

Habitat-specific effectiveness of feral cat control for the conservation of an endemic ground-nesting bird species

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Summary

1. Invasive non-native species are one of the greatest drivers of the loss of biodiversity world-wide. Consequently, removing or controlling invasive predators should generally benefit vulnerable native species. However, especially on islands, where most mammalian predators are introduced, these predators may also prey on other invasive mammals. Removing only apex predators may lead to increases of meso-predators that may in turn increase predation pressure on native wildlife.

2. We examined the benefits of a feral cat *Felis catus* control programme on nest survival of a critically endangered ground-nesting bird, the St Helena Plover *Charadrius sanctaehelenae* in two habitat types, harbouring c. 30% of the global population of this species. We monitored nest success and the activity of introduced mammals (cats, rabbits *Oryctolagus cuniculus*, rats *Rattus rattus* and *Rattus norvegicus*, and mice *Mus musculus*) over 2 years, before and after controlling feral cats.

3. Live trapping removed 56 feral cats from our study areas. In the semi-desert, rabbit and mouse activity increased, but rat activity remained low after feral cat control. In pastures, rat and mouse activity increased after feral cat control, while rabbit activity remained constant.

4. Nest survival of plovers increased more than threefold in the semi-desert, but increased only marginally in pastures. This difference may be due to an increase in rat activity and potentially rat predation following cat control in pastures, whereas no increase in rat activity was observed in the semi-desert.

5. *Synthesis and applications.* Our study shows habitat-specific consequences of feral cat control on ground-nesting bird productivity after 1 year, probably mediated by differences in the availability of alternative prey. The results highlight the importance of experimental trials and a thorough understanding of the interactions between multiple invasive species before predator-control operations are implemented over larger scales. On islands with multiple invasive species, there may not be a simple generic approach to predator management (other than removing all invasive species simultaneously).

Key-words: camera trapping, invasive species, meso-predator release effect, predator control, shorebird, spatially explicit mark–recapture, wader

Introduction

Invasive non-native species are one of the greatest drivers of human-caused loss of biodiversity world-wide (Simberloff *et al.* 2013). The presence of invasive species is particularly severe on many islands, where native biodiversity

either evolved in, or adapted to, the absence of predators. Mammalian predators such as mustelids, cats *Felis catus* and rats *Rattus* spp. have been introduced to many islands and have caused the decline or extinction of many island-endemic species. Over the past 40 years, conservation managers have removed invasive mammals from increasingly large islands to reduce the negative effects of these species on native biodiversity (Nogales *et al.* 2004;

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Howald *et al.* 2007). Despite continuing improvements in eradication techniques, the simultaneous removal of all invasive species from an island poses a complex challenge that has seldom been overcome (Oppel *et al.* 2011; Glen *et al.* 2013).

While the simultaneous removal of all introduced species from an island would probably yield the highest benefits for native biodiversity, the focussed removal or control of mammalian predators has frequently been an effective tool to protect native biodiversity (Lavers, Wilcox & Donlan 2010; Smith *et al.* 2010; Hartway & Mills 2012). Predator management on islands where most or all predators are introduced species can be highly complex due to trophic interactions between predators and native prey species. For example, the control or removal of apex predators such as cats or mustelids may reduce predation and hence increase population size, of other introduced species such as rodents and rabbits *Oryctolagus cuniculus*. The meso-predator release effect describes the detrimental effects on native biodiversity that can occur if the meso-predator species that is released from predation in turn preys on native species (Rayner *et al.* 2007; Bergstrom *et al.* 2009; Ritchie & Johnson 2009). The extent of the meso-predator release effect is likely to vary between islands and habitats, for reasons not always well understood (Bolton *et al.* 2007; Rayner *et al.* 2007; Bodey *et al.* 2011). Given the variable effects of predator management, it is essential to examine trophic responses to predator control to ensure that the species of conservation concern actually benefit (Tompkins & Veltman 2006).

In this study, we examined the impacts of controlling an introduced apex predator on the reproductive success of a ground-nesting bird species, while simultaneously monitoring the response of other introduced mammal species. Our study focussed on the St Helena Plover *Charadrius sanctaehelenae*, a critically endangered wader that inhabits natural semi-desert and pasture. The species is endemic to the island of St Helena, which has already lost six endemic bird species likely due to the effects of introduced mammals (Ashmole 1963). The St Helena Plover declined substantially between the 1980s and 2000s (population in 2013 *c.* 500 individuals), probably as a consequence of lower grazing intensity in pastures and subsequent vegetation growth. Recent conservation management for the species has focused on increasing stocking levels and removing alien vegetation from suitable pasture breeding sites (McCulloch 2009). Habitat management alone, however, may not be sufficient to increase population growth rate of ground-nesting waders (Burns *et al.* 2013; Smart *et al.* 2013), and introduced cats, rats, rabbits and mice *Mus musculus* occur in St Helena Plover breeding habitat. Feral cats have been identified as the main predator of St Helena Plover nests (Burns *et al.* 2013), but cats also prey heavily on rats if they are available (Nogales & Medina 1996; Bonnaud *et al.* 2010; Hervías *et al.* 2013). Rats are known predators of many native birds on islands, including the St Helena Plover

(Burns *et al.* 2013). It is therefore possible that removing feral cats may lead to an increased abundance and/or activity of rats and negative effects on nest success.

We monitored breeding success and the activity of cats, rodents and rabbits for 2 years, before and after the experimental control of feral cats. This allowed us to assess whether nest success differed between the baseline and the control year in two habitats and whether any change could be explained by corresponding changes in the activity of introduced mammal species.

Materials and methods

STUDY AREA AND EXPERIMENTAL DESIGN

St Helena is a volcanic island in the South Atlantic (15°58'S, 5°43'W). St Helena Plovers inhabit various habitats, mainly grazed farmland and open sandy plains of a semi-desert. This study focussed on grasslands at 'Man and Horse' and semi-desert at 'Prosperous Bay', which together host *c.* 30% of the global population (Burns 2011). The pasture study area, at the south-western tip of St Helena, encompassed 250 ha of sheep grazed grassland, bordered to the south by near vertical cliffs and to the north by a steep-sided valley. The semi-desert study area encompassed 215 ha of a larger semi-desert complex in the east and comprised rolling hills with patches of riparian woodland.

The project employed a before–after experimental design. In the first year (July 2011–April 2012), we monitored baseline breeding success of St Helena Plovers, and baseline activity of introduced mammals. From May through September 2012, we conducted an intensive feral cat-trapping operation, and we continued monitoring breeding success and mammal activity for another breeding season from September 2012 until April 2013. In most mammal monitoring approaches, activity and abundance are confounded, and we therefore refer to 'activity' throughout this study, which may reflect changes in abundance or changes in the mobility of individuals of all mammal species.

FERAL CAT TRAPPING AND REMOVAL

St Helena has a human population of *c.* 4000 people, who own >1000 domestic cats, most of them free-ranging. We used live cage trapping rather than poison bait to allow any domestic cats to be released (see Supporting information for details). This procedure required more effort but was considered critical to maintain public support (Ratcliffe *et al.* 2010). Cat trapping was initiated after the first year of baseline surveys, and traps were baited with food, placed where cats had been previously recorded and checked daily. Trapped cats were first compared against a photographic library of domestic cats to avoid euthanizing domestic cats. Cats were then anaesthetized and scanned for a micro-chip, a legal requirement for domestic cats in St Helena. Domestic cats were returned to their owners, and cats that did not match known domestic cats and did not have a micro-chip were euthanized. The control procedures were carried out by staff trained by a veterinary surgeon, approved by the state veterinary service of St Helena and agreed with Defra's Ethical Review Panel to ensure that they were aligned with best practice in the UK. Due to the live trapping and the delay between capture and

euthanasia, the identification of dietary items in stomach contents was not possible.

Intensive feral cat trapping continued until 24 September 2012 at both sites. From September 2012 until the end of the project in April 2013, feral cat trapping was carried out only every second week to limit the number of re-colonizing individuals. Cat traps were placed in strategic thoroughfares where cats had been recorded with camera traps (see Appendix S1, Supporting information).

FERAL CAT AND RABBIT MONITORING

We used 32 passive infrared motion sensor cameras (Bushnell Trophy Cam, Bushnell Outdoor Products, Overland Park, KS, USA) triggered by temperature alterations and movements to detect feral cats and rabbits. Cameras were placed on a 100 × 100 m grid; no bait was used to attract animals to cameras. Because the grid contained several hundred locations, we used a random subset of locations for each 2-week period and moved cameras to a new random subset of grid points every 2 weeks. The coordinates of each camera location were recorded using a GPS unit (Garmin eTrex, Garmin, Schaffhausen, Switzerland).

We used a general activity index to estimate site- and year-specific activity indices of rabbits and feral cats (Bengsen *et al.* 2011). Briefly, this index and associated standard errors were estimated with a generalized linear mixed model (GLMM) using the daily number of detected cats or rabbits at a given camera trap as response variable, site and management as fixed factors, and camera trap location as a random grouping variable. To test whether feral cat control affected activity indices, we constructed four candidate models and evaluated the support for each using an information-theoretic approach (Burnham & Anderson 2002). We hypothesized that cat or rabbit activity could be either constant across sites and treatments (null model), vary between sites (site model), vary between sites and by treatment (site + management), or that the treatment effect was different between the two sites (site × management). We fitted the four models for each species using a negative binomial GLMM with R package 'glmmADMB' (Bolker *et al.* 2009; Skaug *et al.* 2011) in R 2.15.1 (R Development Core Team 2010) and used Akaike's information criterion for inference to assess whether there was any support for feral cat removal to have affected cat and rabbit activity.

FERAL CAT ABUNDANCE ESTIMATION

To assess whether feral cat trapping removed a significant proportion of the population, inhabiting the study areas required an estimate of feral cat abundance. Because the activity index is a function of abundance and detectability, rather than true abundance, we estimated cat abundance using spatially explicit capture–recapture (SECR) models (Oppel *et al.* 2012). SECR models use the individual identification of animals at different locations within the study area to estimate each individual's home range centre (Efford 2004; Efford, Dawson & Borchers 2009; Royle *et al.* 2009) and thus provide an estimate of true abundance for a given study area. We individually identified cats on camera trap images by their unique coat markings (see Appendix S2, Supporting information) and fitted SECR models separately for each study site using program 'SPACECAP' (Gopalaswamy *et al.* 2012) in R 2.15.1 (R Development Core Team 2010). We present cat

abundance estimates for each study area as posterior mean with 95% credible intervals (hereafter 'CrI', see Appendix S2, Supporting information for details).

RODENT MONITORING AND ESTIMATION OF RODENT ACTIVITY INDICES

The relative activity of rodents (rats and mice) was monitored using ink-tracking tunnels. We established 60 and 80 tracking tunnels in the semi-desert and the pastures, respectively, that were arranged in lines of 10 tracking tunnel stations spaced 50 m apart. Origin and direction of each transect line were generated by using a random point generator and a random direction from the starting point. Tracking tunnels were set up in August 2011 and pre-baited for 3 months to allow rodents to get accustomed to the tunnels. Between November 2011 and April 2013, we inserted tracking paper laced with tracking ink and a small amount of peanut butter into each tunnel once per month. Tracking paper was collected one day after deployment, thus recording rodent activity in one night. Tunnel records where the tracking paper was rendered unrecognizable were removed from analysis.

For each month and site, we estimated a general activity index for each rodent species following the same approach as for camera trap data (Bengsen *et al.* 2011), with the unique tracking tunnel station as a random factor to account for serial autocorrelation in using the same tracking tunnel stations repeatedly over several months. We employed the same approach for inference as for camera trapping data and hypothesized that rodent activity could be either constant across sites and treatments, vary between sites, vary between sites and by treatment, or that the treatment effect was different between the two sites. In contrast to the camera trap data, we fit models with a binomial distribution (tracking tunnel data yield only detection/non-detection data) for each species using the function 'lmer' in R package 'lme4' in R 2.15.1 (R Development Core Team 2010).

NEST MONITORING AND ESTIMATION OF NEST SURVIVAL

Nest monitoring followed procedures described in Burns *et al.* (2013). Briefly, we continuously searched for and found nests by following behavioural cues of the birds. Once found, nests were visited approximately weekly and were checked from a distance to avoid disturbance. Nests were classified as successful if chicks of an appropriate age were seen close to the nest scrape. The nest was deemed to have failed if the nest scrape was empty and parent birds were in the area but not exhibiting behaviour typical of adults with young chicks, or if the parent birds were not seen within *c.* 100 m of the nest.

To test whether feral cat control influenced nest survival, we estimated daily nest survival probabilities in Program MARK (White & Burnham 1999), interfaced with R 2.15.1 via the 'RMark' library (Laake & Rexstad 2008). We constructed six models of daily nest survival and used an information-theoretic approach to quantify support for each (Burnham & Anderson 2002; Dinsmore, White & Knopf 2002). Based on previous knowledge of St Helena Plover nest survival, we hypothesized that nest survival would differ between habitats, and we included a habitat effect in all models (Burns *et al.* 2013). We evaluated two models that assumed that nest survival would not change after feral cat removal, one including only the site effect and another that

included the site and an additive effect of nest initiation date. We then introduced an additive effect of cat removal to these two models, examining whether cat control had an additional effect on nest survival that was similar at both study sites. Finally, we evaluated two models that assumed that the effect of feral cat removal would differ between the two study sites by incorporating a site \times management interaction. This interactive effect was justified by the different habitat type and presumed density of feral cats and alternative prey in the pastures and the semi-desert, which could conceivably lead to different benefits of cat control on St Helena Plover nest survival. Other factors that frequently affect nest survival in temperate environments, such as weather and food availability, were not considered because they are remarkably constant and unlikely to affect nest survival over the protracted breeding season of St Helena Plovers.

We used the most parsimonious model for inference and estimated site-specific nest survival by raising the estimates of daily nest survival to the power of 30, assuming that nests must survive 30 days to hatch successfully (Burns *et al.* 2013). We present model-derived estimates of nest survival with 95% confidence intervals.

Results

FERAL CAT TRAPPING EFFORT AND NUMBER OF CATS REMOVED

During the 3 months of intensive cat trapping, 37 feral cats were removed from the two study sites (19 in pastures, and 18 in the semi-desert). To minimize re-colonization, trapping effort was continued until the end of the project. The total trapping effort at both study sites amounted to 4287 trap nights and required 491 person days to set and check traps and refresh bait. By the end of the project in April 2013, a total of 56 feral cats were removed from the two study sites (29 in pastures, and 27 in the semi-desert). In addition, three domestic cats were captured in the semi-desert and returned to their owners. One of these individuals was captured twice.

FERAL CAT ABUNDANCE AND TURNOVER

During 4957 camera trap days prior to feral cat control, we recorded 141 cat encounters, while during 3882 camera trap days after feral cat control, we recorded 98 cat encounters. Thus, feral cat control did not succeed in removing all feral cats from either of the two study sites. There was reasonably strong support for a management effect on the general activity index of cats derived from camera traps (Table 1). Because the most parsimonious model included 'management' as an additive effect, the estimated cat activity index decreased by 25% in both pastures and the semi-desert (Fig. 1).

Of the 239 cat detections, 137 were of sufficient quality to be individually identifiable (52% and 58% of all cat detections in pastures and the semi-desert, respectively). None of the cats identifiable on camera were known domestic cats. Prior to cat control, at least 15 different

Table 1. Model selection table showing different generalized linear mixed models to examine the effect of feral cat control ('management') on introduced mammal abundance measured using tracking tunnels (rats and mice) or camera traps (cats and rabbits) at two sites in St Helena between November 2011 and April 2013

Species	Model	<i>k</i>	AIC	Δ AIC	ω AIC
Rat	Site \times management	5	2274.22	0.00	1.00
	Site + management	4	2302.17	27.94	0.00
	Site	3	2329.76	55.54	0.00
	Constant	2	2404.90	130.67	0.00
Mouse	Site \times management	5	2092.16	0.00	0.55
	Site + management	4	2092.58	0.42	0.45
	Site	3	2298.87	206.71	0.00
Rabbit	Constant	2	2358.25	266.09	0.00
	Site \times management	6	6322.06	0.00	0.94
	Site + management	5	6328.04	5.98	0.05
	Site	4	6330.52	8.46	0.01
Cat	Constant	3	6375.80	53.74	0.00
	Site + management	5	1995.46	0.00	0.59
	Site \times management	6	1997.46	1.99	0.22
	Site	4	1997.68	2.22	0.19
	Constant	3	2006.00	10.54	0.00

k, number of estimable parameters; AIC, Akaike's information criterion; Δ AIC, difference in AIC units to the most parsimonious model; ω AIC, relative weight of evidence for each model.

individuals were registered in pastures, and 17 different individuals in the semi-desert. After feral cat control, 15 and nine different individuals were identified in pastures and the semi-desert, respectively. Three individuals in the pastures were positively identified both before and after feral cat control, and only one identifiable individual was detected before and after feral cat control in the semi-desert. Thus, we identified a total of 27 and 25 individual feral cats in pastures and the semi-desert, respectively. Of the individuals identified from camera trapping, 48% ($n = 13$) and 24% ($n = 6$) were removed by feral cat trapping in pastures and the semi-desert, respectively. Thus, only 45% and 22% of captured feral cats had previously been identified with camera traps in the respective study area.

The SECR model yielded abundance estimates of 26 and 37 feral cats using the pastures and semi-desert prior to feral cat control, respectively (Table 2). Because the pastures were bordered by cliffs and the sea, the area over which feral cats could roam was much smaller (303 ha) than in the semi-desert (953 ha), and the estimated density of feral cats in pastures (0.087 cats ha⁻¹, 95% CrI 0.056–0.132) was more than twice as high as in the semi-desert (0.039 cats ha⁻¹, 95% CrI 0.021–0.060). These densities are similar to cat densities on other islands (Nogales *et al.* 2004).

RODENT AND RABBIT ACTIVITY

On images taken by camera traps, we counted 720 rabbits before cat control (553 in pastures, 167 in the semi-desert)

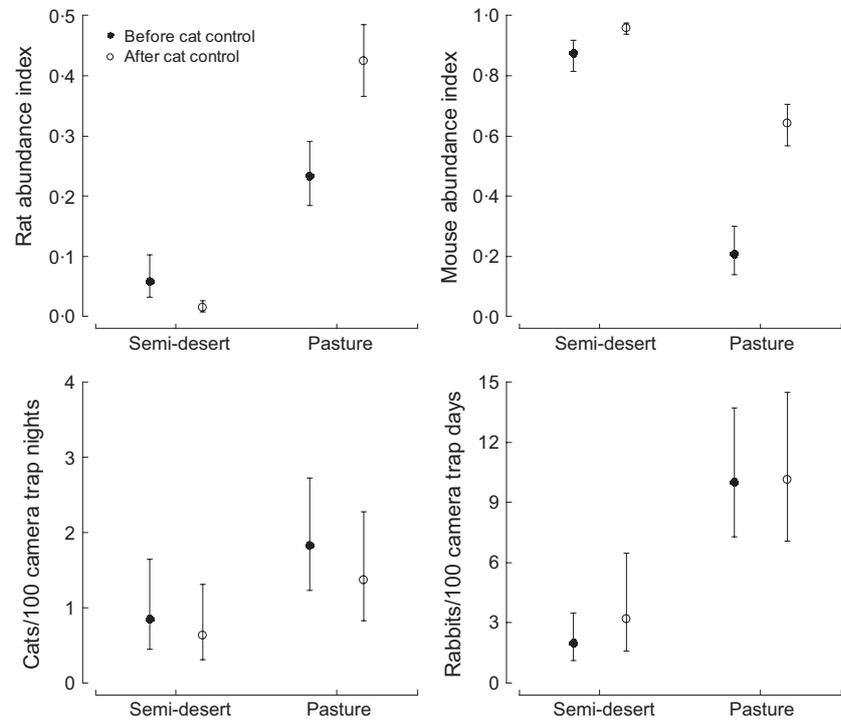


Fig. 1. General abundance indices ($\pm 95\%$ confidence intervals) of introduced mammals at two important nesting sites of St Helena Plovers in the semi-desert and pastures in the months before and after feral cat control. The abundance index for rodents indicates the proportion of tracking tunnels with rodent footprints; the abundance indices for cats and rabbits are derived from camera traps.

Table 2. Mean ($\pm 95\%$ credible intervals) abundance, detection probability and movement radius of feral cats in two habitat types in St Helena, estimated with a spatially explicit capture–recapture model based on camera trap data collected prior to feral cat management in 2012. The ‘super-population’ refers to the number of cats that regularly use the respective study area

Habitat	Parameters	Mean	2.5% CrI	97.5% CrI
Semi-desert (953 ha)	Detection probability at camera trap	0.020	0.008	0.034
	Mean movement radius (km)	0.335	0.234	0.455
	Number of cats (super-population)	37	20	57
Pastures (303 ha)	Detection probability at camera trap	0.020	0.007	0.037
	Mean movement radius (km)	0.358	0.230	0.511
	Number of cats (super-population)	26	16	39

and 757 after cat control (556 in pastures and 201 in the semi-desert). The model that assumed that the effect of feral cat control differed between study sites received the most support from the data (Table 1). The general activity index of rabbits increased by 61% after feral cat control in the semi-desert, but remained stable in pastures (Fig. 1).

Our tracking tunnel data indicated substantial differences in rodent activity between the two study sites (Fig. 1). Rats were much more abundant in the pasture habitat than in the semi-desert; in contrast, mice were more abundant in the semi-desert and were recorded in 80% of tunnels (Fig. 1).

For rats, the model that assumed that the effect of feral cat control differed between study sites received the most support from the data (Table 1). Rat activity increased by 63% in the pasture site after feral cat control, but decreased marginally in the semi-desert (Fig. 1). For mice, both the interaction and the additive model received similar support from the data (Table 1), indicating that the effect of cat control was similar between the two study

sites. Mice increased in both the pastures and the semi-desert after feral cat control, but the increase in pastures by 87% was much higher than the increase in the semi-desert (16%). However, this effect might be due to the recording capacity of tracking tunnels in the semi-desert (Nathan *et al.* 2013), where mice were recorded already at >80% of tunnels in the year prior to feral cat control, and the magnitude of increase that could have been recorded was therefore limited.

NEST MONITORING AND ESTIMATION OF NEST SURVIVAL

We monitored a total of 109 St Helena Plover nests during our study, 53 nests during the baseline year and 56 nests after feral cat control was initiated. In the semi-desert, 20 of 31 nests failed while feral cats were present, and 5 of 33 nests failed after feral cats had been controlled. In pastures, 9 of 22 nests failed while cats were present, and 7 of 23 nests failed after cats had been controlled.

Overall nest survival of St Helena Plovers between 2011 and 2013 was 0.57 (0.45–0.67). Feral cat control had a strong positive effect on daily nest survival, and none of the models that did not include the management factor received any support from the data (Table 3). However, the increase in nest survival after feral cat management was much greater in the semi-desert than in pastures: nest survival increased from 0.23 (95% confidence interval 0.11–0.39) to 0.77 (0.53–0.90) in the semi-desert and from 0.55 (0.32–0.73) to 0.65 (0.41–0.82) in pastures (Fig. 2).

Discussion

The experimental control of feral cats demonstrated a clear beneficial effect on nest survival of the St Helena Plover, but the effect size differed markedly between pasture and semi-desert habitat. Cat control resulted in a more than threefold increase in nest survival in the semi-desert, but only a marginal increase in nest survival in

Table 3. Model selection table showing different models to examine the effect of feral cat control ('management') on daily nest survival probability of St Helena Plovers at two sites between November 2011 and April 2013

Model	k	AIC_c	ΔAIC_c	ωAIC_c
Site \times management	4	237.79	0.00	0.49
Site \times management + nest initiation	5	239.37	1.59	0.22
Site + management	3	239.67	1.88	0.19
Site + management + nest initiation	4	241.04	3.26	0.10
Site + nest initiation	3	249.77	11.99	0.00
Site	3	251.26	13.47	0.00

k , number of estimable parameters; AIC_c , second-order Akaike's information criterion for small sample size; ΔAIC_c , difference in AIC_c units to the most parsimonious model; ωAIC_c , relative weight of evidence for each model.

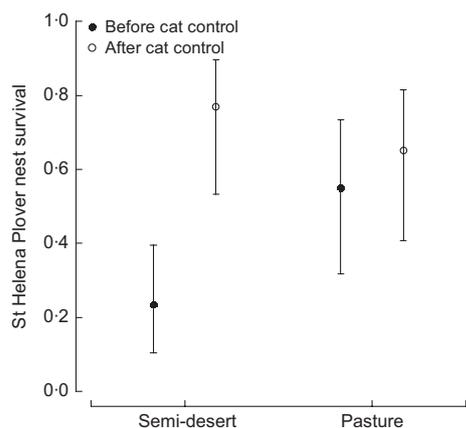


Fig. 2. Estimated nest survival ($\pm 95\%$ confidence intervals) of St Helena Plover at two important nesting sites in semi-desert and pasture in the months before and after feral cat control. Estimates are derived from the most parsimonious model explaining variation in daily nest survival (Table 3).

pastures. Understanding these different responses is critical for management of threatened species, because these results confirm that secondary effects of predator control can be habitat or location specific (Tompkins & Veltman 2006; Rayner *et al.* 2007).

Predator management has been shown to benefit several ground-nesting bird species, but it is also known that removing only top predators may have different consequences for the target species depending on ecosystem and ecological community (Bolton *et al.* 2007; Bodey *et al.* 2011). Generally, the magnitude of the meso-predator release effect is influenced by the composition of the prey community and by ecosystem productivity (Elmhagen & Rushton 2007; Ritchie & Johnson 2009; Brashares *et al.* 2010). For example, Rayner *et al.* (2007) found that rat predation of ground-nesting seabirds after the removal of feral cats was much stronger at higher elevation than at lower elevation sites, and they attributed this difference to more alternative food sources for rats at lower elevation (Rayner *et al.* 2007). Bolton *et al.* (2007) showed that efficacy of top predator removal varied with the density of the top predator and that wader nest survival at sites with low predator density did not necessarily increase after top predator removal. Our finding that the effect of cat control on St Helena Plover nest survival was much stronger in the semi-desert than in pastures is consistent with the prediction that available resources for the meso-predator may impose a bottom-up control of the meso-predator population in the less productive of the two habitats. The semi-desert area is drier, has poorer and shallower topsoil and little vegetation cover and is therefore likely to have fewer food resources available for rats. In addition, foraging preferences of feral cats may have differed between the two habitats owing to a different prey community composition. Cats are generally considered opportunistic foragers that consume the most available prey in each habitat and on each island (Bonnaud *et al.* 2010; Hervías *et al.* 2014). Feral cats in the semi-desert may consume mostly mice and rabbits, while cats in pastures may consume mostly rodents, and it is therefore plausible that cat control did not lead to a strong increase of rats in the semi-desert because rats were more limited by available food resources than by cat predation. Our case study therefore suggests that, even on a small island, the impact of feral cat management can differ between sites and habitats, necessitating a thorough understanding of predator interactions and limitations within an ecosystem context before predator management is implemented (Tompkins & Veltman 2006).

We found substantial changes in nest survival in the semi-desert and rodent activity in pastures despite only moderate changes in cat activity after feral cat control. The response of both target species and meso-predator activity following predator control is known to be several times stronger than the change in predator activity itself (Vance-Chalcraft *et al.* 2007; Ritchie & Johnson 2009). The disproportionate effect is likely a result of release of

both direct and indirect effects from top predators (Peckarsky *et al.* 2008). For example, feral cats may limit rabbit and rodent activity not only by predation, but also by constraining behaviour (Medina *et al.* 2013). Because a lower number of top predators in an area may reduce the perceived risk to prey species (Brown, Laundré & Gurung 1999; Bonnington, Gaston & Evans 2013), the reduction in cat activity following our cat control may have resulted in increased activity and roaming behaviour of rabbits and rodents, thus resulting in higher indices recorded by camera traps and tracking tunnels, respectively. Because behavioural changes may take some time to become apparent at the population level following positive selection for bolder individuals, it is possible that the effects we found may intensify if cat control was maintained over a longer time period than the 1 year of our study (Brashares *et al.* 2010). Although the design of our study does not allow us to distinguish between elevated levels of abundance and activity, we argue that this distinction may be irrelevant from a management perspective: rodents are opportunistic predators of bird nests; hence, higher activity and broader roaming behaviour would likely result in higher encounter rates and predation events even if abundance of rodents remained constant. Thus, the benefit of cat control on St Helena Plovers may be diminished by either increasing activity or increasing abundance of rats.

The habitat-specific increase in nest survival following cat control could reflect a genuine response or a failure in the experimental design, either to detect change in nest survival or to reduce cat numbers adequately. We consider it likely to be a genuine response for several reasons: insufficient cat control may have limited the overall increase in nest survival, but is unlikely to explain the habitat-specific effects on nest survival; faster re-colonization of pastures by feral cats may also have limited the increase in nest survival but is unlikely because the pasture site was more remote than the semi-desert; domestic cats may have predated St Helena Plover nests, but we only observed domestic cats in the semi-desert and never in pastures; an abnormal baseline year in pastures may have obscured a stronger increase in nest survival, but including data from another pasture site ($n = 80$ nests), where feral cat control was performed following a slightly different protocol, also suggested little increase in nest survival following cat control; finally, extreme environmental conditions (drought) that occurred during the second half of the feral cat control may have limited rat population recovery in the semi-desert, but no sign of rat recovery in the semi-desert was evident in the 5 months prior to onset of the drought. Thus, we consider the most likely explanation for the habitat-specific increase in nest survival to be a genuine effect of cat control (see Table S1, Supporting information for alternative possible explanations for observed patterns). The control of cats in pastures led to a marked increase in rats, another known predator of our target species (Burns *et al.* 2013). An

increase in rats did not occur in the semi-desert, where rabbits and mice increased following cat control. Thus, it is possible that reduced cat numbers led to an increase in rat activity and hence rat predation of nests in pastures. This increase may have partially offset any reduction of nest predation by cats, a finding consistent with predictions from the meso-predator release effect.

Besides ecological complexity, predator-control operations are often logistically challenging and expensive (Moseby, Stott & Crisp 2009; Bengsen, Butler & Masters 2012). Particularly on inhabited islands, such as St Helena, where the use of poison bait is often not appropriate, costs can be very high (Ratcliffe *et al.* 2010). Costs can be estimated based on salary and equipment. Maintaining, setting and checking traps and humanely euthanizing cats, as well as liaising with cat owners to raise awareness and minimize risks to domestic cats, required two full-time staff prior to and during the peak breeding season. Other major costs may include equipment (e.g. £1764 for 40 traps), narcotics (£4.50 per 5 kg cat), bait (provided free of charge by local fish factory) and transport (fuel costs and vehicle maintenance £280 per month). Thus, the approximate annual cost of feral cat management over two sites covering 465 ha was ca £25 000 at 2012 fuel costs and St Helena salary levels. Furthermore, to effectively increase nest survival in pastures, the feral cat control may need to be combined with rat control. Alien plants that form dense thickets provide food and shelter for rats, and their removal would also be necessary to minimize the increase in rat populations after feral cat control. These management actions would require additional staff and resources. While annual costs of c. £50 000 may be prohibitive for some islands, the UK government recently invested £240 million for the construction of an airport in St Helena to increase economic revenue from tourism. Because the St Helena Plover is considered a substantial asset to attract foreign visitors, the annual cost of predator control appears to be a negligible investment given the cost for the airport.

Regardless of costs, the effectiveness of feral cat control on inhabited islands may benefit from new approaches, such as the development of a novel toxin (Eason *et al.* 2010), integrated with automated walk-through traps (Blackie *et al.* 2011) that can detect micro-chips and avoid poison delivery to domestic cats. Our cat-trapping efforts used a humane and publicly acceptable procedure with little or no risk to domestic pets, but were only moderately effective. The activity indices from camera trapping indicated only a modest reduction in cat activity despite the removal of 56 individuals. Because very few individual cats were detected both before and after cat control, our data suggest rapid and constant re-colonization of both sites. Such ongoing re-colonization will likely render any benefits of feral cat control short-lived (Bengsen *et al.* 2011; Bengsen, Butler & Masters 2012).

To reduce ongoing re-colonization to areas where feral cat control is used as a management tool, management

must also include the domestic cat population, which is the source of many feral cats. In St Helena, legislation in effect since 2012 mandates that all domestic cats must be registered and micro-chipped, and there is a financial incentive for cat owners to have their pets neutered. This legislation aims to reduce the number of unwanted kittens that contribute to the feral cat population. Additional measures to reduce the pressure of domestic cats on wildlife would be legislation that mandates that domestic cats must be kept indoors at night (Calver *et al.* 2011). The long-term implementation of more effective cat control, and thus the persistent reduction of feral cat numbers in St Helena Plover nesting habitat, may lead to long-term changes in the ecological community that may differ from the response that we observed in the year of our study (Tompkins & Veltman 2006).

MANAGEMENT RECOMMENDATIONS

Controlling or removing non-native predators from islands can be an effective management tool to safeguard native biodiversity. Our study shows, however, that it is critical to understand the trophic interactions between multiple invasive species in all habitats where control is considered, to avoid implementation of a predator-control or predator-removal programme that ultimately fails to deliver biodiversity benefits (Tompkins & Veltman 2006; Rayner *et al.* 2007; Brashares *et al.* 2010). On islands with multiple invasive species, there may not be a simple generic approach to predator management (other than removing all invasive species simultaneously). We therefore recommend that trial studies and experiments such as the one described here should be conducted prior to the large-scale adoption and implementation of predator-removal programmes. In addition to feral predator management, tighter regulation and control of domestic source populations of the same species are often necessary to ensure lasting benefits of predator-control programmes. For St Helena in particular, our experiment demonstrated a clear benefit of cat control in the semi-desert, which is the natural habitat for the St Helena Plover, but also for several hundred endemic invertebrate and plant species. Invertebrates and plants may suffer from elevated mouse and rabbit numbers in response to feral cat control, and these effects require more research. Ultimately, a comprehensive invasive species management plan for the entire island is required to ensure that endemic species that still persist on St Helena can survive in the future.

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Data accessibility

Data uploaded as online supporting information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Procedure for cat trapping and euthanasia.

Appendix S2. Estimation of cat abundance using spatially explicit capture–recapture.

Table S1. Alternative explanations for observed patterns in nest survival after feral cat control.

Tables S2. Database including all raw data of tracking tunnels, camera traps, and nest monitoring.