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Predation pressures on sooty terns by cats, rats and common mynas on Ascension Island in the South Atlantic

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Abstract Despite the presence of invasive black rats (*Rattus rattus*), common mynas (*Acridotheres tristis*), and feral domestic cats (*Felis catus*), sooty terns (*Onychoprion fuscatus*) breed in large numbers on Ascension Island in the tropical South Atlantic Ocean. These introduced predators impact the terns by destroying eggs or interrupting incubation (mynas), eating eggs (mynas and rats), eating chicks (rats and cats), or eating adults (cats). Between 1990 and 2015, 26 censuses of sooty terns and five of mynas were completed and myna predation was monitored on 10 occasions. Rat relative abundance indices were determined through trapping around the tern colonies and rat predation was monitored by counting chick carcasses. Cat predation was quantified by recording freshly killed terns. Prior to their eradication in 2003, cats had the greatest impact on sooty terns and were depredating 5,800 adults and 3,600 near-fledging chicks (equivalent to the loss of 71,000 eggs) each breeding season. We estimated that 26,000 sooty tern eggs (13% of all those laid) were depredated by approximately 1,000 mynas. Rats were not known to depredate sooty terns prior to cat eradication but in 2005, 131 of 596 ringed (monitored) chicks (22%) were depredated by rats. In 2009 chick carcass density was 0.16 per m[2]. Predation by rats hugely increased in the absence of cats and was the equivalent of 69,000 eggs. Care is needed when applying our findings to seabirds globally. The scarcity of alternative food sources and seasonally high density of easily available prey in the sooty tern colony may have magnified predation by cats, rats and mynas.

Keywords: Non-native species, population size, predation rate, United Kingdom Overseas Territory (UKOT)

INTRODUCTION

Comparative studies of global declines in faunal biodiversity have concluded that harvesting, habitat loss and introduced invasive species are leading causes (see refs in Young, et al., 2016). Of extinction events for which causes have been investigated, 54% have been attributed in part to invasive species (Clavero & Garcia-Berthou, 2005). Globally, terrestrial invertebrate invaders have reduced faunal diversity by 29% (Cameron, et al., 2016). Lowe, et al. (2000) compared the severity of alien species on animal and plant diversity by compiling a list entitled "100 of the world's worst invasive alien species". The list includes invasive predators that are commensal with man; they pose major threats to seabirds and they persist following anthropogenic introduction to 90% of all island archipelagos (Towns, et al., 2006). Global seabird population size has declined by 70% between 1950 and 2010 (Paleczny, et al., 2015) with introduced commensal predators being one of the major proposed causes of such declines (Moors & Atkinson, 1984).

Of introduced predators, feral domestic cats (*Felis catus*) (Medina, et al., 2011) and black rats (*Rattus rattus*) (Jones, et al., 2008) inflict the most severe impacts on native avifauna. Common mynas (*Acridotheres tristis*) (hereafter referred to as 'mynas') also have significant negative impacts on native avifauna through competition for food and nest sites (Grarock, et al., 2012). When cats, rats and mynas invade islands on which seabirds are breeding, cats have a direct effect on the size of the seabird population through predation of adults (van Aarde, 1983) while rats and mynas have a less immediate, but a more indirect, effect through predation of eggs or chicks (Jones, et al., 2008). Therefore, rats and mynas reduce breeding success and inflict downstream impacts on seabird demography through reduced recruitment to the breeding population (Harper & Bunbury, 2015). The direct impacts of cats on breeding seabirds are more readily observed than the indirect effects of rats and mynas that are more difficult to quantify because rat and myna predation is less obvious and is confounded by rats scavenging on chicks that have died from causes other than direct predation (e.g. starvation).

Alien invasive predators are the potential cause of precipitous declines in the population size of breeding sooty terns (*Onychoprion fuscatus*) on Ascension Island during the 20th century (Hughes, et al., 2017a). Sooty terns are the most numerous avian species in tropical waters and Ascension Island accommodates the largest breeding population in the Atlantic (Schreiber, et al., 2002). Three of the world's 'worst' invasive predators are found in the seabird colonies on Ascension Island. Black rats probably arrived when HMS Roebuck was abandoned close to the island in 1701 (Ashmole & Ashmole, 2000), and by 1725 rats were so numerous that a castaway on the island lived in fear of being eaten alive (Ritsema, 2006). In 1815 domestic cats were introduced to control the rat population. Mynas were introduced in the 1880s to reduce damage to crops by black cutworms (*Agrotis ipsilon*) (Duffey, 1964). Common mynas in their home range (i.e. India) are regarded as a beneficial species (BirdLife International, 2015) because typically more than 80% of their food mass comprises insects regarded as pests (e.g. cutworms – larvae of Noctuidae). Since the arrival of these invasive species on the island, the once vast colonies of seabirds, estimated to contain > 10 million birds (Ashmole & Ashmole, 2000), have dwindled to less than half a million birds (Bell & Ashmole, 1995). Of the 11 seabird species that breed on Ascension Island, only sooty terns now breed in large numbers on the main island. Numerically, 97% of all seabirds breeding on the main island are sooty terns (Hughes, 2014). Remnant populations of other seabird species nest on cat- and rat-free offshore stacks and Boatswainbird Islet (Ratcliffe, et al., 2009).

In 1958 and 1959, cats were the only non-native predatory species known to depredate seabirds and an aspiration for their eradication was conceived (Ashmole, 1963). During a feasibility study for cat eradication in 1992, rats were also considered a major threat to seabirds (Ashmole, et al., 1992) but the threat that mynas posed was not recognised at that time. More recently, in the Seychelles, Feare, et al. (2015) recorded mynas inflicting intense predation on seabird eggs. On Ascension Island cats were eradicated in 2003 (Bell & Boyle, 2004) and

rat control measures (Pickup, 1999) were implemented. The eradication of apex predators is generally associated with an increase in the abundance of smaller predators with this trophic interaction referred to as 'mesopredator release' (Prugh, et al., 2009). However, Russell, et al. (2009) modelled the effects of mesopredator release and concluded that the negative impact of more mesopredators is outweighed by the benefit of apex predator removal, allowing recovery of prey populations. If we apply their conclusions to Ascension Island then cat eradication should have resulted in an increase in the population size of sooty terns but, to date, no such effect has been detected (Hughes, et al., 2017a).

Here, we have collated data from published outputs and from a 25-year Army Ornithological Society (AOS) dataset on introduced species to calculate the relative impacts of cat, rat and myna predation on the sooty tern breeding population.

METHODS

Study area and period

Ascension (07º57′S, 14º24′W, 97 km²) is one of the volcanic islands that make up the UK Overseas Territory (UKOT) of St Helena, Ascension and Tristan da Cunha, and is isolated in the tropical South Atlantic Ocean midway between South America and Africa (Fig. 1; Hughes, et al., 2010). Its nearest neighbour is the island of St Helena some 1,300 km to the south-east. The territory is an Important Bird Area (IBA reference number SH009; BirdLife International, 2017). More than half of its surface consists of cinder plains, ash cones and basaltic lava flows. The average annual rainfall is 144.0 mm (Anon., 1998) and plant species richness on the plain is < 11 species (Duffey, 1964). The dry coastal plain is the traditional nesting site for seabirds and sooty terns nest at Mars Bay and Waterside in the south-west corner of the island (Fig. 1).

Fieldwork lasted two weeks per breeding season and was timed to coincide with the peak of the sooty tern breeding season (see further details in Reynolds, et al., 2014). Time in the field amounted to 1,691 person-days.
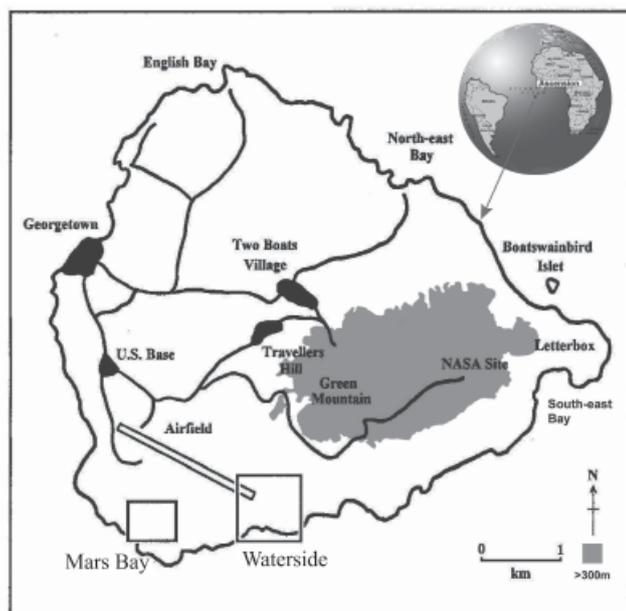
Fig. 1 Map of Ascension Island in the South Atlantic showing sites of human habitation and ground above 300 m (shaded). Sooty terns nest in the south-west corner of the island in the areas marked as 'Mars Bay' and 'Waterside'.

Prey population size

Sooty terns, the primary avian prey species of rats, cats and mynas, are a migratory species and are absent from Ascension Island for approximately three in every 9.6 months that constitute the sub-annual cycle of the species (Reynolds, et al., 2014). Modal clutch size of sooty terns is one (Schreiber, et al., 2002). The population was censused on 26 occasions between 1990 and 2015. We calculated the number of eggs laid by measuring the area of the two breeding colonies using conventional land survey techniques and determined egg density by counting eggs in quadrats (see full details in Hughes, et al., 2008).

Myna population size and their predation pressure on sooty terns

Censuses of the myna population were obtained from a consolidation of counts in 1994, 2004, 2005, 2006 and 2015 and included counts of birds feeding on the two rubbish tips, in 116 1-km grid squares covering the whole island, and at night-roosts.

Rates of predation were estimated by marking focal sooty tern eggs and following their fates. In each sooty tern breeding season, egg predation by mynas was measured for approximately seven days (i.e. for 25% of the incubation period of 28.8 days; Ashmole, 1963) and mean egg failure rates for the core and periphery of the colony (Hughes, et al., 2008) were calculated using the Mayfield method (Johnson & Shaffer, 1990). Causes of egg failure were categorised according to egg damage likely caused by mynas: 'consumption' was defined as the opening of a viable egg and feeding on some (usually < 10%) of the contents, and 'puncturing' was defined as the creation of a single small hole that destroyed egg integrity. The ratio of consumed:punctured sooty tern eggs was obtained from quadrat counts of depredated eggs. To establish causation of egg desertion, sets of focal eggs that contained deserted eggs were separated into two categories: those containing eggs consumed or punctured by mynas, and those that did not. We had previously found that the apparent association between these egg fates was significant (see full details in Hughes, et al., 2017b).

Cat population size and their predation pressure on sooty terns

On Ascension Island the cat population size in 1958 was estimated to be in the hundreds (Ashmole, 1963). Of the 1,100 feral cats that were removed from the island in the eradication programme of 2002, approximately 50 were removed from the tern colonies (Bell & Boyle, 2004).

Predation of adult sooty terns was monitored by removing all corpses of terns from the breeding area and then re-visiting the colonies to record the number of freshly killed birds. The mortality data gathered over two weeks may sometimes under-estimate the level of predation. Ashmole (1963) found that towards the end of each season cats began to take large chicks as well as adults. To compensate for this unknown level of chick predation, cats were assumed to take equal numbers of adults and chicks for 110 days (i.e. the period when some adults incubate while others feed chicks close to fledging; see full details in Hughes, et al., 2008). Because cats have been observed consuming seabird eggs elsewhere, albeit on rare occasions (Plantinga, et al., 2011), we also assessed this source of egg loss by inspecting cat middens for cat-predated eggs.

Rat population size and their predation pressure on sooty terns

The size of the rat population on Ascension Island has not been estimated but anecdotal data indicate that it has been (and remains) large. For example, 70,148 rats were killed between 1878 and 1887 (Hart-Davis, 1972). Relative abundance of rats in the tern colonies was estimated using a simple index calculated as the number of rat captures per 100 trap-nights (C/100TN) corrected for traps tripped (after Cunningham & Moors, 1983). During field seasons 50 'Victor' break-back rat traps baited with peanut butter and cornflakes were set out in pairs along the edge of both tern breeding colonies. Nest density was too high to allow traps to be set within the colonies without significantly disturbing breeding birds. Trapping occurred over two consecutive nights.

We studied the rate of chick predation by rats by counting chick carcasses (Towns, et al., 2006). We eliminated the possibility that starvation was the ultimate cause of chick mortality by recording the muscle score and body mass of live chicks in the same parts of the colonies as carcass surveys. The shape of the pectoral muscles was scored between 0 and 2 according to the prominence of the keel as described in Gosler (1991). A muscle score of 0 on this scale is indicative of low body condition most likely caused by malnourishment. Body mass of live chicks was recorded to the nearest 1 g with a Pesola spring balance. Chicks aged 28–30 days that were underweight weighed approximately 80 g and those that were in higher condition were > 150 g (Ashmole, 1963).

Prior to cat eradication in 2002 we found two cavities in rocks on the perimeter of the tern colonies that contained many broken sooty tern eggs but only later did we attribute the find to rat predation. Rats will roll eggs away from avian nests to a place of safety where they can open them (Zarzoso-Lacoste, et al., 2011). After cat eradication, we studied the rate of egg predation by rats by marking focal eggs and recording their losses. The rate of egg losses to rats was calculated as for that to mynas. We calculated the level of egg predation by rats prior to cat eradication by scaling up our findings from the above focal study. We used rat indices to generate relative rat abundance estimates before and after cat eradication.

Comparison of the three predation pressures

To evaluate the impact of chick and egg losses on the size of the breeding population of sooty terns, ratios of adults to chicks, and adults to eggs were required. In other words, on average, how many eggs need to hatch, and thus how many chicks need to survive until recruitment, to replace one adult in the breeding population? Furthermore, cats depredate near-fledging chicks while rats take half-grown chicks and thus we also required a ratio of eggs to both cat- and rat-depredated chicks.

The ratio of near-fledging chicks to adults was obtained from demographic data and estimates of adult and juvenile survival rates were calculated from ringing-re-capture data of adults and near-fledging chicks that were ringed during the same breeding seasons and re-captured in subsequent seasons (see further details in Reynolds, et al., 2014). Adult and juvenile survival rates, age at first breeding and mean age of birds in the breeding population were determined each breeding season by the re-capture from each cohort of adults and new recruits, and a mean with a 95% confidence limit (CL) calculated using the program MARK (White & Burnham, 1999).

The ratio of eggs to near-fledging chicks (i.e. those depredated by cats) was calculated from density counts of eggs and near-fledging chicks in quadrats (Bibby, et al., 2000; Schreiber & Burger, 2002). The ratio of eggs to half-grown chicks (i.e. those depredated by rats) was calculated by taking the average of near-fledging chick survival (see above) and nestling survival rates. The age at which nestlings leave the nest was approximately five days (Schreiber, et al., 2002). We calculated nestling survival rate for the five days by applying a hatchability rate of 0.91 (i.e. the number of eggs that hatched at the end of the incubation period; after Koenig, 1982) and a predation rate from Ascension frigatebirds (*Fregata aquila*) of 0.98 (i.e. the number of nestlings that escape frigatebird predation; BJH, unpubl. data) to the incubation success rate.

RESULTS

Sooty tern population size

Each season between 1990 and 2015, sooty terns laid on average 180,000 ± 8,000 (1 standard error [SE]) eggs (range: 70,000–270,000 eggs, n = 26 censuses). The mean number of nestlings in the tern colony each season was 94,000 ± 14,000 (n = 12 breeding seasons). The mean size of the breeding population was 360,000 ± 14,000 (95% CL) birds (Fig. 2).

Myna population size and their predation pressure on sooty terns

Between 1992 and 2015 the mean size of the myna population was 935 ± 265 (95% CL) birds (Fig. 3a). We found no evidence to suggest that mynas killed tern chicks. Mynas were recorded every field season in the tern colonies. Between 2000 and 2008 we monitored 1,238 eggs (935 on the periphery and 303 in the core). Of the 331 nest failures at the periphery of the colonies, 87 (26.3%) failed as a direct result of mynas. We calculated the mean egg failure rate at the periphery of the colonies as being 0.35 ± 0.07 (± 1 SE) eggs per season (n = 10 breeding seasons). The core of each colony appeared largely free from egg predation by mynas. The mean rate of egg loss to mynas in the two colonies was 0.19 ± 0.04 eggs per pair of terns (range: 0.02–0.37 eggs per pair, n = 1,238 breeding pairs over 10 breeding seasons). The ratio of consumed:punctured sooty tern eggs was 1:1.83 (n > 500 eggs in five sample quadrats across three breeding seasons). In summary, of all sooty tern eggs lost to mynas, 21% were consumed, 39% were punctured and 40% were deserted. We calculated that sooty tern mean egg losses to myna predation per season amounted to 26,000 ± 12,000 eggs (range: 4,000–50,000 eggs) that represented an average of 13% of all eggs laid (n = 10 breeding seasons).
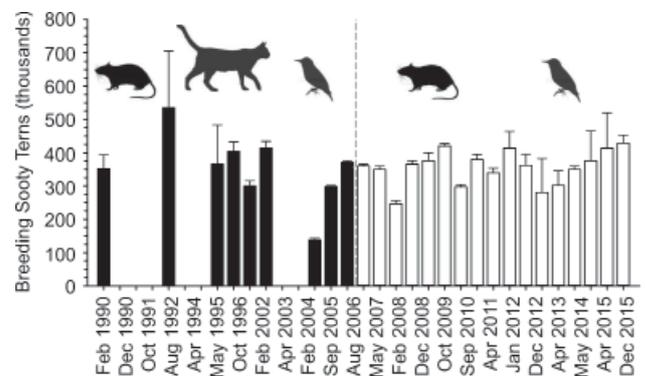
Fig. 2 Estimated size of the sooty tern breeding population (mean + 95% confidence limits) on Ascension Island between 1990 and 2015. Filled columns are censuses carried out during the cat-rat-myna (three) predator regime while open columns are those conducted during the rat-myna (dual) predator regime. Note that the sub-annual breeding cycle results in birds breeding twice in 1996, 2004, 2008, 2012 and 2015.
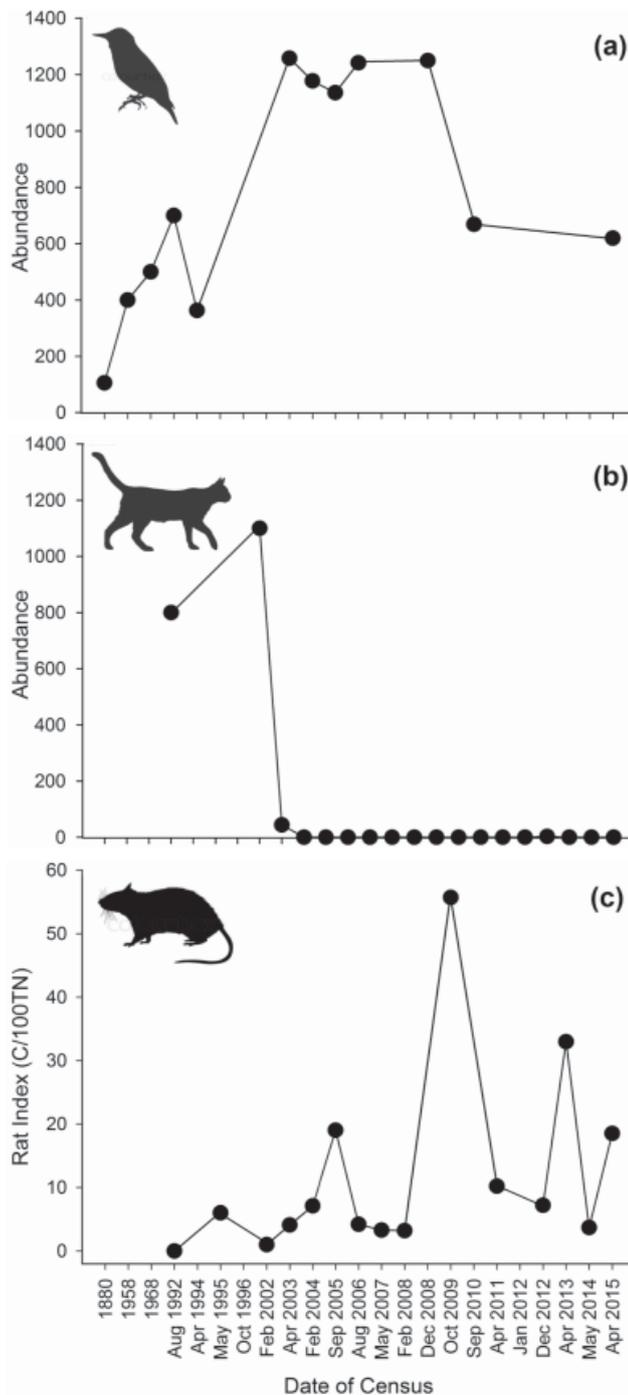
Fig. 3 Population sizes of the three introduced species that prey on various life stages of sooty terns breeding on Ascension Island in the South Atlantic: (a) common mynas, (b) domestic cats, and (c) black rats. Note that in (a) and (b) population estimates are based upon whole-island counts while (c) provides a relative abundance index calculated as the mean number of rats captured (C) per 100 trap-nights (TN) at both colonies (see further details in the Methods).

Cat population size and their predation pressure on sooty terns

We were unable to quantify cat numbers in the sooty tern colonies. Estimates of the size of the feral cat population across the whole island are shown in Fig. 3b. The number of adult sooty terns killed by cats from collection of corpses in 1990, 1992 and 1994 amounted to 2,996, 340 and 310, respectively. The mean number of adults killed by cats in the two colonies was 29 per night ($n = 32$ nights over

three breeding seasons). Towards the end of the sooty tern breeding season cats were killing near-fledging chicks as well as adults. If cat predation continued at the same intensity in the second half of the season as in the first, the overall percentage of the adult population depredated by cats would have been 1.8% (or 5,800 birds on average, $n = 3$ breeding seasons). Predation of chicks was not monitored but we estimated that the overall percentage of chicks that were depredated or died of starvation because a parent was killed by cats, was 3,600 chicks (i.e. 29 cat kills per night for the four months that chicks were in the colony, yielding a total of 3,600 chicks, 3.8% of the chick population of 94,000). We found no evidence that feral cats were taking any sooty tern eggs.

Rat population size and their predation pressure on sooty terns

During 473 days of fieldwork prior to the eradication of cats, no rat predation of tern chicks was observed. Between 1992 and 2002 the mean relative abundance of rats pre-cat eradication on the dry coastal plain close to the two tern colonies was 1.3 ± 1.0 (± 1 SE) C/100TN (range: 0–6.0 C/100TN, $n = 6$ trap-lines over three breeding seasons). Between 2005 and 2015 after the cat eradication the mean relative abundance of rats was 15.2 ± 3.8 C/100TN (range: 0–74.5 C/100TN, $n = 25$ trap-lines over 12 breeding seasons) (Fig. 3c).

Carcasses of chicks depredated by rats were first observed in 2005 when 131 of 596 ringed chicks (22.0%) were depredated. In 2009 mean carcass density in quadrats was 0.16 (range: 0–0.9 per m², $n = 68$ quadrats). The area of the colony was 12.21 ha and thus it contained an estimated $19,500 \pm 27,000$ carcasses (20%) of the chick population. We found no evidence of mass starvation as live chicks had a mean muscle score of 1.05 ± 0.31 (range: 0–2, $n = 998$ chicks) and a mean body mass of 157.5 ± 29.2 g (range: 54.8–220.0 g, $n = 946$ chicks). In 2005 and 2009 the mean number of chicks depredated by rats was 20,000 (21% of the chick population).

During nine sooty tern breeding seasons between 2003 and 2012, we monitored 1,067 single egg clutches (792 on the periphery and 275 in the core) for rat predation. Of the 327 nest failures, 314 were on the periphery and 13 were in the core of the colonies. Of the 327 that failed, 51 (15.6%) were missing eggs and these were attributed to rat predation. The mean rate of egg loss to rats was 0.17 ± 0.06 (± 1 SE) eggs per pair of terns (range: 0.00–0.49 eggs per pair, $n = 1,067$ breeding pairs over nine breeding seasons). Assuming rats only depredated eggs at the periphery of the colonies as so few eggs failed in the core, the overall percentage of the eggs depredated in the tern colony by rats was 4.8% representing an egg total of 9,000 ($n = 9$ breeding seasons).

From a comparison of mean relative abundances of rats pre- (1.3 C/100TN, $n = 3$ breeding seasons) and post-cat eradication (15.2 C/100TN, $n = 12$ breeding seasons), we estimated that the rat population was only 8.6% as large prior to, compared with after, the cat eradication. We also estimated that rats depredated 800 eggs per season prior to cat eradication.

Comparison of the three predation pressures

A summary of the comparative predation pressures in terms of egg losses (i.e. the lowest currency to represent all tern life stages) is provided in Fig. 4. We generated ratios to eggs laid of survival estimates at various life stages using life-history data in Hughes (2014). The ratios generated were eggs preyed upon by mynas (1:1); chicks succumbing to rat predation (2.99:1); chicks preyed upon by cats (4.13:1); and adults preyed upon by cats (9.67:1).
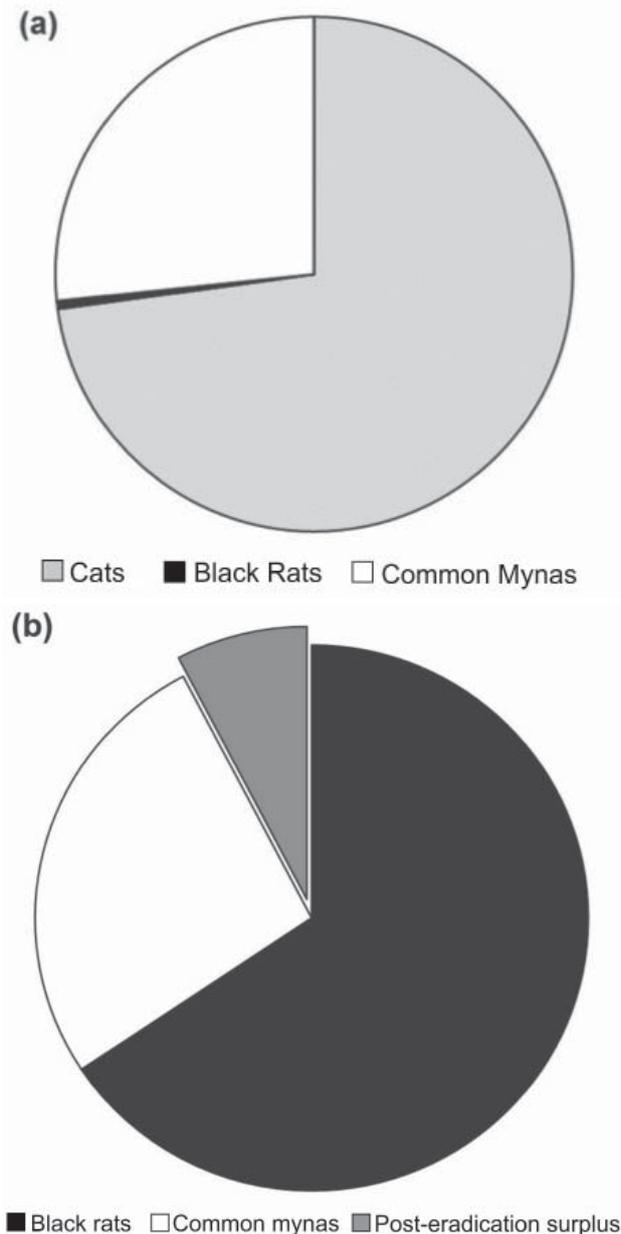
Fig. 4 (a) Pre- and (b) post-cat eradication losses of sooty tern egg equivalents (i.e. eggs and post-hatching chick and adult life stages) to three introduced predator species on Ascension Island in the South Atlantic. The average number of eggs laid was 180,000. Note that in (b) there are only two predators contributing to losses of egg equivalents while the third category represents the benefit to the tern population of cat eradication, equating to 2,000 eggs (see further details in the Results).

The mean number of eggs lost to myna predation per sooty tern breeding season was 26,000. We calculated that losses of chicks to rats translated into the 'loss' of 60,000 eggs (i.e. 20,000 chicks × 2.99). Rats also directly removed 9,000 eggs from the breeding colony. The sum of rat predation translated into the 'loss' of 69,000 eggs. Cats depredated 5,800 adults and 3,600 near-fledging chicks translating into egg losses of 56,000 (i.e. 5,800 adults × 9.67) and 15,000 (i.e. 3,600 near-fledging chicks × 4.13), respectively. Therefore, the sum of cat predation translated into the 'loss' of 71,000 eggs.

DISCUSSION

We compared carcass counts of adults killed by cats with those of chicks killed by rats to assess their relative impacts on the tern population. Carcass density of chicks killed by rats was likely to provide an under-estimate of chick losses as decomposition of corpses was rapid and rough ground made it easy to overlook them. Carcass counts of adults and near-fledging chicks killed by cats (and adjusted by the adult:chick ratio), and those of chicks solely killed by rats, were similar to each other, varying by 18%. If we take into account that rats also depredated 9,000 eggs then the variation between rat and cat predation is just 3%. Of the three sources of predation on the tern population, cats had the greatest impact on the tern population but following their eradication, rats replaced them as the primary source of predation pressure (Fig. 4).

The third source of predation on the island was mynas that depredated 26,000 eggs every sooty tern breeding season but their overall impact on the population size of sooty terns was less than half that of cats or rats. Mynas depredated more tern eggs than did rats (i.e. 26,000 *versus* 9,000) and very many more than did cats. Bell and Boyle (2004) found egg remains in stomachs of one of five cats culled close to the tern colony. We found no evidence that mynas depredated chicks or adults. Mynas depredated more tern eggs than rats or cats depredated chicks and before cat eradication (i.e. pre-2002) mynas had a greater detrimental impact on the size of the breeding tern population than did rats. There were large variations between sooty tern breeding seasons in the relative abundance of rats in the tern colonies (Fig. 3c) and in the extent of egg losses to mynas (i.e. 0.02–0.37 eggs per pair) suggesting that sooty terns were not the main driver of the population dynamics of these two omnivorous predators (Towns, et al., 2006).

Other comparative studies

A meta-analysis by Baker, et al. (2013) of threats to native avian species posed by introduced ones concluded that introduced invasive avian species are not a major threat. However, we found that mynas posed a major threat to native sooty terns on the island (Hughes, et al., 2017b). For every egg that mynas consumed, they punctured or caused desertion of four others. The only quantitative comparative study of seabird egg predation by mynas was of 350 wedge-tailed shearwaters (*Puffinis pacificus cuneatus*) on Hawaii where mynas punctured 74 (21%) of all eggs laid during one season (Byrd, 1979).

Ashmole (1963) estimated that on Ascension Island cats were killing approximately 10,000–20,000 sooty tern adults (i.e. 0.5 to 1.0% of the adult population) and up to 40% of chicks in 1958 and 1959. On Juan de Nova Island in the Mozambique Channel in the western Indian Ocean where predator/prey constituent members were similar to those on Ascension Island, Peck, et al. (2008) found that cats were killing 2,205 sooty terns per week (0.1% of the breeding population).

Prior to cat eradication, we saw no live rats in the tern colony and we did not suspect any rat predation of tern life stages. Similarly, Ashmole (1963) saw no such incidents of predation by rats during numerous day and night visits to the tern colonies in 1958 and 1959. On Juan de Nova Island where black rats co-exist with cats, and both depredate sooty terns, Ringler, et al. (2015) reported that losses of sooty terns to rats were relatively low. On Ascension Island losses of sooty terns to rats increased dramatically when cats were eradicated (Fig. 4). The severity of the predation post-eradication was similar to that found by Jones, et al. (2008) in their meta-analysis of the severity of rat predation.

Mesopredation

We found that the intensity of predation by rats varied depending on whether rats were the apex predator. Under the cat-rat-myna predator regime, rats exerted the least predation pressure on the tern population (Fig. 4a) but following apex predator (cat) removal, they exerted the greater predation pressure in the dual predator regime (Fig. 4b). Cats were eradicated from the tern colony in 2002 (Bell & Boyle, 2004) and the rat population increased seven-fold in size following their eradication as determined from the relative abundance index (Fig. 3c). The eradication of cats is seen as particularly beneficial to seabirds (Nogales, et al., 2013) but, to the best of our knowledge, this only applies to islands without rats in the first place (e.g. Natividad Island, Marion Island in the sub-Antarctic and Baker Island in the Pacific). We found clear evidence that when black rats are 'released' by apex predator removal the size of the rat population increased and rats started to depredate tern chicks. Rats as apex predators exerted a predation pressure on terns that was 97% of that in the regime of cats and rats. Our findings are at odds with those of Ringler, et al. (2015) who predicted that cat eradication would be beneficial to sooty terns. They also oppose McCreless, et al. (2016) who found that the potential for extirpation of seabird populations was greater in the twin predator regime of cats and rats and they also disagree with Ratcliffe, et al. (2009) who reported that on Ascension Island five seabird species had re-colonized the mainland following the eradication of cats. There are three possible explanations for this disparity: 1) despite major changes in predator population sizes (Fig. 3), there has been little fluctuation in that of breeding sooty terns on the island (Fig. 2) which suggests that predation may not be the primary driver of the tern's population size; 2) a change in the habitat on the tern colonies on Ascension Island occurred concurrently with cat eradication which rats, with their catholic diets, took advantage of by switching to alternative food sources such as seeds of the invasive plant mesquite (*Prosopis juliflora*) (Pickup, 1999); and 3) the sub-annual breeding cycle of sooty terns on Ascension Island may provide rats with more opportunities to breed than if sooty terns were breeding annually as they do elsewhere in their range (Reynolds, et al., 2014).

CONCLUSIONS

Care is needed when applying our findings related to predation pressures on Ascension Island sooty terns to other seabird species on the island and to other places in the world. When sooty terns are present, the super-abundance of prey as represented by eggs, chicks and adults may magnify predation pressures. As far as we are aware, our study is the first to provide a comparison of predation pressures by cats, rats and mynas on seabirds. Such empirical evidence of invasive species' impacts on native avifauna is critical for the prioritization of management options directed towards introduced species (Jeschke, et al., 2014; McCreless, et al., 2016). Here, we present strong evidence that mynas can be major egg predators of seabirds. We have quantified changes in predation pressures resulting from the eradication of cats and we have highlighted that rats in the absence of cats have impacted upon breeding success of sooty terns sufficiently to bring into serious question the benefits of cat eradication to the recovery of the sooty tern breeding population on Ascension Island. Conversely, pressures on sooty terns from predators have declined by 3% following the removal of cats. How rats have largely replaced the predation pressure posed by cats following their removal and why the population of sooty terns on Ascension Island has not recovered in response to seabird conservation efforts to date are questions that require considerable future investigation.

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