Popul Ecol (2017) 59:213–224
DOI 10.1007/s10144-017-0588-z

THE SOCIETY OF POPULATION ECOLOGY

ORIGINAL ARTICLE

Long-term population trends of Sooty Terns *Onychoprion fuscatus*: implications for conservation status

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Received: 8 March 2017 / Accepted: 23 June 2017 / Published online: 13 July 2017

Abstract Seabirds have suffered dramatic declines in population over recent decades. The most abundant seabirds of tropical oceans are Sooty Terns *Onychoprion fuscatus* and they have an IUCN Red List category of 'Least Concern'. Ascension Island has the largest colony of Sooty Terns in the Atlantic Ocean and censuses between 1990 and 2013 have shown that its population size is static. In this study we have used historical data and recent censuses to describe the population status of Sooty Terns on Ascension Island over a century. We show that the breeding population contained over 2 million individuals in the 1870s and remained at this level for at least 70 years. However, the population declined from >2 million birds in 1942 to 350,000 birds by 1990. The population trend spanning a period equivalent to three generations of the species (63 years; 1942–2005) showed an approximate 84% decline in population size. Using IUCN criteria this suggests that Sooty Terns on Ascension could be considered 'Critically Endangered'. We conclude that a re-evaluation of Sooty Tern conservation status is necessary at the local level and possibly globally. Our study highlights that for long-lived species historic demographic data should be considered when determining conservation status.

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Keywords Census · Historical population size · IUCN Red List · Tropical pelagic seabirds · United Kingdom Overseas Territories

Introduction

Determining the conservation status of species according to a formal set of criteria is now widely regarded as essential for conservation action. Over recent decades the Red List of Threatened Species produced by the International Union for Conservation of Nature (hereafter referred to as the 'IUCN Red List') has been adopted internationally as the main framework within which the conservation status of animal and plant taxa are assessed (see review by Rodrigues et al. 2006). A major criterion among birds is based upon population trend over 10 years, or three generations, whichever is longer.

Compared with many other avian taxa, seabirds present challenges when assessing their conservation status because they are typically long-lived, migratory and widely distributed, and individuals may not breed annually. Nevertheless, seabirds are the subject of many long-term monitoring programmes which have revealed that, compared with other taxa, seabird populations have declined rapidly over recent decades (Croxall et al. 2012), with the combined global population size of all seabirds having declined by nearly 70% between 1950 and 2010 (Paleczny et al. 2015).

Sources of data for establishing population trends

Ornithology has a rich history of scientific monitoring programmes that have quantified changes in distribution and size of bird populations at different spatial scales,

often over many decades (e.g., Hagemeijer and Blair 1997; Balmer et al. 2013). Data from these monitoring programmes have provided essential reference points for estimating population trends over multiple generations in many short-lived birds. Among long-lived species, however, such multi-generational demographic data are scarce (Newton 2013). In some species historical data have been used for setting population baselines and from these population trends have been developed (e.g., Sweetnam et al. 1999; Igl and Johnson 2005; McClenachan et al. 2012). Such retrospective investigation of population trends has been applied, for example, to populations of Passeriformes (Gooch et al. 1991) and Anseriformes (Cooch et al. 2001).

Conservation status of Sooty Terns

Sooty Terns *Onychoprion fuscatus* are the most numerous of seabirds in the three tropical ocean systems (IUCN 2015). They are the only seabird species with a large global population [estimated at 23–25 million birds (Schreiber et al. 2002)], in which the trend in population size is unknown. Despite a lack of information on population trend they have been assigned a conservation status of 'Least Concern' (IUCN 2015), presumably because they are regarded as sufficiently numerous. However, the total population size of Sooty Terns is reported to be falling (Schreiber et al. 2002) most likely because of the combined threats of over-exploitation of pelagic fish species (upon which they are dependent for successful foraging) (Danckwerts et al. 2014), climate change (Foden et al. 2013), and egg harvesting (Feare et al. 2007).

In this study we determine general changes in the size of the population of breeding Sooty Terns on Ascension Island since the nineteenth century. We also determine population change over the period of three recent generations. Generation length is defined as the average age of parent birds in a current cohort (IUCN 2012). In Sooty Terns the average age of adults is 21 years (Schreiber et al. 2002) and accordingly we have constructed a population trend over a recent 63-year period. This is a similar timeframe to an assessment of the world's monitored seabirds carried out by Paleczny et al. (2015). Breeding population sizes were determined from calculated areas of colony occupancy and estimates of breeding density.

Methods

Study area

Ascension Island (07°57′S, 14°24′W; 97 km^2) is one of the three volcanic islands that make up the United Kingdom 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 (Hughes et al. 2010). It lies some 800 km south of the equator, 2000 km from continental land masses and its nearest neighbour is St Helena which is 1100 km to the south-east. Wideawake Fair is the site of the Sooty Tern breeding colony on Ascension Island and is an Important Bird Area (IBA reference number SH009; BirdLife International 2016).

Study species and fieldwork

Sooty Tern breeding colonies are distributed pan-equatorially (Schreiber et al. 2002), and the population breeding on Ascension Island in the South Atlantic may be the most closely monitored. Ascension Island holds approximately 2% of the global, and 40% of the Atlantic Ocean, population of Sooty Terns (Schreiber et al. 2002). There are multiple sources of long-term demographic data for breeding Sooty Terns on this island from which it has been possible to estimate their distribution and number as early as 1877.

Sooty Terns generally breed in large colonies composed of smaller sub-colonies that contain birds at equivalent reproductive stages. In total, colonies can number in excess of 1 million birds (Schreiber et al. 2002) and this makes counting all individuals or incubated eggs impractical. In the Indian Ocean, Le Corre and Jaquemet (2005) estimated the population size of Sooty Terns at colonies during incubation by mapping the colonies and then determining their area of coverage. Counts of eggs in quadrats were used in the estimation of breeding density which was multiplied by the area to estimate the number of Sooty Tern breeding pairs. This census method is appropriate for Sooty Terns on Ascension Island as the edge of each sub-colony (defined as spatially separate areas occupied by breeding birds) is well-defined, enabling sub-colony area to be surveyed reliably with clutches easily found on substrate devoid of vegetation (Fig. 1). Sooty Terns do not build a nest and clutches are laid in different areas of the breeding colony each season. They lay a modal clutch size of one (Schreiber et al. 2002) although Feare and Larose (2014) showed that on rare occasions 2-egg clutches can be found as a result of adoption of an egg from an adjacent nest.

Chapin (1946) mapped the sub-colonies from the air and the ground in 1942 while Ashmole (1963) mapped them in 1958 during 18 months of the British Ornithologists' Union's (BOU's) Centenary Expedition (Dawson 2008). The survey methods used to map the sub-colonies are unknown but the appearance of the maps and their scale strongly suggested that they were sketched onto map sheet Ascension 11, scale 6 inches to 1 mile (1:10,560), surveyed by E. Y. Daniel RMLI and issued by the Director of Works Department of the Admiralty in 1901. The maps prepared

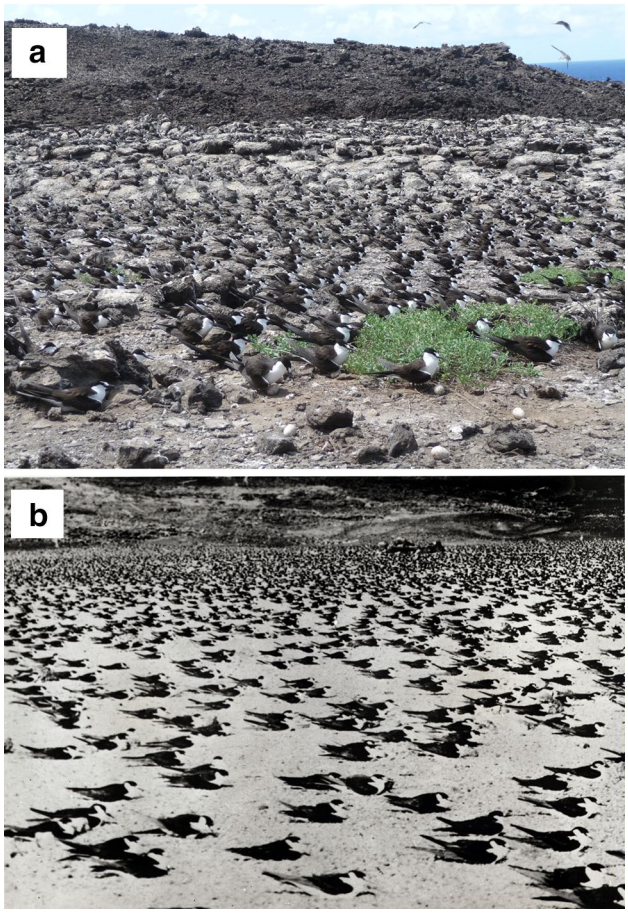

Fig. 1 Sooty Tern colonies on Ascension Island in the South Atlantic in **a** 2011 (photo: ADG), and **b** *circa* 1910 [photo: © The Porthcurno Collections Trust 2017 (Porthcurno 1910–1930)]. The Wideawake airfield was built on this colony's location in 1942

by Chapin (1946) and Ashmole (1963) were scanned in GIS (as described above) and the area of the colony calculated. Breeding densities were calculated from counts of eggs in 1942 in two rectangular quadrats of 1000 square feet (92.9 m^2) (Chapin 1946) and from counts of eggs in 1958 in 247 5×5-yard (4.6×4.6 m) grid squares (Ashmole 1963). This latter grid covered almost the whole area of a small (approximately 1 ha) sub-colony referred to as "First Fair". To check the accuracy of our method of calculating the area of the sub-colonies, we compared our calculated area of First Fair with that obtained by overlaying the sub-colony with grid squares. The numbers of birds breeding on Ascension Island in 1942 and 1958 were calculated by multiplying the total area occupied each breeding season by breeding density (as described above).

W. R. P. Bourne during a 1-day visit to the island on 14th October 1984 annotated a map from Ashmole (1963) showing sub-colonies that were no longer occupied (W. R. P. Bourne, personal communication). The map was once again scanned in a GIS and areas quantified as described above.

To census the population between 1990 and 1998, we mapped the sub-colonies using compass and tape traverses. We surveyed the colony in March 1990, October 1996, September 1997 and June 1998, and estimated breeding density close to the seasonal peak in breeding (Hughes et al. 2008). Sooty Terns on Ascension Island breed relatively synchronously every 290 days but there was a spread of approximately 59 days in the timing of laying within a breeding season (Reynolds et al. 2014). Timing of the census effort was carefully planned to coincide with the peak in incubation efforts; if it was too early, many birds would have been absent from the breeding grounds while if it was too late, highly mobile chicks would have made quantitative estimations of breeding density (from counting tending adults) impossible. The breeding grounds were searched systematically for sub-colonies. Typically, sub-colonies range in size between 0.1 and 6 ha, and in number between three and 14 in any given breeding season (Hughes 2014). The perimeter of each sub-colony was mapped, scanned in GIS (as described above) and the area occupied by breeding birds calculated. Breeding density was determined in the field from randomly placed 10 m^2 circular quadrats. Transects were placed at random through sub-colonies where birds were incubating. At every 10 paces a pole was positioned on the ground and a 1.784 m length of string attached to it was used to describe a circle of 10 m^2. The number of clutches within each quadrat was counted by two observers. The mean breeding density of adjacent sub-colonies was used to calculate the size of the population in the sub-colonies where eggs were hatching so that disturbance of newly hatched chicks (and their parents) was minimized. Breeding density was calculated by dividing the number of clutches counted in each quadrat by its area (in m^2).

Three more maps of the tern colony on Ascension Island were used to provide population estimates. R. Prytherch (personal communication), who surveyed the sub-colonies with K. E. L. Simmons, provided BJH with a copy of his scaled drawings of the sub-colonies mapped in October 1993, September 1996, and October 1997. The maps were scanned in GIS (as described above) and the area of the colony calculated. Ratcliffe et al. (1999) completed a Sooty Tern population census in September 1997 but did not produce a map of the colony, instead calculating the area from a 5×5 m grid that covered each of the sub-colonies.

Historical breeding population size and sub-colony locations

Historical demographic data are available from maps of the island surveyed by Bedford (1838) that show the locations of breeding sub-colonies. The species provided a rich

food source to the first settlers who harvested many eggs according to reports from visiting naturalists (Hart-Davies 1972). Maps and photographs of this breeding colony and eye witness accounts of the size of the breeding population are available. Scientific studies of the breeding population on Ascension Island were made in 1942 when birds were displaced to build an airfield on the island (Chapin 1946, 1954), and in 1958 during the BOU's Centenary Expedition (e.g., Ashmole 1963; Ashmole et al. 1994). Both Chapin (1946) and Ashmole (1963) produced scaled drawings of the Sooty Tern breeding colony, calculated breeding density and estimated the population size. However, despite having surveyed the colony and calculated breeding density, neither study determined colony area nor used this in the estimation of population size. In recent years the size of populations breeding within large colonies has been estimated routinely from mean breeding density and colony areas (e.g., Mitchell et al. 2004; Le Corre and Jaquemet 2005). The first census carried out by us was completed in 1990 (Hughes et al. 2008) and since then the population has been censused in almost every breeding period (Hughes 2014).

Processing of 19th-century historical data

Pauly (1995) and Bonebrake et al. (2010) make the case for using all forms of historical data when attempting to determine historical population size, and we have done so. Eye witness accounts and photographs that provided support for our findings of the historical population size were collated (Appendix 1). We searched a wide range of literature and other sources for potentially useful information on Sooty Tern population size in the nineteenth century. The astronomer Sir David Gill in 1877 drew a map, reproduced in Penrose (1879), delineating the boundaries of the terns' sub-colonies on the island. The map was scanned in GIS as 300 dpi jpeg images using a TruScan Vidar Scanner. The file was then rectified using Erdas Imagine 9.2 (Leica 2008) to give the un-projected image a true location on the ground. This was achieved by referencing the original map to existing re-projected imagery/mapping. Once the files were given a projection, the area was digitized as Shapefiles using ESRI's ArcMap 9.2 (ESRI 2009). This GIS software was available through the MOD Joint Aeronautical and Geospatial Organization (managed by ADG), and this enabled the area of these digitized sub-colonies to be calculated. A photograph of the colony taken by Jenner (1899) and records of egg harvests enabled us to compare breeding densities in the nineteenth century with those in the twentieth and twenty-first centuries. The population size in 1877 was estimated by multiplying the area occupied by Sooty Terns by their mean breeding density in the twentieth and twenty-first centuries (following Bonebrake et al. 2010 and Rebstock et al. 2016).

Population estimates in the 21st century

Between 2000 and 2013 we used Garmin 12 Global Positioning System (GPS) receivers (Garmin, Kansas City, KS, USA) to record waypoints around the perimeter of the sub-colonies. The recorded GPS waypoints were imported into the GIS and the areas of the sub-colonies calculated. Breeding density was determined in the field from randomly placed 10 m^2 circular quadrats (as described above).

Population trend

Paleczny et al. (2015) determined population trends of seabirds globally between 1950 and 2010, and we estimated the population trend of Sooty Terns on Ascension Island over a similar timeframe. The changes in population size and area of occupancy by Sooty Terns in three generations were calculated between 1942 (Chapin 1946, 1954) and 2005, i.e., 1942 plus three Sooty Tern generation lengths of 21 years.

Results

Figure 2 shows the occupancy of Ascension Island by Sooty Tern breeding colonies in 1877, 1942, 1958 and 2013, and the areas of each colony are presented in Table 1. Sooty Terns no longer nest in most of the historical sub-colonies but have formed sub-colonies elsewhere in the south-west corner of the island. Wideawake Fair, described by Chapin (1954), and First Fair, described by Ashmole (1963), were destroyed when the airfield was built in 1943 and extended in 1965. The area of First Fair calculated from 250 5×5-yard (20.9 m^2) grid squares covering the sub-colony was 0.58 ha. The area calculated from the map in Ashmole (1963) was determined to be 0.89 ha following scanning into GIS. The annotations on the map in Ashmole (1963) made by W. R. P. Bourne (personal communication) in 1984 indicated that the area occupied by breeding terns had declined to approximately 56 ha (Table 1). The areas occupied by Sooty Terns during 24 breeding seasons between 1990 and 2013 (Fig. 2) are shown in Table 2.

Egg counts on sandy substrates in two rectangular quadrats of a total area of 92.9 m^2 yielded a breeding density of 1.60 clutches m^{-2} in 1942 (Chapin 1954), while those in 247 grid squares on sandy substrates when eggs were hatching provided a breeding density of 2.15 clutches m^{-2} in 1958 (Ashmole 1963). Breeding densities of birds nesting on rocky substrates and estimated prior to hatching

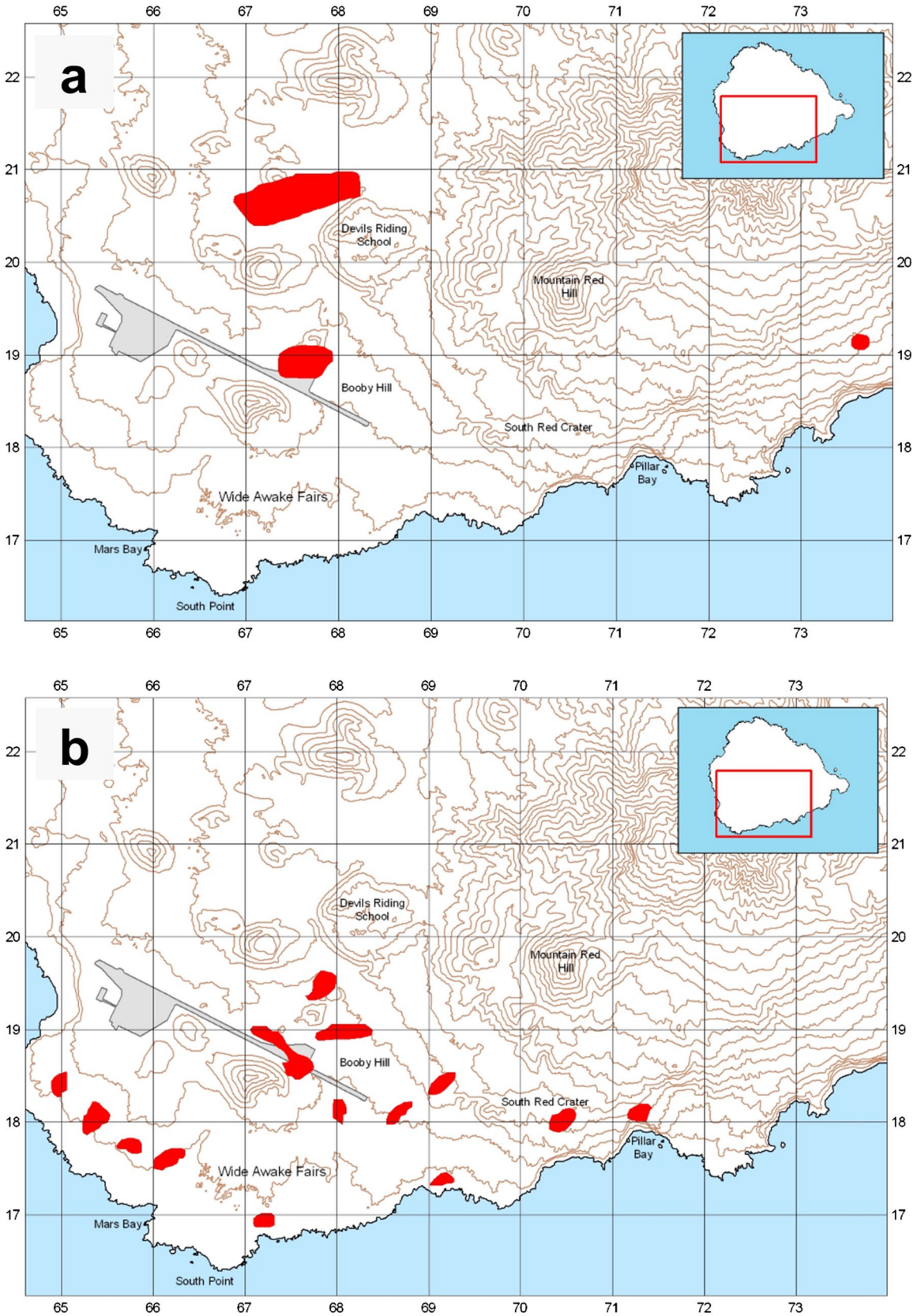

Fig. 2 GIS re-scaled historical maps showing the size and location of the breeding colonies of Sooty Terns on Ascension Island in the South Atlantic in **a** 1877 (Penrose 1879), **b** 1942 (Chapin 1954), **c** 1958 (Ashmole 1963), and **d** 2013

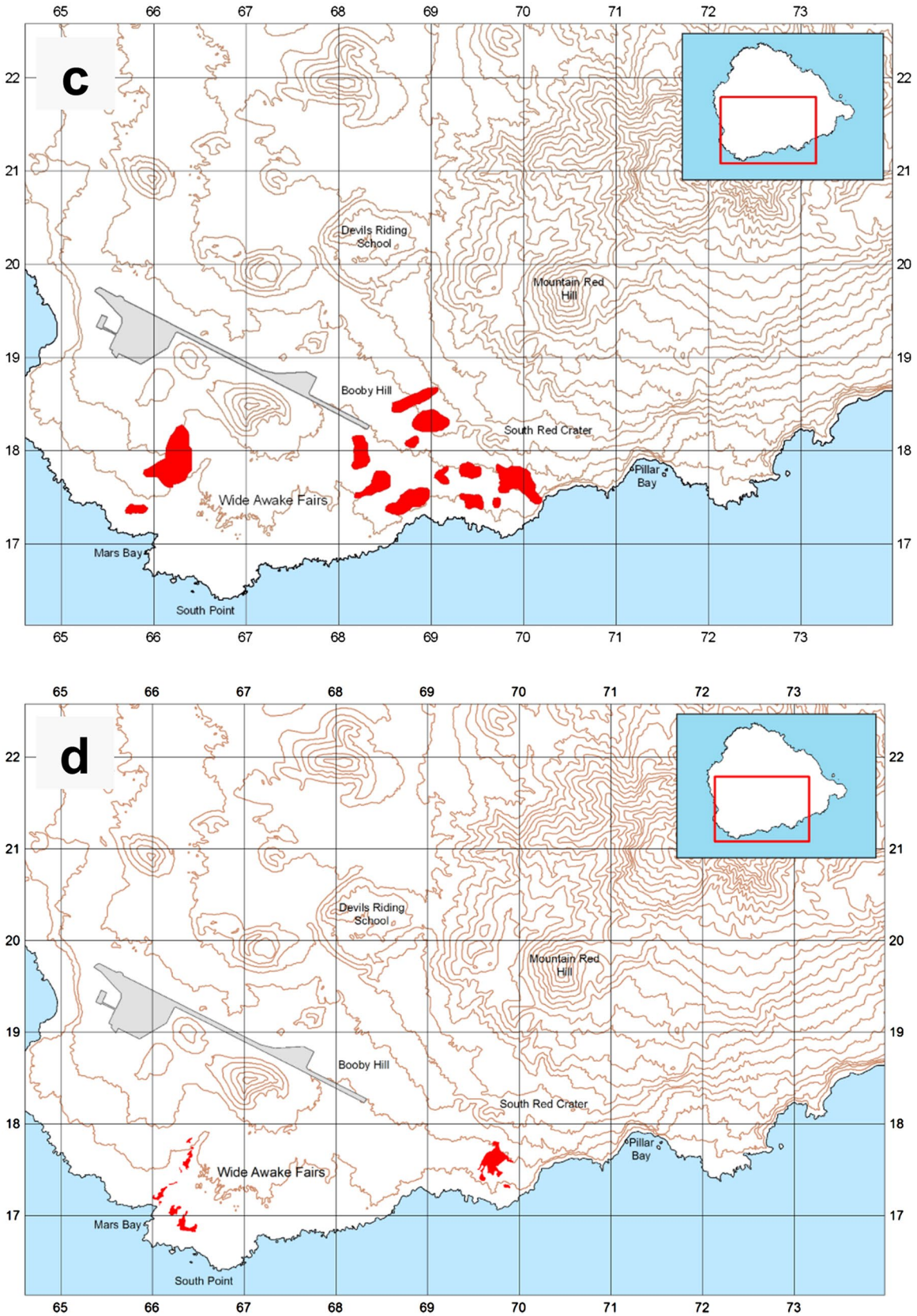

Fig. 2 (continued)

Table 1 Details of the breeding colonies of Sooty Terns on Ascension Island in the South Atlantic surveyed in 1877, 1942, 1958 and 1984

Surveyor	Date of survey	Number of sub-colonies	Survey scale (1:)	Area (ha)
D Gill	December 1877	3	123,700	71.56
JP Chapin	October 1942	14	63,360	73.30
NP Ashmole	January–December 1958	12	31,680	77.23
WRP Bourne	October 1984	10	31,680	Approximately 56

The survey scale of '1:' is an imperial scaling measurement that describes 1 inch on the map referring to 31,680 inches (1/2 mile), 63,360 inches (1 mile) and 123,700 inches (2 miles) on the ground

Table 2 Areas of nesting colonies and the breeding densities of Sooty Terns on Ascension Island in the South Atlantic as determined from independent surveys

Breeding season	Surveyor	Area of colony (ha)	Mean AoNs (m^{-2})
March 1990	BJH	14.38	1.85
October 1993	R Prytherch	**16.34**	
January 1996	R Prytherch	**11.18**	
October 1996	BJH	9.67	1.93
September 1997	N Ratcliffe	**9.12**	**1.61**
October 1997	R Prytherch	**11.37**	
June 1998	BJH	10.43	1.85
November 2000	RA survey team	3.63	1.90
September 2001	BJH	6.90	2.16
July 2002	RA survey team	9.62	1.93
April 2003	BJH	10.46	1.72
February 2004	BJH	9.25	1.89
December 2004	BJH	7.07	1.74
October 2005	BJH	11.36	1.61
August 2006	BJH	15.68	1.20
May 2007	BJH	14.19	1.48
February 2008	ADG	9.72	1.53
December 2008	BJH	13.58	1.40
October 2009	ADG	12.21	1.09
May 2010	AIG and S Riddick	**13.49**	
April 2011	ADG	10.69	1.69
January 2012	BJH	**Approximately 7**	1.95
December 2012	ADG	8.13	1.79
August 2013	ADG	11.10	1.81

The apparently occupied nest (AoN) densities within each breeding season are pooled across colonies. Estimates in bold text are derived from secondary data (generated from fieldwork by non-military surveyors). In 2000 and 2002 Royal Artillery (RA) British Army surveyors and staff from the Ascension Island Government (AIG) conservation department were employed to map the Sooty Tern colonies on occasion

from egg counts in 10 m^2 quadrats between 1990 and 2013 varied between 1.09 and 2.16 clutches m^{-2} with the mean of 1.71 ± 0.26 clutches m^{-2} ($n = 20$ breeding seasons; Table 2).

The breeding population on Ascension Island in 1877 contained an estimated 2.45 million birds. The breeding populations in 1942 and 1958 calculated from data provided by Chapin (1946) and by Ashmole (1963) contained 2.35 and 3.32 million birds, respectively. The breeding population between 1990 and 2013 varied in size between 140,000 and 540,000 birds with a mean of $350{,}000 \pm 73{,}000$ birds ($n = 24$ censuses; Fig. 3).

The population size of Sooty Terns breeding on Ascension Island declined during the 63-year (three generation cycle) period between 1942 (2.35 million) and 2005 (0.37 million) by 84% (Fig. 3). The area occupied by breeding colonies shrank by 85%.

Discussion

Globally, Sooty Terns have a conservation status of 'Least Concern' (IUCN 2015), and therefore are not considered a prime target for conservation action. However, our findings show that over the recent three generation time period (1942–2005) the Ascension Island population has declined by 84%. This indicates that this population of Sooty Terns could be considered 'Critically Endangered'. This disparity between the current global conservation status and our regional findings is of concern because even avian species with large populations are not immune from extinction; consider, for example, the cases of Passenger Pigeons *Ectopistes migratorius* (Halliday 2003) and Carolina Parakeets *Conuropsis carolinensis* (Snyder 2004).

The value of demographic data from different sources

Our estimate of the colony area occupied by Sooty Terns in 1877 (Table 1) is supported by an eye witness account. In 1873 Sir C. Wyville Thomson visited the Sooty Tern colony on Ascension Island during the Challenger Expedition and recorded that the breeding place was "some square miles in extent" (1 sq. mile = 259 ha) and that during the breeding season 120,000 eggs are sometimes "gathered in a single week" (Thomson 1877). We calculated that >2 million Sooty Terns bred on Ascension Island in 1942 and

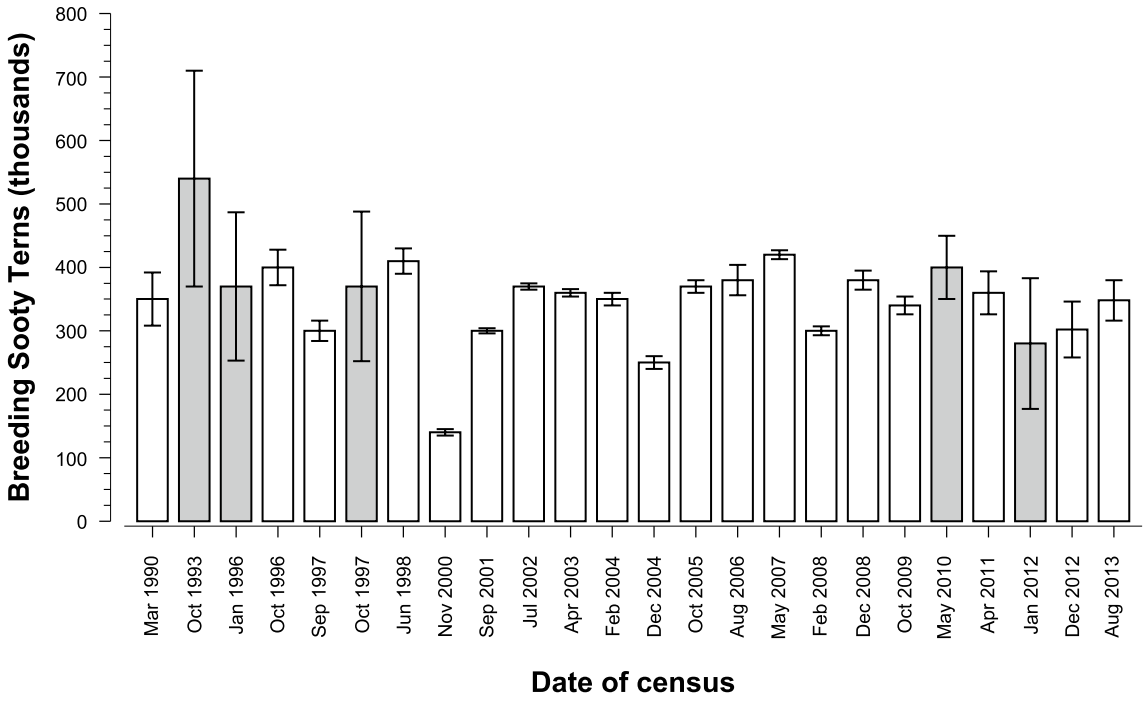

Fig. 3 Estimated size of the Sooty Tern population (mean number of individuals ± 95% confidence limits) breeding on Ascension Island in the South Atlantic between 1990 and 2013 (inclusive). Most estimates are based on our field (primary) data (*open bars*) while some are based on secondary data (*grey bars*) (generated from fieldwork by non-military surveyors). Note that the sub-annual breeding cycle results in birds breeding twice in 1996, 2004, 2008 and 2012

maps showing the colony area in 1942 (Fig. 2b) compared with in 2013 (Fig. 2d) illustrate the scale of the population decline in terms of the reduced area occupied by breeding birds. Our estimate of the population size in 1877, our calculation of the population size in 1958 (Ashmole 1963), and W. R. P. Bourne's 1984 revision of a map produced by Ashmole (1963), provide strong support for both an estimated population size in 1942 of 2.35 million birds and a current population estimate of 350,000 ± 73,000 birds. There is some anecdotal evidence (personal communications with K. E. L. Simmons who was living on the island at that time) identifying the early 1960s as being when the decline in the Sooty Tern population began.

Historical (mostly non-quantitative) records are increasingly being used in an attempt to quantify historical animal population sizes (Bonebrake et al. 2010; Thurstan et al. 2016). For example, on St Paul's Rocks, another island in the tropical Atlantic Ocean, Luiz and Edwards (2011) used historical records to substantiate anecdotal accounts of the decline in the size of reef shark *Carcharhinus* spp. populations. Our baseline population size for Sooty Terns was determined from quantitative data but a near-approximation to the calculated population size can be obtained from our collection of eye witness accounts and photographs (Appendix 1).

Reliability of population estimates

There are biases associated with censuses of colonially nesting birds. These include difficulties in counting breeding birds in colonies in inaccessible coastal sites and seasonal variation in the proportion of the population that is breeding (Bibby et al. 2000). Relatively few Sooty Terns, i.e., <20 nests (Stonehouse 1962), nest on inaccessible parts of Ascension Island such as Boatswainbird Islet and offshore stacks in a given season, and therefore any such bias is systematic and minor. A far greater source of bias originates from long-term variation in the proportion of the island's Sooty Tern population that breeds each cycle. We lack data from marked individuals that would allow, for example, estimation of the percentage of sub-adults from different age cohorts that recruit into the breeding population (e.g., Lebreton et al. 2003), and of the percentage of previously successful breeders that skip a subsequent breeding season. In the latter case, Devney et al. (2009) examined what they defined as "breeding participation" of Brown Noddies *Anous stolidus* and Sooty Terns (pelagic feeders), and Greater Crested Terns *Thalasseus bergii* (an inshore feeder) and found a relationship in the first two species between specific environmental conditions and the numbers of breeding pairs at a colony site in the Pacific

Ocean. Their findings suggested that birds were probably skipping breeding in years when pelagic food availability was lower as a result of oceanographic phenomena such as El Niño.

Across 21 breeding seasons between 1942 and 2013 (inclusive), breeding density varied between 1.09 and 2.16 clutches m^{-2}. We found little evidence to suggest that measuring breeding density using different information resulted in marked differences in estimates. For example, we estimated breeding density (1) in quadrats with sizes that varied between 10 and 93 m^2, (2) on sandy or rocky substrates, or (3) when eggs are hatching or at pre-hatch, and each of these returned similar breeding density estimates. Historical scaled drawings have been used effectively to delineate the periphery of study areas (Crazier 1976). There was good agreement (range 72–77 ha) in the colony areas obtained from historical maps surveyed by Gill in 1877 and reproduced in Penrose (1879), Chapin (1946) and Ashmole (1963) (Table 1). To map the colony, these ornithologists drew the outline of each sub-colony on the existing large scale map of the island. R. Prytherch used this technique in 1996 and 1998 and the colony areas obtained from his maps were only 3% larger than the mean area obtained from GPS surveys. We found little evidence that the accuracy of historical drawings was greatly inferior to modern maps of the breeding colonies and this is supported by Benavide and Koster (2006) who concluded that surveyors and mapmakers in the seventeenth century could map with very high precision. Therefore, we believe that our population estimates over the long and more recent time periods can be relied upon to give a good account of population change.

Population decline of Sooty Terns: an Atlantic phenomenon?

It is possible that the decline in Sooty Terns on Ascension Island could have been compensated for by increases elsewhere. Ascension Island birds could have been displaced to other colonies within an Atlantic metapopulation, but this seems unlikely because populations have declined, not increased, elsewhere. On the Culebra Archipelago in Puerto Rico the Sooty Tern population declined by 82% between 1970–1971 and 1980–1982 (Furniss 1983). On the Dry Tortugas in Florida the population suffered an 80% decline from 380,000 in 1950 to 80,000 during 1986–1991 (Florida Fish and Wildlife Conservation Commission 2003). On St Helena (the nearest neighbour of Ascension Island) there has been an 89% decline between 1952 and 1988 (Rowlands et al. 1998). However, coupled (or decoupled) contemporaneous data showing variation in breeding population sizes at different locations tell us little (if anything) about breeding dispersal rates between different colony sites; movement data from birds that can inform demographics of Ascension Island Sooty Terns can only be derived from marking and retrapping of known individuals (e.g., Spendelow et al. 2016).

The Ascension Island population is isolated (Hughes et al. 2010, 2015) and we can only assume that the decline was the result of insufficient recruits to the breeding population to maintain population size. The impact of keeping the airfield clear of nesting birds, adverse weather conditions in 1963 and 1985, and the commencement of a commercial, foreign flagged, longline tuna fishery that started in 1988 (J. Brown, personal communication) are factors that almost certainly have contributed to the population decline but a thorough investigation of causes contributing to reduced recruitment is urgently required.

Population decline of Sooty Terns: a global phenomenon?

Given similar contemporaneous reductions in population sizes of this species elsewhere in its range, the steep declines that we have shown for Ascension Island Sooty Terns are not unexpected. Between 1950 and 2010 seabird populations worldwide have declined by 69.7% with the greatest decline occurring in pelagic species aggregating in large assemblages to breed (Paleczny et al. 2015). In the Pacific Ocean steep declines occurred in the second half of the twentieth century in the Sooty Tern breeding colony of >10 million birds on Christmas Island where >90% of adults have been lost (Schreiber et al. 2002) and in French Polynesia and South Orkney population size has declined by >95% (Paleczny et al. 2015).

Impacts of Sooty Tern population decline on the marine ecosystem?

Throughout their range, Sooty Terns gather in large numbers to breed (Schreiber et al. 2002). They are near-obligate commensals with tuna and other predatory fish that drive small pelagic fish to the surface where terns feed on them (Au and Pitman 1986). Therefore, when they numerically dominate breeding seabird communities (as Sooty Terns once did and still do on Ascension Island), they can deplete pelagic small fish reserves markedly. For example, Danckwerts et al. (2014) found that the breeding seabird population of the western Indian Ocean numbered 19 million birds, of which 85% numerically comprised Sooty Terns. They calculated that the seabird population consumed between 150,000 and 500,000 metric tons of prey with 81% of consumption by Sooty Terns. They argued that consumption of fish prey by seabirds was of the same magnitude as other modes of extraction from the marine ecosystem such as longline and purse seine landings. Sooty Terns in the mid-Atlantic will

certainly play an equivalent role in removing a significant percentage of prey from lower trophic levels of the marine ecosystem (Brooke 2004) with recent declines in their population probably having pervasive effects through mechanisms such as density dependence. We know little about how this may disrupt marine ecosystem function. Equally, however, we have not identified the cause(s) of the long-term population decline of Sooty Terns that could have followed a decline in the availability of small pelagic fish; under such circumstances, reduced numbers of Sooty Terns may not be altering fish stocks.

A re-assessment of Sooty Tern conservation status?

We estimated that between 1942 and 2005 the population size of Sooty Terns on Ascension Island declined by 84% but from 1990 until 2013 it has remained relatively constant (Fig. 3). According to IUCN Red List criteria, this reduction of the Sooty Tern population on Ascension Island of >80% over three generations, could suggest that this population should be placed in the 'Critically Endangered' category. However, the IUCN Red List Categories and Criteria (Version 3.1 2012) cautions against applying threatened categories at the global scale to regional populations because "…it must be recognized that a global category may not be the same as a national or regional category for a particular taxon. For example, taxa categorized as Least Concern globally might be Critically Endangered within a particular region where numbers are very small or declining, perhaps only because they are at the margins of their global range." (p. 12) Such precautions are clearly necessary but the population of Sooty Terns breeding on Ascension is neither small nor is this population at the margins of its global range. Moreover, although similarly robust and detailed demographic data for three generations may not be available for populations of Sooty Terns elsewhere, many populations appear to show steep declines over similar timeframes. Our Ascension Island data, plus estimates from other populations, suggest that a re-evaluation of the conservation status of Sooty Terns, based upon population trends over three generations, is needed.

Prior to our study the long-term trend in the Sooty Tern population size on Ascension Island was not known and because of the stability in the population size between 1990 and 2013, the population was not targeted by conservationists for closer scrutiny. To avoid the shifting baseline syndrome (Pauly 1995), long-lived animals need to be at the focus of long-term ecological and historical studies, such as ours on Ascension Island. Seminoff and Shanker (2008) identified major problems with the use of threatened categories when setting regional conservation management priorities for marine turtles. Their conclusion would seem to mirror our own regarding Sooty Terns.

Causes of the Sooty Tern population decline?

Many factors can have contributed to the pronounced decline that we have identified in the population of Sooty Terns breeding on Ascension Island. As with other populations of seabirds, these may include depletion of foraging resources, predation by introduced predators, mortality due to collisions with man-made structures, and direct exploitation by humans (see review by Oro 2014). In the absence of specific evidence about which parts of the breeding and recruitment cycle have been disrupted in our study population, we suggest that it would be unwise to speculate at this stage on which factors are at play. The 'Critically Endangered' categorization has often been the trigger for the investigation of causal factors leading to decline and we would hope that this will be the case for this species and population.

Acknowledgements We would like to thank members of the AOS and the other military ornithological societies in the UK for helping to census Sooty Terns on Ascension Island. We thank Robin Prytherch and Bill Bourne for surveys of the tern colony and the Porthcurno Telegraph Museum for copies of their historical photographs. We are also grateful to Stuart Riddick and Ascension Island Government staff for field data that enabled us to calculate the Sooty Tern population size in May 2010. We would like to thank two anonymous referees and the editor, Roger Jovani, for helpful comments that significantly improved the manuscript. Some financial support was received from the Royal Society for the Protection of Birds (RSPB) but this work was predominantly supported by financial contributions of participating AOS members.

Appendix 1

Eye witness accounts

Estimates of the number of Sooty Terns seen on Ascension Island by eye witnesses were collected as they can provide anecdotal support for our calculations of population size in the nineteenth and twentieth centuries. However, eye witness estimates of the numbers of Sooty Terns seen on Ascension Island are not the same as estimates of Sooty Tern population size because at any one time approximately half the Sooty Tern population are foraging at sea during the incubation period and few adults remain overseeing large assemblages of chicks. Independent eye witness estimates of the Sooty Tern population size on Ascension Island during the twentieth century are shown in Table 3.

Table 3 Details of eye witness accounts of the number of Sooty Terns in the colony on Ascension Island in the South Atlantic between 1876 and 1957

Date of estimate	Witness' name	Account	Source
1876	Sir C Wyville Thomson (Challenger expedition)	"The birds are in millions…"	Thomson (1877)
August 3, 1922	George H Wilkins (Quest expedition)	"…nesting in hundreds of thousands…"	Wilkins (1923)
1923	George F Simmons (Blossom expedition)	"…birds assembled by the millions…"	Simmons (1927)
1942	James P Chapin	"…there may possibly have been a million"	Chapin (1954)
1942–1946	Colonel J Noel Tomlinson, Island Administrator	"… cannot decide whether there are two million or only one million…"	Chapin (1946)
1957	Sir James Harford, Governor of St Helena	"…perhaps one million birds"	Harford (1958)

Breeding densities from photographs

We discovered 22 pre-1960 photographs of the Ascension Island Sooty Tern colony. To visualize historical breeding density, the reader is encouraged to inspect our collection of photographs at: http://www.armybirding.org.uk/what-we-do/ascension.

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