



Short communication

No overall benefit of predator enclosure cages for the endangered St. Helena Plover *Charadrius sanctaehelenae*

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Predator enclosure cages are designed to increase the clutch survival of ground-nesting birds. Predator enclosures provided for the endangered St. Helena Plover *Charadrius sanctaehelenae*, however, did not result in differences in clutch survival between protected and control nests and may have resulted in elevated adult mortality. Enclosures did not exclude all cats, the dominant nest predator, and it is likely that cats caused the adult mortalities observed close to the enclosures. A population model indicates that even if predator enclosures had excluded all cats, the benefits of increased clutch survival would have been more than negated by the estimated decrease in adult survival. The overall effect of predator enclosures needs to be clarified for other species, taking into consideration annual productivity and adult survival, to understand the circumstances in which predator enclosures are beneficial.

Keywords: adult mortality, clutch survival, nest protection, shorebird conservation, wader, Wirebird.

In many bird species, predation is a major cause of nest failure (Newton 1998) and this can be particularly severe when the predator community is supplemented by non-native species. Much effort has gone into increasing clutch survival for endangered bird species, either through predator control or through one of a suite of non-lethal methods, such as habitat management or

predator enclosure cages (Gibbons *et al.* 2007). Predator enclosure cages have become a common technique in conservation management for ground-nesting birds. A recent meta-analysis found the overall effect of enclosures on hatching success to be significantly positive (Smith *et al.* 2011), although the results of individual studies have been mixed (e.g. Mabee & Estelle 2000), and the overall positive result would be negated by the addition of only a small number of currently unpublished, non-significant, results to the analysis. Furthermore, predator enclosures can also be associated with elevated adult mortality (Smith *et al.* 2011), potentially reducing or negating any positive influence of increased clutch survival on the population growth rate. Therefore, carefully controlled trials are required when predator enclosures are being used on a new species or in a new locality. Here we report on such a trial for the St. Helena Plover *Charadrius sanctaehelenae*, listed as Critically Endangered (McCulloch 2009, BirdLife International 2010).

The St. Helena Plover (also known as the St. Helena Wirebird) is a small plover endemic to the island of St Helena. Its population size has stabilized recently (mean population 2008–2012 = 369 ± 33.9 sd individuals; Saint Helena National Trust unpubl. data) after declining by more than 40% between 2000 and 2005 (McCulloch 2009). Scrub encroachment and other habitat changes are likely to have played a large part in this decline but increased predation pressure may also have been involved (McCulloch 2009, Burns 2011). As on other isolated oceanic islands, many species have been introduced to St Helena since its discovery by humans in 1502 (Ashmole & Ashmole 2000). St Helena has no native mammals and invasive mammals now make up the majority of terrestrial vertebrate biomass. Recent nest camera recordings found only introduced species depredating St. Helena Plover eggs, with domestic or feral cats *Felis catus* emerging as the most important nest predator (65% of recordings, *n* = 13), and rats *Rattus norvegicus* or *Rattus rattus* and Common Mynas *Acridotheres tristis* taking a smaller proportion of eggs (Burns 2011). Predator enclosures were deployed in areas of low clutch survival (Burns 2011) to boost productivity whilst longer-term conservation options were evaluated.

METHODS

The study was carried out in a semi-desert area of St Helena (15°58'S, 5°43'W), named Prosperous Bay, between 8 January and 2 March 2010. The study area covers 7.4 km² and represents a quarter of the species' global breeding range and adult population; 92 adults were counted in this area during the 2010 census (Saint Helena National Trust unpubl. data). The Plovers also nest on grazed land and the same predator species have

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been recorded by nest cameras in both habitats (Burns 2011). Enclosure design and rationale is shown in Figure 1. Nests were visited every 2 days. The first nest was randomly allocated to the treatment (enclosure) or the control (no enclosure) group and subsequently nests were allocated alternately to each group. Nest age was estimated using a calibration of egg density to egg age (Furness & Furness 1981) previously calculated for this species (F. Burns unpubl. data) and enclosures were only erected at nests that had been incubated for a week to minimize the risk of nest abandonment, which has been recorded in other enclosure studies (Hardy & Colwell 2008, Maslo & Lockwood 2009). Nests that failed during the first week of incubation were not included in the study. 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 scrape was empty and parent birds were in the area but not exhibiting any behaviour typical of adults with young chicks, or if the parent birds could not be seen within 100 m of the nest. Nests were assumed to have been abandoned if left unattended for over 24 h. Daily clutch survival was calculated using the Mayfield method (Mayfield 1975). A second study area was initially considered but insufficient nests survived the required week necessary to be included in the trial. Site-specific variation in survival of control nests could lead to a misestimate of the effective-

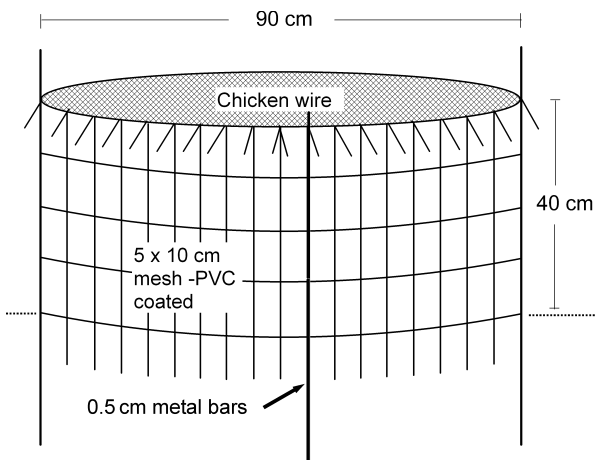


Figure 1. Diagram of the enclosure. Enclosure design was based on the skull dimensions of domestic cats and reference to previous studies (Mabee & Estelle 2000, Johnson & Oring 2002). It is not possible to exclude smaller nest predators, such as rats and Common Mynas, using an enclosure cage, while still allowing access to the parent birds. Enclosures were formed from a cylinder of PVC-coated wire mesh (5 × 10 cm, gauge ~ 2.5 mm) and fitted with a chicken wire roof (2.5-cm square mesh). Enclosures were secured using tent pegs, and four metal bars threaded through the enclosure mesh and into the ground provided additional support.

ness of enclosures. The effectiveness of enclosures was, however, modelled at the level of the entire population (see analysis section below). An infra-red motion-sensitive nest camera was set up at one treatment nest to try to identify nest predators; the design followed that of Bolton *et al.* (2007).

Analysis was carried out in program R (R Core Development Team 2004). Adult mortality during incubation was only observed in association with enclosures (see Results). To assess the impact of this increased adult mortality on the net benefit of predator enclosures to the population, the combination of adult survival (S_A) and clutch survival (S_C) that would lead to a stable population, assuming other vital rates remain unaffected, was plotted. The demographic values used are averages of four St. Helena Plover populations, together representing half the species' global range and breeding population. In relation to the predicted stable population we assessed the effect of the potential increase in S_C from enclosure use, assuming enclosures exclude cats and that S_A remains unchanged and the effect of both the potential increase in S_C and the concurrently observed decrease in S_A (details and calculations are given in Supporting Information Appendix S1).

RESULTS

Adult birds rapidly resumed incubation after enclosure installation (mean time to resume incubation where enclosure accepted = 11.45 ± 1.24 (se) min, $n = 11$ nests). On the one occasion where both adults did not accept the enclosure it was removed after 1 h and the nest excluded from the analyses. Daily clutch survival rate was not affected by the presence of enclosures (Control = 0.953, $n = 11$, Treatment = 0.952, $n = 11$; $Z = 0.2132$, $P = 0.5844$). These estimates of daily clutch survival correspond to a hatching success of 22.7% in control nests and 23.8% in treatment nests. The incidence of nest abandonment did not differ between the treatment group ($n = 1$) and the control group ($n = 2$). All remaining hatching failure ($n = 7$ and $n = 6$, respectively, in all these nests none of the eggs hatched) was attributed to predation, as evidenced by the disappearance of eggs, but in most cases the identity of the nest predator was unknown. It is uncertain, therefore, whether enclosures reduced the effect of cats on clutch survival and this was balanced by an increase in predation by another species, or if there was no change at all.

The camera deployed at one treatment nest showed a cat entering the enclosure through the mesh and eating the eggs (Supporting Information Video S1). The cat took several minutes to access the enclosure but exited rapidly. The parent bird was not seen in the video during this time. There were no signs of damage to the

exclosure, implying that the 5×10 cm mesh used is too large to exclude all cats. One exclosure showed signs of attempted entry, with the wire mesh being slightly misshapen. In this case the parent birds were still incubating, suggesting that not all cats could access the exclosures.

In the final week of the trial the remains of adult birds were found at two nests, each associated with an exclosure. The nest camera was located at one of these nests but the predation of the adult itself was not captured on video. Footage shows a cat eating the unattended eggs on the same evening. It is, however, likely that a cat was responsible for the adults' deaths. The two adult predation events occurred *c.* 800 m apart, potentially within the home-range of a single cat. It is unclear, however, whether an individual cat had learned to associate the exclosures with birds and was responsible for both deaths. It is not clear from the video evidence, or any other evidence, how the adult birds were caught. Most feathers were found within 1 m of the exclosures but not inside, suggesting that the birds were caught leaving or returning to the nest. No evidence of adult mortality was found associated with any control nests.

Using current estimates of demographic parameters, the St. Helena Plover population is predicted to decrease (Fig. 2). Given the observed rates of brood and juvenile survival, the potential increase in clutch survival from the use of exclosures, assuming exclosures effectively excluded cats, would be insufficient to reverse this decline, even though it would have the effect of raising the population growth rate. The potential increase in clutch survival is estimated using the proportion of filmed nest predation events attributable to cats (65%; Burns 2011). We assumed that predator exclosures would be used on half of all nests and calculated the increase in hatching success by removing half of the average daily nest failure attributable to cats (full details and calculations are shown in Appendix S1). Altering the daily failure rate rather than the overall hatching failure accounts for the fact that although the hunting behaviour of other predator species may not change when predator exclosures are used, they will nonetheless encounter nests more frequently, as fewer clutches will have been removed by cats. The decrease in adult survival observed in this study, if applicable throughout the Plover's range, is likely to more than negate any potential increase in clutch survival resulting from the use of exclosures.

DISCUSSION

Smith *et al.*'s (2011) meta-analysis found an overall trend towards increased clutch survival from predator exclosure use. Their analysis compared eight long-term studies of exclosures; seven of these were of North

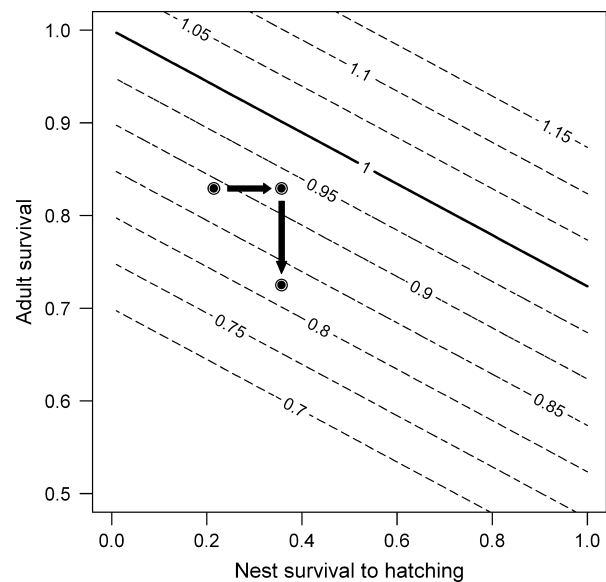


Figure 2. Potential impact of predator exclosures on the adult survival (S_A) and clutch survival (S_C) of the St. Helena Plover. Solid line: conditions (S_A and S_C) required to give a stable population size calculated using observed population averages for juvenile and brood survival (see Appendix S1). Dashed lines: the same relationship but for the indicated population growth rates. The points show three scenarios following the order of the arrows: (i) baseline of observed S_A and S_C ; (ii) the potential increase in S_C from exclosure use, assuming that exclosures exclude cats and that S_A remains unchanged; (iii) both the potential increase in S_C and the concurrent observed decrease in S_A .

American *Charadrius* species, of which five were Piping Plover *Charadrius melodus*. Conversely, our study found no difference in clutch survival rates between the study groups. It is likely that the exclosures did not exclude all cats and made nests easier for cats to locate. A mesh of 5×10 cm is the most common mesh size used for exclosures, and therefore our results are of broader relevance, in particular for those managing populations where cats are key nest predators (Dowding & Murphy 2001, Moore 2005). Some exclosures for Piping Plover (Rimmer & Deblinger 1990, Mabee & Estelle 2000) and Snowy Plover *Charadrius nivosus* (Mabee & Estelle 2000) have used the next smallest mesh size commercially available, 5×5 cm. St. Helena Plovers are similar in body size to these species, although they are significantly taller due to their long legs (tarsus 40.7 mm, compared with 19.4 and 27.5 mm for Piping and Snowy Plovers, respectively; F. Burns unpubl. data, Cohen 2005, Lislevand *et al.* 2007). It is therefore unclear whether the Plovers would enter such an exclosure and, if they did, whether such a mesh size would impede their exit.

The St. Helena Plover is the sixth species in which increased adult mortality has been associated with predator exclosure cages (Smith *et al.* 2011 and Supporting Information Table S1). Usually, predation upon adult St. Helena Plovers is rare and evidence is seldom found (McCulloch 2009). Cases of elevated adult mortality have been reported from a variety of prey and predator species, habitats, locations and exclosure designs, with no general risk factors apparent. It is not fully understood why birds incubating inside exclosures are more vulnerable to predation. Predator exclosures may increase the visibility of normally cryptic nests. Learning to associate exclosures with nests may allow predators to detect nests earlier and approach cautiously, thereby getting closer before being seen by the parent bird. Predation of several adults over a short period of time at exclosures close to each other suggests predator learning (this study, Hardy & Colwell 2008, Murphy *et al.* 2003, Neuman *et al.* 2004). Furthermore, exclosures do not protect nidifugous chicks. Where predators learn to associate exclosures with nests, survival to fledging may be suppressed. Several studies have found that the observed increase in clutch survival does not translate into an increase in productivity (Neuman *et al.* 2004, Pauliny *et al.* 2008).

To assess the effectiveness of exclosures, it is necessary to quantify the trade-off between elevated clutch survival and suppressed adult survival at the population level. It is clear that even a modest decrease in adult survival could substantially reduce the potential positive effect of predator exclosures on the population (Fig. 2). Without the necessary demographic estimates, our results cannot be extrapolated to other cases where elevated adult mortality has been found. Nevertheless, the increase in population growth rate from exclosure use is likely to be substantially reduced, and increased adult mortality may mean that targets to stabilize or increase the study population are not met. Few studies have investigated the population-level or long-term effects of exclosures on populations (Murphy *et al.* 2003, Neuman *et al.* 2004, Watts *et al.* 2012) and therefore the impact of decreased adult survival may be overlooked. There may be some additional benefits of exclosures not considered here, for instance protection from trampling. Nevertheless, it remains unclear under which circumstances exclosures could form part of an effective conservation management plan.

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SUPPORTING INFORMATION

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

Appendix S1. Details of demographic estimates used in the population model (Table S1) and of the three scenarios depicted in Figure 2 and a summary of adult mortality associated with predator exclosures in waders (Table S2).

Video S1. A case of nest predation by a cat within a predator exclosure.