ranking competing models (models incorporating main effects and interactions between mink presence and site characteristics).

Results

Effect on breeding numbers

During 2009–2013, a total of 35 shags (33 adults and two chicks) presumably killed by mink were recorded in the breeding colonies in our study area (Fig. 2b). Most records of predated adults ($N = 24$; 73 %) occurred in 2009 (Fig. 2c). Mink abundance and the number of shags killed by mink were not correlated ($r_5 = 0.02$, $P = 0.97$); however there was a statistically significant and a strong negative correlation between mink abundance and the annual growth rate of the shag breeding population in the following year ($r_5 = -0.96$, $P = 0.009$). In 2010 we recorded the highest number of scats during the shag breeding season and the shag breeding population decreased by 26 % in the following year (Fig. 2e). The annual growth rate of breeding population was not found to be correlated with the number of shags found dead ($r_5 = 0.17$, $P = 0.78$). Overall, the breeding population decreased during the study period, but, in contrast, breeding numbers increased in the two nearby mink-free colonies (see ESM, Fig. S1).

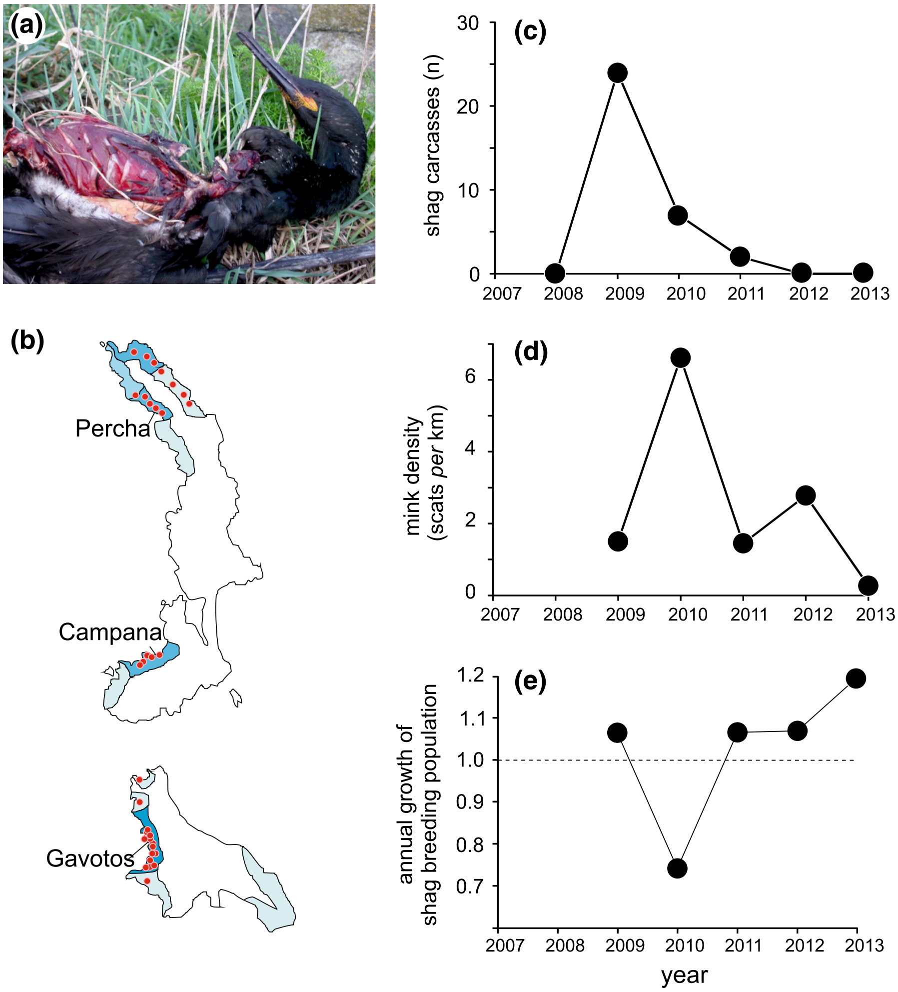

Fig. 2 Mink abundance, predation and changes in the breeding population of European shags at Illas Cíes. **a** Photograph of a freshly predated adult shag. **b** Location of preyed adult shags (*red dots*, $N = 33$) observed during the 2009–2013 breeding seasons (*blue colour intensity* indicates breeding density in the 12 subcolonies). **c** Annual records of preyed adult shags. **d** Annual variation in the abundance of mink (scats *per* km). **e** Annual growth rate of the shag breeding population (λ; to the following year (i.e. from year t to year $t + 1$). The *dashed line* represents a stable population ($\lambda = 1$)

In total, 47 mink were removed by the National Park wardens from 2009 to 2012. Most captures ($N = 28$; 60 %) were made in 2009, the first year with confirmed predation on shags, and captures decreased gradually until 2013, when no mink were captured (total number of mink removed: 2009:28, 2010:10, 2011:5, 2012:4, 2013:0).

Effect on nest-site selection

The model of site occupation with the lowest AIC included two interactions: steepness × mink presence and drainage × mink presence (Table 2), suggesting that the effect of steepness and drainage on the probability of occupation of a nest-site changed after the arrival of mink in the breeding colonies (Fig. 3; Table 3). Thus, the association between the probability of occupation of steeper sites increased after the arrival of the mink, but, the correlation between the occupation probability of a site and its drainage score disappeared after mink arrival, mainly due to reduced occupation of nest-sites with better drainage scores (Fig. 3c). Similar changes in nest-site selection were found when the analyses were restricted to the Campana subcolony (steepness × mink presence, drainage × mink presence, $P < 0.020$). There was low support (Table 2), for a change in selection of nest-sites with high cover (Fig. 3; Table 3) and visibility scores (Fig. 3; Table 3) after the presence of mink.

Effect on the reproductive success of nest-sites

The reproductive success of shags was higher in the period before the arrival of mink in the colonies (before mink: 1.21 ± 0.05, after mink: 0.79 ± 0.10 chicks per pair; LSD, $P = 0.018$). The comparison

Table 2 Summary of the model selection statistics for the models of (a) nest-site occupation and (b) reproductive success

Model	(a) Site occupation		(b) Reproductive success	
	AIC	ΔAIC	AIC	ΔAIC
Main effects	2309.73	13.76	1702.94	13.85
Cover × Mink period (C × M)	2311.45	15.48	1704.64	15.55
Drainage × mink period (D × M)	2305.09	9.12	1704.58	15.49
Visibility × mink period (V × M)	2311.62	15.65	1702.03	12.94
Steepness × mink period (S × M)	2302.84	6.87	1693.9	4.81
C × M + D × M	2306.94	10.97	1706.16	17.04
C × M + V × M	2313.32	17.35	1703.66	14.57
C × M + S × M	2304.14	8.17	1694.59	5.5
D × M + V × M	2307.06	11.09	1703.03	13.94
D × M + S × M	**2295.97**	**0.00**	1695.88	6.79
V × M + S × M	2304.63	8.66	**1689.09**	**0.00**
C × M + D × M + V × M	2308.92	12.95	1704.36	15.27
C × M + D × M + S × M	2297.51	1.54	1696.60	7.51
C × M + V × M + S × M	2305.87	9.90	1689.29	0.20
D × M + V × M + S × M	2297.97	2.00	1691.05	1.96

The best supported model (i.e. lowest AIC) in bold

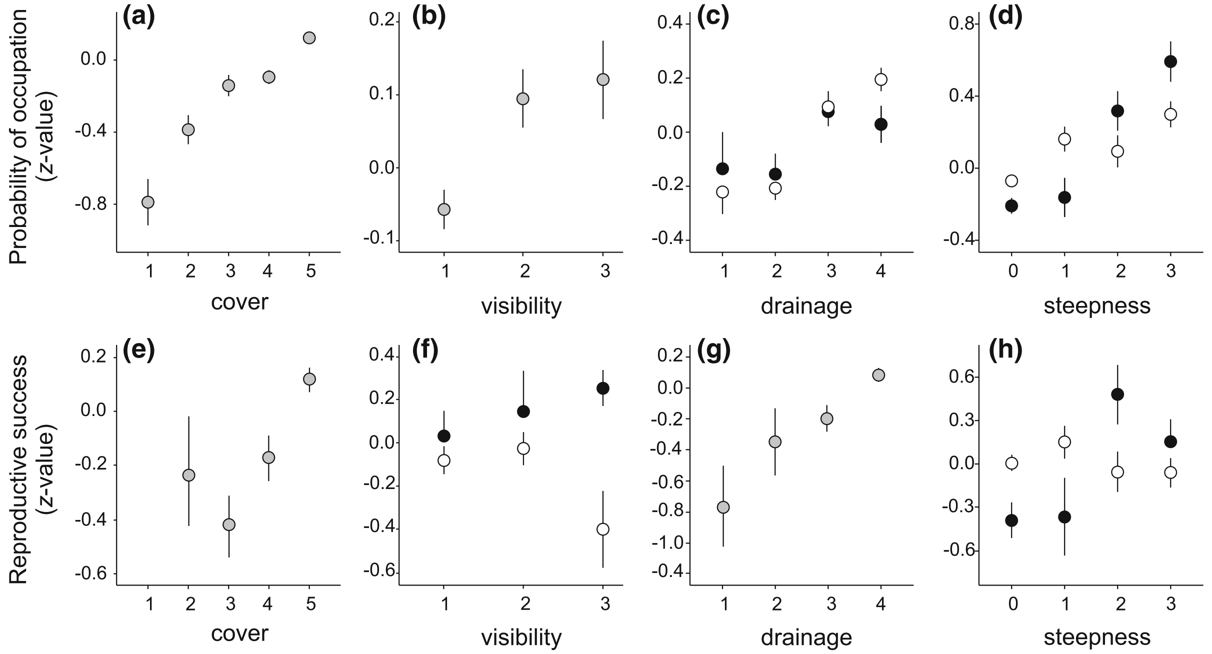

Fig. 3 Probability of occupation (**a–d**) and reproductive success (**e–h**) of standardized values (mean *z*-value ± SE) by annual variation in relation to nest-site characteristics in the three subcolonies. When the interaction with mink period was significant (see ESM) values in predator-free years (*white dots*) and predator years (*black dots*) are shown

with nearby mink-free colonies (see ESM, Fig. S2) revealed a reduced reproductive success not only in 2009, but also in 2008 (one season before the first signs of mink predation were recorded, see above).

Overall (1994–2013), the observed reproductive output of a nest-site was highly dependent on cover (Fig. 3e; Table 3), and drainage (Fig. 3g; Table 3), but there was low support for models including the

Table 3 Summary of best supported generalized mixed models for (a) nest-site occupation and (b) reproductive success (number of full grown chicks per nest)

Source of variation	(a) Site occupation				(b) Reproductive success			
	Estimate ± SE	*F*	*df*	*P*	Estimate ± SE	*F*	*df*	*P*
Intercept	−2.11 ± 1.10				−2.38 ± 0.60			
Subcolony (Percha)	−1.06 ± 0.29	16.05	2,1919	<0.0001	0.12 ± 0.38	0.91	1178	0.403
Subcolony (Campana)	−1.51 ± 0.27				0.34 ± 0.27			
Mink period	−0.55 ± 1.01	0.30	1,1919	0.585	0.30 ± 0.41	0.51	1422	0.473
Cover	0.36 ± 0.10	12.06	1,1919	<0.0001	0.20 ± 0.07	8.76	1422	0.0033
Drainage	−0.23 ± 0.21	0.35	1,1919	0.555	0.20 ± 0.08	5.74	1422	0.0170
Visibility	0.33 ± 0.12	7.32	1,1919	0.0069	−0.40 ± 0.19	2.39	1422	0.123
Steepness	0.44 ± 0.10	10.63	1,1919	<0.001	0.37 ± 0.11	6.16	1422	0.0135
Mink period × drainage	−0.41 ± 0.14	9.36	1,1919	0.0023	–			
Mink period × steepness	−0.36 ± 0.11	10.93	1,1919	0.0010	−0.48 ± 0.19	13.45	1422	0.0003
Mink period × visibility	–				−0.42 ± 0.11	6.27	1422	0.0127

change of these associations by mink presence (Table 2). The model with the lowest AIC included two interactions (steepness × mink presence and visibility × mink presence). Thus, after the arrival of mink the reproductive success of a site was strongly related to its steepness but not in previous years (Fig. 3; Table 3) and shags breeding in nest-sites with high visibility score showed reduced reproductive success. These interactions were also supported when the analysis was restricted to Campana sub-colony ($P < 0.001$).

Discussion

Substantial predation on adult shags occurred in the year when mink were detected for the first time at the breeding colonies though the number of shags killed dropped abruptly in the following years. The relative abundance of mink during the shag breeding season (estimated as the relative abundance of scats), predicted negative annual population growth rates in the following year, probably through effects on the number of breeding pairs (Fig. 4; see below). After the arrival of mink in the breeding colonies shags apparently selected nest-sites with low risk of predation, a habitat shift that increased the use of lower quality nest-sites (Fig. 4; see below). Along with the effect of culling on mink numbers, we suggest that behavioural plasticity in nest-site selection allowed shags to cope with this invasive carnivore.

A possible confounding factor is the presence of feral cats, although we think that cats cannot explain the observed patterns. First, there were no records of adult shags killed by terrestrial carnivores before the arrival of mink in the breeding colonies even though the presence of feral cats in shag breeding areas has been repeatedly documented since the start of our long-term monitoring program in 1994 (Velando and Munilla 2008). Additionally, fresh mink scats were found close to some freshly killed shags and shags were killed at Illa Sur, a cat free island. In the years when cats were present and mink was absent, most shag nests were accessible to terrestrial predators (Velando and Freire 2003), without any apparent negative impact on adult or chick survival. Notably, the population increased largely from 1994 to 1999, and in that period cats were widespread in the colonies (Velando and Munilla 2008). Altogether, evidence suggests that the effects observed in this study are largely attributable to mink.

Mink presence, predation and changes in breeding numbers

Severe mortality events have been reported on several seabird populations following the arrival of feral mink in breeding areas (e.g. Folkestad 1982; Craik 1995, 1997).

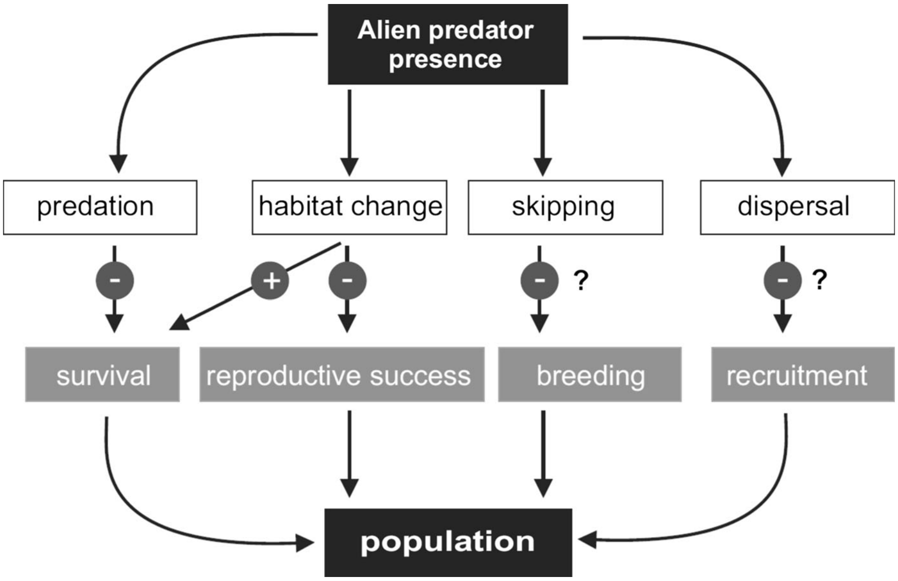

Fig. 4 Possible pathways of the effects of mink presence on the population dynamics of European shags at Illas Cíes. Initially, mink directly reduced adult and chick survival by predation. We also recorded a habitat shift towards safer nest-sites which is likely to reduce the risk of predation on adults at the expense of reproduction. Mink abundance predicted shag population growth, which suggests reduced recruitment and/or non-breeding events (skipping), but these possibilities were not addressed in the current study (see text)

In our study, the highest mink predation rate on adult shags was recorded in 2009 (24 adults c. 4 % of the breeding population), the year when the first signs of mink predation were observed at breeding colonies. It is unlikely that shags were lost to mink before 2009 because the population has been monitored and censused either partly (Faro island) or completely each year since 1994. On the other hand, we found only two preyed chicks, but predation of chicks could be underestimated, as small chicks may be consumed entirely (Dunstone 1993). Most shags were preyed during courtship and incubation and were found near or inside a nest-site. At the study site, many nests are placed under rocks and boulders and the attending adults are particularly vulnerable to terrestrial predators.

The reduced mortality of shags since 2009 could be due to plastic responses to predator presence (such as changes in nest-sites, skipping breeding or/and dispersal, Fig. 4; see below), or to culling campaigns. Although the scat surveys should be taken with caution (Zuberogoitia et al. 2006), the number of mink scats and captures decreased over time, especially after 2010, probably as a result of the control program. Overall, 47 mink were removed during 2009–2012 (Romero and Piorno 2012) and by 2015 the islands were apparently free of mink (R. Romero, unpublished data). Thus, we cannot entirely separate the effect of behavioural responses of shags from the effect of mink culling campaigns on shag survival. Nevertheless, few shags were predated in 2010, the year of the highest mink density according to scat surveys. This result suggests that there were other mechanisms than culling by which shags could avoid predation.

Invasive alien predators may elicit plastic responses in prey species (Lima 2009), which preclude local population extinctions (Brzeziński et al. 2012). In our study, the abundance of mink during the breeding season correlated with the population growth rate in the next year but not with observed mortality. These results suggest that mink disturbance triggered behavioural responses in shags, such as non-breeding (skipping) or dispersal. Skipping a breeding event due to bad weather conditions at sea during the pre-breeding period is a common feature of shag biology (Aebischer and Wanless 1992; Velando and Freire 2002; Velando et al. 2005b), a possible response with adaptive consequences when the risk of predation in the colonies is high. Additionally, the activity of predators in colonies may influence adult or juvenile dispersal (Oro et al. 1999). In our study area, adult shags are characterized by high site fidelity (Velando and Freire 2002; Barros et al. 2013). During our study, of 78 adult shags ringed after mink arrival and resighted anywhere, only one moved to another colony, so adult dispersal is not likely to be responsible for the observed patterns. Juvenile dispersal could explain the correlation between mink density and population growth if potential recruits avoided mink-inhabited colonies (Lima 2009). We cannot discard this possibility because, during the study period, only six juveniles ringed at the study area were observed to recruit [i.e. birds observed in breeding colonies and hatched from 2007 onwards; the average age of first reproduction in the study population is 2.53 years (Velando and Freire 2002), and most shags recruit within 3 years (Aebischer 1986)]. Nevertheless, the six recruits observed established in the study area and no recruits were observed in the other islands of the National Park, which were also extensively monitored (e.g. Velando et al. 2015, see also ESM).

Changes in nesting behaviour

This study tested the hypothesis that the presence of mink in breeding areas produced a change in the nest-site selection of European shags towards nest-sites located on steeper slopes including ledges on vertical cliffs. Nest-sites located on vertical cliffs are usually inaccessible to terrestrial carnivores, which explains the cliff-nesting behaviour of many seabirds (Regehr et al. 1998), including the European shag (Nelson 2006). At Illas Cíes, prior to mink arrival in the breeding colonies, European shags typically bred in cavities under detached granite rocks and boulders situated in areas readily accessible to terrestrial predators (see Velando and Freire 2003). Nest-sites placed on steep slopes and vertical cliff faces may also facilitate the escape of the attending adults, especially in species that, as European shags, do not take off easily (Nelson 2006). As far as we know, the invasion of the colonies by mink is the only environmental factor that is likely to explain this evident habitat shift. The rapid change in nesting behaviour, a switch from accessible to inaccessible nest-sites, may also explain, in part, the reduction in adult mortality over time (see above). Safe nest-sites may be limited at the colony, and this could constrain the population growth in the presence of mink. The culling effectively eradicated minks from this protected area, thereby eliminating this possible constraint.

In this study we found that neither the coverage of the nest-sites selected by shags changed after mink arrival. Over the fifteen study-years, European shags selected nest-sites with lateral and overhead cover and good visibility (see Velando and Freire 2003). In our long-term study, these nest-site characteristics were associated positively with observed reproductive success. Nevertheless, after the arrival of mink in the colonies, the probability of occupation of the nest-sites with better drainage decreased slightly. Reproductive success was low in those nest-sites with poor drainage (i.e. with side walls sloped toward the nest), which increases the probability of nest flooding. In these colonies, heavy rains during incubation commonly produce egg loss by flooding (Velando and Freire 2003). Thus, it is possible that, after mink arrival, shags selected safer nest-sites at the expense of quality.

Effects on reproductive success

The strong relation between the success of a nest-site and its steepness score suggests higher survival rates of chicks from inaccessible nest-sites during the mink period. By contrast, the lower quality of inaccessible nest-sites due to poorer drainage, may have negatively affected reproductive success. Nonetheless, the possible cost of selecting safer nest-sites can be negligible in certain circumstances, for example when safer and high quality nests are available.

Overall, reproductive success was lower after mink arrival compared with mink-free years. This temporal comparison should be taken with caution because other causes may underlie the reproductive impairment observed. In 2003, the Illas Cíes colony was affected by the *Prestige* oil spill (Velando et al. 2005a, b), with long-term consequences on reproductive success (Barros et al. 2014). A previous spatial and temporal study made on 18 colonies to analyse the effect of the *Prestige* oil-spill on reproduction found that the presence of mink further reduced reproductive success by 28 %, although this effect was not statistically significant ($P = 0.053$; Barros et al., 2014). On the other hand, previous studies failed to find an effect of climate oscillations on reproductive success (Barros et al. 2014). The comparison between Illas Cíes and two nearby mink-free colonies (see ESM) indicated that, in 2009, the season when mink were first detected at breeding colonies, the reproduction in our study area was impaired. This analysis also indicated a poor reproduction in the previous season (2008). It is possible that mink visited the colonies 1 year before the first signs of their presence were recorded or, alternatively, that reproduction in these islands was still impaired by the *Prestige* oil-spill. The negative effects of mink presence on shag reproduction, if any, were transient, as reproductive performance in mink-infested colonies was similar to nearby mink-free colonies during 2012 and 2013.

Indirect effects of mink disturbance on the reproductive success of shags are also possible, because under high predation risk, a reduction of parental investment is expected (Lima 2009). Inca terns (*Larosterna inca*) nesting in sites with high predation risk made fewer visits to their nests, with detrimental effects on chick growth (Velando and Marquez 2002). In our study, the interaction between steepness and mink presence period on reproduction indicates that steepness is an important factor affecting reproductive output when predators are present. Thus, in the years after mink arrival, shags nesting in safer, steeper (i.e. with high steepness scores) produced more fledglings compared to those breeding in ground level nest-sites, an effect that was not found in mink-free years. Additionally, after mink arrival, low concealed nest with sites (i.e. those with high visibility scores) showed reduced reproductive success. A high predation risk may induce physiological-stress responses with detrimental effects on reproduction (Travers et al. 2010) and fitness (Eggers et al. 2006; Travers et al. 2010). Lastly, under predation risk, shags could prioritize nesting in safe nests at the expense of their reproductive quality. Although our results suggest a negative small effect of a mink-related habitat shift on reproductive success, this effect was restricted to nest-site drainage and thus this possibility should be taken with caution (see above).

Conclusions and implications for management

In this study, we showed that mink presence affected European shags via direct (predation of breeding adults) and indirect (shift in nest-site selection) effects. The onset of mink predation in 2009 was followed by a sharp drop in breeding numbers, and likely contributed to the overall negative trend observed in the European shag population at Illas Cíes in subsequent years. Our study suggests that shags were able to cope with mink predation by selecting nest-sites that afforded greater protection from terrestrial carnivores. Our study highlights that the effects of invasive predators on prey are complex, and shows how predator-triggered plasticity in behaviour allows to reduce the impact of introduced predators.

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References

Aebischer NJ (1986) Retrospective investigation of an ecological disaster in the shag, *Phalacrocorax aristotelis*: a general method based on long-term marking. J Anim Ecol 55:613–629

Aebischer NJ, Wanless S (1992) Relationships between colony size, adult non-breeding and environmental conditions for Shags *Phalacrocorax aristotelis* on the Isle of May, Scotland. Bird Study 39:43–52

Barros A, Álvarez D, Velando A (2013) Cormorán moñudo—*Phalacrocorax aristotelis*. In: Salvador A, Morales MB (eds) Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org. Accessed 24 June 2015

Barros A, Álvarez D, Velando A (2014) Long-term reproductive impairment in a seabird after the *Prestige* oil spill. Biol Lett. doi:10.1098/rsbl.2013.1041

Bennett PM, Owens IPF (1997) Variation in extinction risk among birds: chance or evolutionary predisposition? Proc R Soc Lond B 264:401–408

BirdLife International (2000) Threatened birds of the world. Lynx Edicions and BirdLife International, Barcelona

Bixler KS (2010) Why aren't Pigeon Guillemots in Prince William Sound, Alaska, recovering from the Exxon Valdez oil spill? M.Sc. Thesis, Oregon State University, Corvallis, Oregon

Björsson TE, Heirstensson P (1991) Mink in southern Breidfjordur Bay. In: Macdonald D, Strachan R (eds) The mink and the water vole. Analyses for Conservation 7. Wildlife Conservation Research Unit and the Environment Agency, Oxford, pp 3–12

Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinction and mammalian introductions on oceanic islands. Science 305:1955–1958

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bonesi L, Macdonald DW (2004) Evaluation of sign surveys as a way to estimate the relative abundance of American mink (*Mustela vison*). J Zool 262:65–72

Bonesi L, Palazón S (2007) The American mink in Europe: status, impacts, and control. Biol Conserv 134: 470–483

Bonesi L, Chanin P, Macdonald W (2004) Competition between Eurasian otter Lutra lutra and American mink *Mustela vison* probed by niche shift. Oikos 106:19–26

Brzeziński M, Natorff M, Zalewski A, Zmihorski M (2012) Numerical and behavioral responses of waterfowl to the invasive American mink: a conservation paradox. Biol Conserv 147:68–78

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. A practical information-theoretic approach. Springer, New York

Craik C (1995) Effects of North American mink on the breeding success of terns and smaller gulls in west Scotland. Seabird 17:3–11

Craik C (1997) Long-term effects of North American Mink *Mustela vison* on seabirds in western Scotland. Bird Study 44:303–309

Croxall JP, Rothery P (1991) Population regulation of seabirds: implications of their demography for conservation. In: Perrins CM, Lebreton JD, Hirons GJM (eds) Bird population studies, relevance to conservation and management. University Press, Oxford

Dunstone N (1993) The mink. T & AD Poyser Ltd, London

Eggers S, Griesser M, Nystrand M, Ekman J (2006) Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. Proc R Soc Lond B 273:701–706

Fleming MA, Cook JA (2010) MtDNA and microsatellite DNA provide evidence of fur farm ancestry for mink populations in Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project 070853. Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM

Folkestad AO (1982) The effect of mink predation on some seabird species. Viltrapport 21:42–49

Fontaine JJ, Martin TE (2006) Habitat selection responses of parents to offspring predation risk: an experimental test. Am Nat 168:811–818

Forstmeier W, Weiss I (2004) Adaptative plasticity in nest-site selection in response to predation risk. Oikos 104:487–499

Furness RW, Monaghan P (1987) Seabird ecology. Blackie, Glasgow

García-Díaz P, Lizana M (2013) Reproductive aspects of American minks (*Neovison vison*) in central Spain: testing the effects of prey availability. Mamm Biol 78:111–117

Gobster PH (2005) Invasive species as ecological threat: is restoration an alternative to fear-based resource management? Ecol Rest 23:261–270

Harfenist A, Ydenberg RC (1995) Parental provisioning and predation risk in rhinoceros auklets (*Cerorhinca monocerata*): effects on nestling growth and fledging. Behav Ecol 6:82–86

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Biol 46:10–18

Lima SL (2009) Predators and the breeding bird: behavioural and reproductive flexibility under the risk of predation. Biol Rev 84:485–513

Little RC, Milliken GA, Stroup WW, Wolfinger RD, Schabenberger O (2006) SAS for mixed models, 2nd edn. SAS Institute Inc, Cary

Mainwaring MC, Hartley IR, Lambrechts MM, Deeming DC (2014) The design and function of birds' nests. Ecol Evol 4:3909–3928

Martin TE (1993) Nest Predation and nest-sites: new perspectives on old patterns. Bioscience 43:523–532

Martínez-Abraín A, Velando A, Oro D, Genovart M, Gerique C, Bartolomé MA, Villuendas E, Sarzo B (2006) Sex-specific mortality of European shags after the Prestige oil spill: demographic implications for the recovery of colonies. Mar Ecol Prog Ser 318:271–276

McNeely JA (2005) Human dimensions of invasive alien species. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (eds) Invasive alien species: a new synthesis. Island Press, Washington

Melero Y, Palazón S (2011) Visón americano—*Neovison vison*. In: Enciclopedia Virtual de los Vertebrados Españoles. Salvador A, Cassinello J (ed) Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org/. Accessed 20 May 2015

Mooney HA, Hobbs RJ (2000) Invasive species in a changing world. Island Press, Washington DC

Nelson BJ (2006) The pelecaniformes. Oxford University Press, Oxford

Nordström M, Högmander J, Laine J, Nummelin J, Laanetu N, Korpimäki E (2003) Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic sea. Biol Conserv 109:359–368

Opermanis O, Mednis A, Bauga I (2001) Duck nests and predators: interaction, specialisation and possible management. Wildl Biol 7:87–96

Oro D, Pradel R, Lebreton JD (1999) The effects of nest predation and food availability on life history traits in Audouin's gull. Oecologia 118:438–445

Pereira P (2006) Estudio de la metodología para el control de la población de visón americano en el archipiélago de Sálvora en el Parque Nacional Islas Atlánticas de Galicia. Parque Nacional Islas Atlánticas de Galicia (unpublished report)

Quillfeldt P, Schenk I, McGill RAR, Strange IJ, Masello JF, Gladbach A, Roesch V, Furness RW (2008) Introduced mammals coexist with seabirds at New Island, Falkland Islands: abundance, habitat preferences and stable isotope analysis of diet. Polar Biol 31:333–349

Ratcliffe N, Craik C, Helyar A, Roy S, Scott M (2008) Modelling the benefits of American Mink *Mustela vison* management options for terns in west Scotland. Ibis 150:114–121

Regehr HM, Rodway MS, Montevecchi WA (1998) Antipredator benefits of nest-site selection in Black-legged Kittiwakes. Can J Zool 76:910–915

Romero R, Piorno V (2012) Plan de control de visón americano (*Neovison vison*) en el Parque Nacional de las Islas Atlánticas de Galicia. In: Proceedings of the 7th European conference on biological invasions. Pontevedra (Spain)

Russell RW (1999) Comparative demography and life history tactics of seabirds: implications for conservation and marine monitoring life in the slow lane. Ecology and conservation of long-lived marine animals. Am Fish Soc Sympos 23:51–76

Saether BE, Bakke O (2000) Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653

Schüttler E, Ibarra JT, Gruber B, Rozzi R, Jax K (2009) Abundance and habitat preferences of the southernmost population of mink: implications for managing a recent island invasion. Biodivers Conserv 19:725–743

Short J, Kinnear JE, Robley A (2002) Surplus killing by introduced predators in Australia—evidence for ineffective antipredator adaptations in native prey species? Biol Conserv 103:283–301

Travers M, Clinchy M, Zanette L, Boonstra R, Williams TD (2010) Indirect predator effects on clutch size and the cost of egg production. Ecol Lett 13:980–988

Vidal-Figueroa T, Delibes M (1987) Primeros datos sobre el visón americano (Mustela vison) en el Suroeste de Galicia y Noroeste de Portugal. Ecología 1:145–152

Velando A, Álvarez D (2004) Cormorán moñudo*, Phalacrocorax aristotelis aristotelis*. In: Madroño A, González C, Atienza JC (eds) Libro Rojo de las Aves de España. Dirección General para la Biodiversidad-SEO/BirdLife, Madrid, pp 60–62

Velando A, Freire J (2001) Can the central-periphery distribution become general in seabird colonies? Nest spatial pattern in the European Shag. Condor 103:544–554

Velando A, Freire J (2002) Population modelling of European shag at their southern limit: conservation implications. Biol Conserv 107:59–69

Velando A, Freire J (2003) Nest-site characteristics, occupation and breeding success in the European shag. Waterbirds 26:473–483

Velando A, Marquez JC (2002) Predation risk and habitat selection in the inca tern (*Larosterna inca*). Can J Zool 80:1117–1123

Velando A, Munilla I (2008) Plan de Conservación del Cormorán Moñudo en el Parque Nacional de las Islas Atlánticas. Universidade de Vigo, Spain (unpublished report)

Velando A, Ortega-Ruano JE, Freire J (1999) Chick mortality in European shag *Stictocarbo aristotelis* related to food limitations during adverse weather events. Ardea 87:51–59

Velando A, Álvarez D, Mouriño J, Arcos F, Barros A (2005a) Population trends and reproductive success of the European shag *Phalacrocorax aristotelis* on the Iberian Peninsula following the *Prestige* oil spill. J Ornithol 146:116–120

Velando A, Munilla I, Leyenda PM (2005b) Short-term indirect effects of the Prestige oil spill on a marine top predator: changes in prey availability for European shags. Mar Ecol Prog Ser 302:263–274

Velando A, Barros A, Moran P (2015) Heterozygosity–fitness correlations in a declining seabird population. Mol Ecol 24:1007–1018

Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. N Z J Ecol 21:1–16

Zuberogoitia I, Zabala J, Martínez JA (2006) Evaluation of sign surveys and trappability of American mink. Consequences for management. Fol Zool 55:257–263

Barros et al.

ELECTRONIC SUPPLEMENTARY MATERIAL

1. Breeding numbers and reproductive success: comparison with nearby colonies

Methods

We analysed the changes in the shag breeding population in the National Park of the Atlantic Islands of Galicia, including three groups of islands (Illas Cíes, Illa de Ons and Sagres, Fig. S1). During the period 2007-2014, the breeding pairs in all the colonies in the National Park were counted as the number of apparently occupied nests (nests in advanced stage of construction and with reproduction signs) in April-May. Mink presence was well documented in breeding areas at Illas Cíes, as early as 2009 (see main text), but no signs of mink presence have been recorded in Illa de Ons or Sagres. Therefore, we compared Cies population trends with those trends in the free-mink islands in the National Park. For that, we performed a Generalized Linear Model (GLM) with Poisson errors and log link using the breeding numbers as dependent variable and the island (Cíes, Ons, Sagres) and year as dependent variables.

In the study period, we followed the shag reproduction in the three islands in some years (2007-2009, 2012-2013) according to financial support. Marked nest sites were monitored three to five times during the breeding season (March to June). Nest sites were marked with epoxy resin and the number of monitored nests varied across islands and years (Sagres, n=22-37 nests; Ons, 25-44 nests; Cíes, 29-62 nests). In all cases, nests were monitored at least once during the incubation period and twice during the chick-rearing period. This procedure enabled estimation of reproductive success as the number of chicks surviving to full-size-grown per nest (age >35 days, Velando et al. 2000; Barros et al. 2014). Reproductive success was analysed by a GLM with Poisson errors and a log link, including sampling year and island (Cíes, Ons and Sagres).

Results

The GLM on breeding population counts in the National Park revealed that population trends differed among islands (interaction island x year; Wald χ^2_2= 9.94, P=0.007, Fig. S1). Thus, shag population in the locality with mink presence (Illas Cíes) decreased during the study period (estimate =-0.036±0.009, Fig S1) compared with mink-free islands (Fig S1), which showed a slightly increase in the number of breeders (Ons, estimate =0.046±0.006, Sagres, estimate =0.041±0.019). The population decline in Illas Cíes was especially evident after mink presence in the breeding colonies (i.e. 2009, Fig. S1).

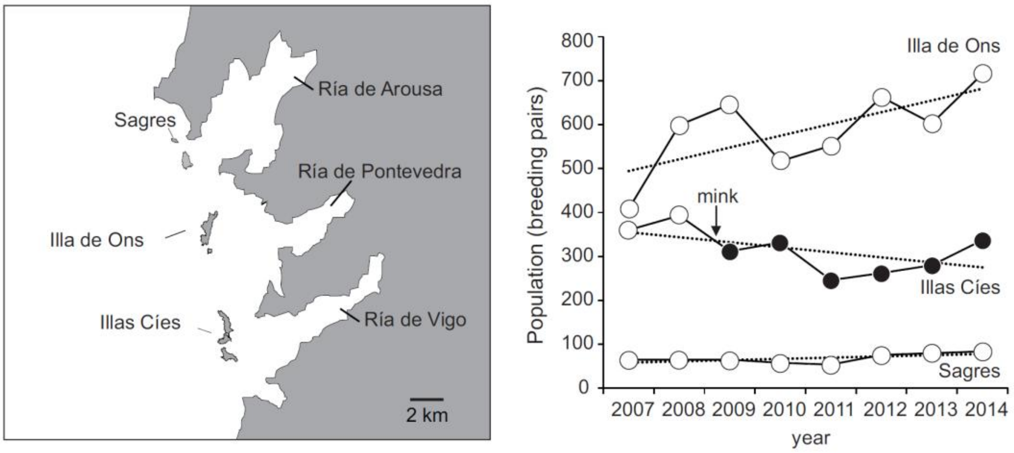

Figure S1. Location of the main shag breeding localities (Sagres, Illa de Ons and Illas Cíes) in the National Park of the Atlantic Islands of Galicia (left panel) and changes in the breeding population during the period 2007-2014 (right panel). Black dots indicate breeding events with mink presence in breeding areas.

Reproductive success varied across islands (Fig. S2, Wald χ^2_2= 15.32, P<0.001) and years (Fig. S2; Wald χ^2_1= 7.97, P=0.005), but the interaction between these terms was not statistically significant (Wald χ^2_2= 4.08, P=0.13). Annual comparisons indicated that reproductive success in Cíes was statistically significant lower compared with free-mink localities only in two years (2008 and 2009; Fig S2).

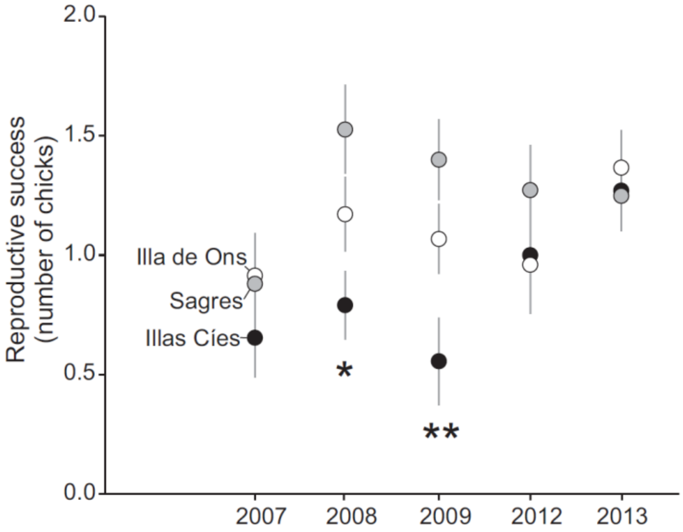

Figure S2. Reproductive success (mean number of chicks per pair±SE) in the National Park of the Atlantic Islands of Galicia. Asterisks indicate statistically significant differences in annual reproductive success between mink (Cíes) and mink-free islands (Ons and Sagres; *p<0.05, **p<0.01).