Re-colonisation and successful breeding of Masked Boobies *Sula dactylatra* on mainland St Helena, South Atlantic, in the presence of Feral Cats *Felis catus*

Bolton. M.[1*], Watt, R.[2], Fowler. E.[3], Henry, L.[3] and Clingham, E.[3]

**Correspondence author. Email: mark.bolton@rspb.org.uk*

[1] *RSPB, UK Headquarters, The Lodge, Sandy, Bedfordshire SG19 2DL, UK;*

[2] *12 Dalmore Crescent, Helensburgh, Argyle and Bute G84 8JP, UK;*

[3] *Agriculture and Natural Resources Department, St Helena Island, South Atlantic Ocean STHL 1ZZ.*

Abstract

Masked Boobies *Sula dactylatra* were apparently extremely abundant on St Helena in the early sixteenth century, when the island was discovered. It is probable that the breeding population was severely depleted by man and introduced mammalian predators following human settlement of the island in 1659. The species had certainly become very scarce by the nineteenth and twentieth centuries, restricted to a few small offshore stacks that remained predator-free. The first fully documented breeding, on Shore Island a small predator-free stack, was as recent as 1988. Since that time, the population has increased substantially, and here we report the first instance of breeding on the St Helena mainland, despite the presence of Feral Cats *Felis catus*, Brown Rats *Rattus norvegicus* and Black Rats *R. rattus*. In July 2009, along 4 km of coastline in the southwest of the island, one pair was discovered with a large downy chick, four pairs were confirmed to be incubating eggs, and a further 25 pairs were apparently incubating eggs. Subsequent monitoring of 28 breeding attempts up to July 2010 revealed moderate levels of breeding success (0.461 young fledged per attempt), which were substantially higher than those of Masked Boobies that have re-colonised Ascension Island in recent years following cat eradication. The ability of Masked Boobies to nest successfully, on occasion, on islands where cats and rats are present, highlights their potential resilience to these introduced mammalian predators, and the circumstances and long-term viability of successful co-existence with such non-native predators warrant further investigation.

Introduction

The role of predation in limiting population size has long been of interest to ecologists (Birkhead & Furness 1985; Furness & Monaghan 1987; Croxall & Rothery 1991; Newton 1998) and is increasingly of relevance to conservation managers wishing to maintain or restore populations of rare or vulnerable species (Gibbons *et al*. 2007; Hilton & Cuthbert 2010). Understanding the population-level impacts of predation is especially important in cases where the main source of predation is

an introduced non-native species. In such cases predator eradication may be technically feasible, but costly, opposed by members of the public, logistically complex, and long-term success may not be guaranteed either due to failure to remove all individuals or by subsequent reinvasion/reintroduction (Oppel *et al*. 2011). Notwithstanding the challenges, introduced mammalian predators (principally Brown Rats *Rattus norvegicus*, Black Rats *R. rattus*, Pacific Rats *R. exulans* and Feral Cats *Felis catus*) have been successfully eradicated from several hundred islands worldwide (Nogales *et al*. 2004; Howald *et al*. 2007). In many cases the anticipated beneficiaries have been seabirds, which, due to their ground-nesting habits and low reproductive rates, may be especially vulnerable to introduced terrestrial predators, against which they have no, or limited, evolved defence. Larger predators such as Feral Cats are likely to impact a wider range of seabird species than the smaller predators (Black Rats, Brown Rats and House Mice *Mus musculus*), due to their ability to tackle even large-bodied adult prey (Burger & Gochfeld 1994). Predation on adults also results in faster population decline than that associated with predation directed predominantly or solely on eggs or chicks (Hilton & Cuthbert 2010). However, the outcome of the co-occurrence of any particular seabird-predator species combination can be difficult to predict, as demonstrated by the unexpected predation of albatross chicks by House Mice on Gough Island (Cuthbert & Hilton 2004). Whilst their large size, aggressive nature and formidable bill may confer on boobies a degree of resilience to cat predation, Ashmole *et al*. (1994) provide detailed field evidence of multiple instances of cat predation of adult Brown *Sula leucogaster* and Masked Boobies *S. dactylatra* on Ascension Island, and there is evidence of cat-related declines and extirpation of several booby species at numerous sites worldwide: Ascension Island, South Atlantic (Stonehouse 1962; Williams 1984; Ashmole *et al*. 1994; Ratcliffe *et al*. 2009); Baker Island, Hawaii (Forsell 1982); Jarvis Island, 1,300 km south of Hawaii (Rauzon 1985); various Indonesian islands (de Korte 1984; de Korte & Silvius 1994). The restoration of booby breeding populations at some of these islands following cat eradication also provides good evidence of population-level impacts of cat predation (e.g. Ratcliffe *et al*. 2009).

St Helena was discovered by the Portuguese in 1502, and the first mammalian predator, the Black Rat, is likely to have been introduced at that time, or soon afterwards (Rowlands *et al*. 1998). The island was not permanently settled until 1659, though cats were introduced sometime earlier, in the sixteenth century, to control the large numbers of rats. Brown Rats did not arrive until around the start of the eighteenth century but were well established throughout the island by 1732, by which time cats were said to have reached plague proportions and were as numerous as rats (Rowlands *et al*. 1998). The earliest accounts of St Helena during the years immediately following human settlement (Ogilby 1670) suggest the avifauna was initially extremely abundant and heavily exploited for human consumption. Extensive sub-fossil bone remains in deposits on St Helena indicate the former existence of large seabird populations on the island, 16 species in total, including three endemic to St Helena (Olson 1975). Remains of Masked Boobies in both the youngest and older deposits indicate the species' presence on St Helena for a consid-

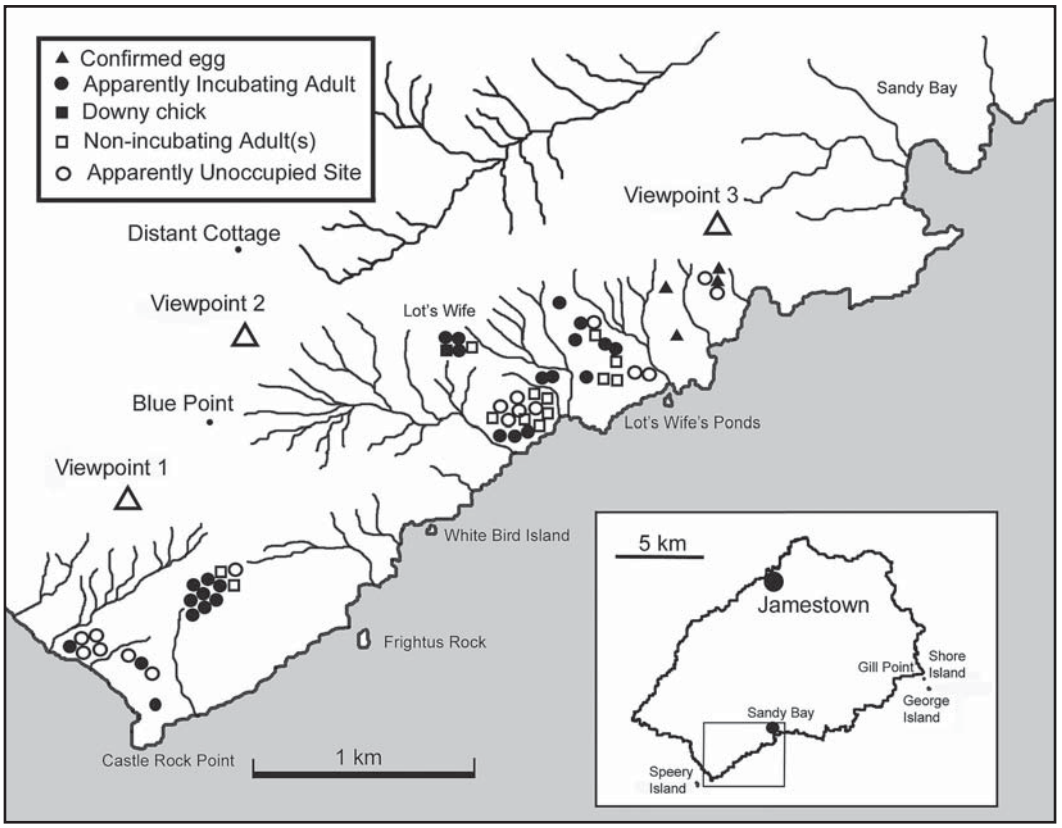

Figure 1. Location of nest sites of Masked Boobies *Sula dactylatra* on St Helena mainland, July 2009.

erable period prior to human settlement. However, a combination of habitat change, human persecution and predation by mammalian predators led to declines and extinction of almost the entire endemic avifauna, including the St Helena Petrel *Pterodroma rupinarum* and the St Helena Bulweria *Bulweria bifax*. The third endemic seabird, the St Helena Shearwater *Puffinus pacificoides* is believed to have become extinct before 1502 (Olson 1975). Currently only eight breeding seabird species are known to remain on St Helena. The earliest confirmed record in recent times of breeding Masked Boobies (on Shore Island) dates from as recently as 1988 (Rowlands *et al*. 1998). Unconfirmed reports suggest breeding may also have occurred in the previous few years, but the absence of previous records suggests the species did not breeder earlier in the twentieth century. Indeed, Stonehouse (1960) remarked on the absence of both Brown and Masked Boobies when he visited St Helena in 1958. Since 1988, breeding has been documented for both Shore Island and George Island (Rowlands *et al*. 1998), but has never been reported on the mainland of St Helena, presumably due to the presence of Feral Cats.

This study resulted from anecdotal reports that Masked Boobies were present on the coast of mainland St Helena, but confirmation of breeding was lacking. Given the current conservation efforts to eradicate introduced mammalian predators from

many islands worldwide, and the common belief that such introduced predators prevent successful reproduction of the majority of native seabird species, the aim of this study was to determine whether Masked Boobies were breeding on mainland St Helena, and to document the location, size and success of any breeding colony.

Methods

Study site: St Helena (15°58'S 05°43'W) lies in the South Atlantic Ocean, 1,913 km from the west coast of Africa and c. 800 km east of the Mid-Atlantic Ridge. The main island (122 km^2) is surrounded by 24 satellite islets and stacks, most within 100 m of the coast and of very limited area, the largest being c. 5 ha. Masked Boobies are known to breed on two of these offshore islets: Shore Island and George Island (Rowlands *et al*. 1998) which lie off the east coast. The search area for the current study lies on the south coast between Castle Rock Point and Sandy Bay (Figure 1).

Search protocols: The area immediately to the north of Lot's Wife's Ponds (Figure 1) was accessed via the cairn-marked footpath leading south-westwards from Sandy Bay, by MB and RW on 28 July 2009. The area between Lot's Wife and Castle Rock Point (Figure 2) was viewed from the ridge from Distant Cottage to Castle Rock Point on 31 July 2009. The areas were searched for signs of nesting Masked Boobies by scanning with Leica 10 x 42BA binoculars from the vantage points marked in Figure 1. All potential nest sites (areas marked with droppings) were inspected as closely as possible. Some nest sites could be approached to within a few metres (Figure 3), but

Figure 2. View looking east-southeast from Viewpoint No. 2 showing the main groups of Masked Booby *Sula dactylatra* nests. Lot's Wife, indicated in Figure 1, is the large stone pillar to the left in the photograph. St Helena, 31 July 2009. © Mark Bolton.

Figure 3. Masked Booby *Sula dactylatra* incubating two eggs at a nest on the slopes south of Viewpoint No. 3. St Helena mainland, 28 July 2009. © Mark Bolton.

the steep and unstable nature of the terrain, and limited time available, meant other sites could only be inspected from distances of over 1 km. All visible nest areas were photographed using a high-resolution digital camera and telephoto lens (15 megapixel Canon 50D, Canon 400 mm/5.6 lens and 1.4x teleconverter, equivalent to a 900 mm lens on a conventional SLR film camera). Amplification of the resultant images allowed identification of individual boobies at ranges of up to 1.5 km. For nests that could not be approached sufficiently closely to inspect their contents, adult Masked Boobies were classified as Apparently Incubating Adults (AIA) if surrounded by a halo of guano on suitably flat nesting terrain and if their posture was consistent with incubation (i.e. body horizontal, not upright, with the belly close to the ground, see Figure 3). Apparent nest sites (marked with guano) where one or more birds were present but not clearly incubating were also counted, as were nest sites where no adults were present. Nests which could be approached closely were observed for up to 20 minutes to determine if eggs were present, when adults shifted their position. Nest locations were plotted on a satellite map by triangulation and reference to landscape features. Since most nests were located on ridges and peaks, nest locations could be plotted accurately.

Breeding success: The areas used by breeding boobies were subsequently visited every month until July 2010 by EF and LH to record: the total number of adults; the number of AIAs; the contents of nests that were accessible for detailed inspection; the number, and growth stage (Dorward 1962) of chicks; and any fledglings present. Nests were individually numbered to facilitate relocation and construction of

individual nest histories. Hatching success (the proportion of eggs surviving from laying to hatching) and fledging success (the proportion of chicks surviving from hatching to fledging) were calculated from daily egg and chick failure rates respectively, raised to the power of the incubation and chick rearing periods (44d and 105d respectively; Dorward (1962)), (Mayfield 1961, 1975). This method accounts for failures that occur before nests are found by observers, which was necessary given the relative infrequency of survey visits. Standard errors of the estimate of hatching success were calculated following Johnson (1979). In dealing with the very small number of nests where the outcome was uncertain we followed Manolis *et al*. (2000), only considering nests for the period for which nest status was known, since this approach has been shown to minimise bias in estimates of nest survival rate. Breeding success (the number of young reared to fledging per breeding attempt) was calculated as the product of hatching and fledging success.

Cat presence: Although no attempt was made to quantify cat density in the area occupied by breeding Masked Boobies, both the access route to the survey areas and the areas occupied by breeding boobies themselves were searched for signs of cats (footprints in soft substrate, faeces) on each visit.

Results

Evidence of breeding: On 28 July 2009 a total of 60 nest sites were located (Figures 1 & 2). One nest site held a large downy chick, four were confirmed to contain eggs (Figure 3) and a further 25 held AIAs. An additional 13 nest sites were occupied by adult Masked Boobies, but incubation behaviour was not evident. The remaining 17 nest sites were unoccupied at the time of our survey. In total 54 adult and four immature birds were counted.

Breeding phenology and breeding success: Monthly surveys between July 2009 and July 2010 revealed breeding activity in every month of the year. There was a steady decline in the number of apparently active nests between the discovery of the colony in July 2009, and October 2009, with chicks hatching throughout this period (Figure 4). In November there was an increase in both the number of AIAs and the number of nests where eggs were confirmed. The number of active nests each month remained fairly stable between December 2009 and April 2010, indicating that failures were balanced by newly initiated attempts during this period. The smallest number of active nests was recorded in May 2010, with the numbers of AIAs increasing thereafter until July 2010. Hatching success was estimated at 0.461 (95% CI 0.291–0.727) and all 16 monitored chicks survived to fledging, yielding an overall breeding success of 0.461 (95% CI 0.291–0.727).

Cat presence: Signs of cats were found in both search areas when the breeding colony was first located in July 2009. Cat footprints were found in sandy soil c. 200 m north of Lot's Wife's Ponds and faeces were found in four locations between Distant Cottage and Blue Point. Cat scats were also noted in seven locations in March 2010 and in one location in July 2010. There was no evidence however, of predation of either adult or young boobies.

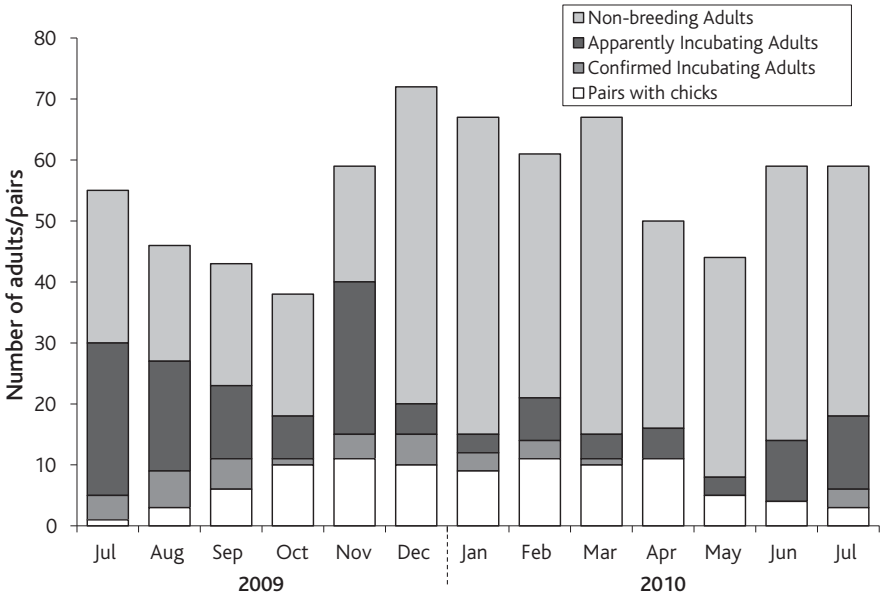

Figure 4. Number of non-breeding and breeding Masked Boobies *Sula dactylatra* counted on monthly surveys, St Helena mainland.

Discussion

Breeding of Masked Boobies on the St Helena mainland was confirmed, with at least 40 active breeding pairs in November 2009. The total number of nesting pairs is likely to be substantially higher than this, due to a high degree of asynchrony in the timing of laying, typical of many tropical seabirds. It is very likely that breeding on the mainland is only a recent phenomenon: Lot's Wife's Ponds is a popular walking trail and the area was visited regularly by competent observers in the preceding years. The presence of boobies in the area was first observed in late 2007 on cliff tops adjacent to Castle Rock Point (A. Darlow pers. comm.) and birds were first recorded on the south coast towards Lot's Wife's Ponds in 2008 (E. Thorpe pers. comm.). The nesting sites extending towards Sandy Bay were first noted in May 2009 (A. Darlow & L. Malan pers. comm.). With the colony still in its establishment phase it was difficult to discern laying phenology with certainty, but there appeared to be two peaks of egg-laying, one in July-August and a second in November. Dorward (1962) similarly found two peaks of laying during his detailed study of Masked Boobies on Boatswainbird Island, Ascension in 1958 and 1959; the majority of birds laid in July with a second, very small peak, in November.

Overall breeding success on St Helena was estimated at 0.461 (95% CI 0.291–0.727), which is considerably higher than that reported from Ascension Island in 1958 (0.097; Dorward 1962) and between 2002 and 2007 (0.190; Ratcliffe *et al*. 2009), and slightly below the lower limit of the range of values from monitoring at Kure Atoll, Hawaii between 1964 and 1969 (0.520–0.864; Kepler 1969, cited in Ratcliffe *et al*. 2009; Woodward 1972) and the value of 0.510

reported from Lord Howe Island, Australia in 2001 (Priddel *et al*. 2005). The relatively high breeding success for a newly established colony is notable, given the presumed inexperience of the birds concerned (though see below). The level of breeding success we found indicates good food resources within foraging range of the colony, and that nest predation was low or absent.

In light of the numerous cases listed above implicating cats in declines and local extirpations of boobies, the recent colonisation of mainland St Helena by substantial numbers of Masked Boobies, and their successful breeding, is unexpected. The impact that an introduced predator has on a native species will depend on a variety of factors, including the body size differential between the two species and the existence and effectiveness of any anti-predator behaviour of the potential prey. Reviewing the impacts of alien predator species on seabirds, Moors & Atkinson (1984) concluded that the impact of cats on booby species was variable, with some species suffering heavy predation, whereas Hilton and Cuthbert (2010) allow the possibility that tropical booby species may be "relatively resistant to most mammalian predators and could conceivably have benefited from reductions in populations of smaller, predator-sensitive species". Other factors influencing the outcome of an introduced predator on a native species include the availability of alternative prey and seasonal variation in the availability of food for the predator, which will determine predator numbers (Moors & Atkinson 1984). Cats on St Helena have a very varied diet, which is likely to depend on locality and season. Rats and mice have been found to form a major component (Olson 1975) and a recent study using nest cameras has shown that cats prey on adults and eggs of the St Helena Plover ('Wirebird') *Charadrius sanctaehelenae* (Burns 2011). At Gill Point (overlooking Shore Island, Figure 1) large middens found in cat dens have included bones and feathers of substantial numbers of Brown Noddies *Anous stolidus*, as well as Band-rumped Storm-petrels *Oceanodroma castro*, Red-billed Tropicbirds *Phaethon aethereus* (MB pers. obs.), and Sooty Terns *Onychoprion fuscata* (Rowlands *et al*. 1998).

Colonisation by Masked Boobies of the St Helena mainland could result from a recent population increase, leading to scarcity of suitable nesting sites on the small offshore stacks for new recruits. Unfortunately, there are no survey data available for the two years leading up to the mainland colonisation, but monthly counts of the number of AIA and apparently occupied nest sites on Shore Island showed a significant decrease in the breeding population between October 2004 and July 2007 (Figure 5). Surveys of George Island carried out on a six-monthly basis indicated a non-significant decline over the same period. The breeding status of Masked Boobies on Speery Island is uncertain. Rowlands *et al*. (1998) list Shore and George Islands as the only known breeding localities of the species, yet between 60 and 90 Masked Boobies are regularly counted atop the towering pinnacle (120 m) of Speery Island (St Helena Agriculture and Natural Resources Department, unpublished data). The stack is too distant from the shoreline for mainland-based counts, and the frequently choppy sea conditions do not permit an easy assessment of the breeding status of all birds from a boat at the foot of the stack.

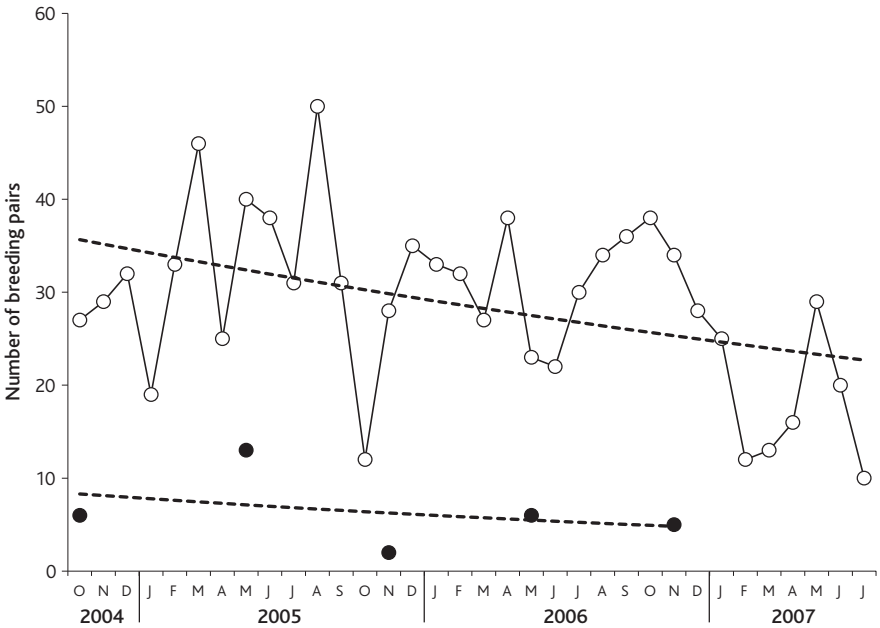

Figure 5. Number of pairs of breeding Masked Boobies *Sula dactylatra* (AIA and Apparently Occupied Sites) on Shore Island (open circles) and George Island (filled circles). Poisson regression lines are shown. Shore Island: Pairs = exp(3.5874–0.0137*month) $F_{1,32}$ = 6.00, P = 0.02; George Island: Pairs = exp(2.1387–0.0218*month) $F_{1,3}$ = 0.41, P = 0.52.

It is possible that small numbers breed. On 2 August 2009, we counted just four AIA Masked Boobies on Shore Island (c. 0.5 ha) and one AIA Masked Booby on George Island (c. 1.7 ha). These islands held 42 and 13 breeding pairs respectively in 2005 (Figure 5), so the colonisation of the southern mainland cliffs by 40 breeding pairs of Masked Boobies may therefore represent a redistribution rather than a population increase. The relatively high breeding success of this mainland colony also suggests that many of the birds had previous breeding experience. Why established breeders should leave the protection of predator-free offshore nesting locations and venture to nest in the presence of ground predators on the mainland is unclear. However, both Shore Island and George Island lie on the east coast exposed to the predominant south-easterly Trade Winds, and are relatively low-lying at 50 m and 30 m respectively. Though smaller in area, Shore Island has consistently held the larger colony (Figure 5) perhaps as a result of its more sheltered position in the lee of George Island, and its higher summit affording greater protection from the salt spray. Rowlands *et al*. (1998) reported that the breeding success of Brown Noddy nests on George Island was low, due to wet conditions as periodic high seas destroyed nests at lower levels, as also occurs on stacks at Ascension (Stonehouse 1960). Although there is no evidence for a recent increase in the severity of stormy weather to have prompted a relocation, and the sites chosen for nesting within the newly-formed colony on the southern cliffs are also in the path of the Trade Winds, the majority of mainland nests were about 100 m a.s.l. and more than 200 m from the shore, beyond the reach of salt spray. The

selection of rocky summits and ridges for nest locations also affords some protection from ground predators such as cats by providing good visibility and a height advantage over an approaching predator.

The successful recolonisation and breeding of Masked Boobies may result from lowered densities of cats locally, or increased availability of alternative, more easily subdued, prey. However, without quantitative information on historic and current densities of cats, or the availability of alternative prey, it is not possible to say with certainty whether the recent mainland colonisation represents a response to reduced cat predation pressure on the mainland. In addition, an increasing number of studies are revealing that a wide range of vertebrate predators show individual dietary specialisation (see review by Bolnick *et al*. (2003)), where individual predators specialise on a particular prey species. The number of prey of a given species taken may show considerable spatio-temporal variation, in response to the number of prey specialists in the predator population.

We emphasise that this case of successful breeding by Masked Boobies in the presence of Feral Cats does not cast doubt on the role of cat predation in population declines of this species demonstrated elsewhere, nor on the value of cat eradication in many seabird restoration programmes. It does, however, highlight the unpredictable nature of predator-prey relationships in the altered trophic webs that result from the introduction of non-native invasive species into island ecosystems. Future changes in the numbers of cats in the vicinity of the booby colony and/or the availability of alternative prey could result in higher levels of predation on booby eggs, chicks or adults. Future monitoring of the St Helena colony would be extremely instructive in resolving the longer-term consequences of Feral Cats on breeding performance and population size of Masked Boobies.

Acknowledgements

We thank Andrew Darlow and Lourens Malan for bringing to our attention the presence of Masked Boobies on the southern cliffs and the possibility that a breeding colony may have become established. We also thank Graham Sim and Ivan Henry for monthly assistance with fieldwork, and Emma Bennett, who established the seabird monitoring programme on St Helena.

References

Ashmole, N. P., Ashmole, M. J. & Simmons, K. E. L. 1994. Seabird conservation and feral cats on Ascension Island, South Atlantic. In: Nettleship, D. N., Burger, J. & Gochfeld M. (eds.) *Seabirds on Islands. Threats, Case Studies and Action Plans. BirdLife Conservation Series No. 1*: 94–121. BirdLife International, Cambridge.

Birkhead, T. R. & Furness, R. W. 1985. Regulation of seabird populations. In: Sibley, R. M. & Smith, R. H. (eds.) *Behavioural Ecology*: 145–167. Blackwell, Oxford.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161: 1–28.

Burger, J. & Gochfeld, M. 1994. Predation and effects of humans on island-nesting seabirds. In: Nettleship, D.N., Burger, J. & Gochfeld, M. (eds.) *Seabirds on Islands: Threats, Cases Studies and Action Plans. BirdLife Conservation Series No. 1*: 39–67. Bird-Life International, Cambridge.

Burns, F. E. 2011. 'Conservation biology of the endangered St. Helena Plover *Charadrius sanctaehelenae.'* PhD Thesis, University of Bath.

Croxall, J. P. & Rothery, P. 1991. Population regulation of seabirds: implications of their demography for conservation. In: Perrins, C. M., LeBreton, J. D. & Hirons, G. M. (eds.) *Bird Population Studies: Relevance to Conservation and Management*: 272–296. Oxford University Press, Oxford.

Cuthbert, R. & Hilton, G. 2004. Introduced house mice *Mus musculus*: a significant predator of endangered and endemic birds on Gough Island, South Atlantic Ocean? *Biological Conservation* 117: 483–489.

Dorward, D. F. 1962. Comparative biology of the White Booby and the Brown Booby *Sula* spp. at Ascension. *Ibis* 103b: 174–220.

Forsell, D. J. 1982. Recolonization of Baker Island by seabirds. *Bulletin of the Pacific Seabird Group* 9: 75–76.

Furness, R. W. & Monaghan, P. 1987. *Seabird Ecology*. Blackie, Glasgow.

Gibbons, D. W., Amar, A., Anderson, G. Q. A., Bolton, M., Bradbury, R. B., Eaton, M. A., Evans, A. D., Grant, M. C., Gregory, R. D., Hilton, G. M., Hirons, G. J. M., Hughes, J., Johnstone, I., Newbery, P., Peach, W. J., Ratcliffe, N., Smith, K. W., Summers, R. W., Walton, P. & Wilson, J. D. 2007. *The predation of wild birds in the UK: a review of its conservation impact and management*. RSPB Research Report No. 23. RSPB, Sandy.

Hilton, G. & Cuthbert, R. 2010. The catastrophic impact of invasive mammalian predators on birds of the UK Overseas Territories: a review and synthesis. *Ibis* 152: 443–458.

Howald, G., Donlan, C. J., Galván, J. P., Russell, J., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P., Pascal, M., Saunders, A. & Tershy, B. 2007. Invasive rodent eradication on islands. *Conservation Biology* 21: 1258–1268.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96: 651–661.

Kepler, C.B. 1969. Breeding biology of the blue-faced booby *Sula dactylatra personata* on Green Island, Kure Atoll. *Publications of the Nuttall Ornithological Club* 8: 1–97

de Korte, J. 1984. Status and conservation of seabird colonies in Indonesia. In: Croxall, J. P., Evans, P. G. H. & Schreiber, R. W. (eds.) *Status and Conservation of the World's Seabirds*: 527–546. International Council for Bird Preservation Technical Publication No. 2, Cambridge.

de Korte, J, & Silvius, M. J. 1994. Pelecaniformes in Indonesia: status, recent changes and management. In: Nettleship, D. N., Burger, J. & Gochfeld, M. (eds.) *Seabirds on Islands. Threats, Case Studies and Action Plans. BirdLife Conservation Series No. 1*: 77–93. BirdLife International, Cambridge.

Manolis, J. C., Andersen, D. E. & Cuthbert, F. J. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* 117: 615–626.

Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73: 255–261.

Mayfield, H. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87: 456–466.

Moors, P. J. & Atkinson, I. A. E. 1984. Predation on seabirds by introduced animals, and factors affecting its severity. In: Croxall, J. P., Evans, P. G. H. & Schreiber, R. W. (eds.) *Status and Conservation of the World's Seabirds*: 667–690. International Council for Bird Preservation Technical Publication No. 2, Cambridge.

Newton, I. 1998. *Population limitation in birds*. Academic Press, London.

Nogales, M., Martin, A., Tershy, B. R., Donlan, C. J., Veitch, D., Puerta, N., Wood, B. & Alonso, J. 2004. A review of feral cat eradication on islands. *Conservation Biology* 18: 310–319.

Ogilby, J. 1670. *An accurate description and complete history of Africa (based on Arnold Montanus' De Nieuwe en Onbekende Wereld)*. T. Johnson, London.

Olson, S. L. 1975. *Paleornithology of St Helena Island, South Atlantic Ocean*. Smithsonian Contributions to Paleobiology, No. 23. Smithsonian Institution Press, Washington D.C.

Oppel, S., Beaven, B. M., Bolton, M., Vickery, J. & Bodey, T. W. 2011. Eradication of invasive mammals on islands inhabited by humans and domestic animals. *Conservation Biology* 25: 232–240.

Priddel, D., Hutton, I., Olson, S. & Wheeler, R. 2005. Breeding biology of masked boobies (*Sula dactylatra tasmani*) on Lord Howe Island, Australia. *Emu* 105: 105–113.

Ratcliffe, N., Bell, M., Pelembe, T., Boyle, D., Benjamin, R., White, R., Godley, B., Stevenson, J. & Sanders, S. 2009. The eradication of feral cats from Ascension Island and its subsequent recolonisation by seabirds. *Oryx* 44: 20–29.

Rauzon, M. J. 1985. Feral cats on Jarvis Island: their effects and their eradication. *Atoll Research Bulletin* 282: 1–32.

Rowlands, B. W., Trueman, T., Olson, S. L., McCulloch, M. N. & Brooke, R. K. 1998. *The Birds of St Helena*. BOU Checklist No. 16. British Ornithologists' Union, Tring.

Stonehouse, B. 1960. *Wideawake Island; the story of the BOU Centenary Expedition to Ascension*. Hutchinson, London.

Stonehouse, B. 1962. Ascension Island and the British Ornithologists' Union Centenary Expedition 1957–59. *Ibis* 103b: 107–123.

Williams, A. J. 1984. Breeding distribution, numbers and conservation of tropical seabirds on oceanic Islands in the South Atlantic Ocean. In: Croxall, J. P., Evans, P. G. H. & Schreiber, R. W. (eds.). *Status and Conservation of the World's Seabirds*: 393–402. International Council for Bird Preservation Technical Publication No. 2, Cambridge.

Woodward, P. W. 1972. The natural history of Kure Atoll, northwestern Hawaiian Islands. *Atoll Research Bulletin* 164: 1–318.