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Long-term dietary shift and population decline of a pelagic seabird — A health check on the tropical Atlantic?

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1	Long-term dietary shift and population decline of a pelagic seabird—A health check on
2	the tropical Atlantic?
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4	Running head Bio-indicators and marine ecosystem function
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25 nitrogen-15, *Onychoprion fuscatus*, sooty tern, South Atlantic, stable isotope

#### 26 Abstract

In the face of accelerating ecological change to the world's oceans, seabirds are some of the 27 best bio-indicators of marine ecosystem function. However, unravelling ecological changes 28 that pre-date modern monitoring programmes remains challenging. Using stable isotope 29 analysis of feathers and regurgitants collected from sooty terns (*Onychoprion fuscatus*) 30 nesting at a major Atlantic colony, we reconstructed a long-term dietary time series from 31 1890 to the present day, and show that a significant dietary shift occurred during the second 32 half of the twentieth century coinciding with an apparent population collapse of 33 approximately 84%. After correcting for the 'Suess Effect',  $\delta^{13}$ C in feathers declined by 34 ~1.5‰ and  $\delta^{15}$ N by 2‰ between the 1890s and the present day, indicating that birds changed 35 their diets markedly over the period of population decline. Isotopic niches were equally wide 36 37 before and after the population collapse but isotopic mixing models suggest that birds have grown ever more reliant on nutrient-poor squid and invertebrates as teleost fish have declined 38 in availability. Given that sooty terns rely heavily on associations with sub-surface predators 39 40 such as tuna to catch fish prey, the rapid expansion of industrialised fisheries for these species over the same period seems a plausible mechanism. Our results suggest that changes to 41 marine ecosystems over the past 60 years have had a dramatic impact on the ecology of the 42 most abundant seabird of tropical oceans, and highlight the potentially pervasive 43 44 consequences of large predatory fish depletion on marine ecosystem function.

45

### 46 1 | INTRODUCTION

Since the middle of the twentieth century, intensified human use of marine resources,
population growth and accelerating industrialization have contributed to a period of
unprecedented change in the ecology of the world's oceans. Some estimates suggest that 90%
of all large fishes in the oceans may already have been extracted (Myers & Worm, 2003) and

many of the largest fisheries in the world are considered to be under threat (Pauly & Zeller, 51 52 2016). Accelerating climate change and marine pollution have also had wide-ranging effects on marine ecosystem function (Lotze, Coll, Magera, Ward-Paige, & Airoldi, 2011), with the 53 54 pace and impacts of change continuing to increase (McCauley et al., 2015). It is estimated that ~1 billion people rely on fish for their daily diet as do 200 million people for their 55 livelihoods (Béné et al., 2016). Given that oceans sustain so many people and are so 56 57 biodiverse, it is imperative that we understand how marine ecosystems function, and how they are changing. 58

59 Seabirds act as sensitive bio-indicators for the direct and indirect effects of anthropogenic pressures on the marine environment through the study of their foraging 60 behaviour, breeding performance and demographics (Furness & Monaghan, 1987). The 61 62 longevity of seabirds, their regular censusing, and the sensitivity of focal species to changes 63 in resource availability make them invaluable 'barometers' by which the health of the marine environment can be monitored (but see Grémillet & Charmantier, 2010). Phenology and 64 65 breeding performance are known to be strongly influenced by oceanic conditions, food availability and fishing activities in both temperate (Frederiksen, Wanless, Harris, Rothery, & 66 67 Wilson, 2004) and tropical (LeCorre, 2001) waters. In the latter case, many foraging seabirds associate with cetaceans and predatory fish such as tuna (*Thunnus* spp.) that drive prey to the 68 69 surface where they are captured by plunge diving and surface feeding (Ballance & Pitman, 70 1999). Prey may be sufficiently abundant but remain unavailable to tropical seabirds without the presence of such underwater predators (Maxwell & Morgan, 2013; Veit & Harrison, 71 2017), particularly where foraging occurs over pelagic waters, far from upwelling areas or 72 73 other physical oceanographic features that naturally result in large congregations of prey at the sea surface (Au & Pitman, 1986). Global declines of large predatory fishes since the 74 middle of the twentieth century as a result of over-fishing, and lack of appropriate 75

76 management measures (Myers, Baum, Shepherd, Powers, & Peterson, 2007; Juan-Jordá, 77 Mosqueira, Cooper, Freire, & Dulvy, 2011), may therefore have had significant impacts on the ecology of tropical oceanic seabirds. Other drivers of global environmental change may 78 79 also have impacted on seabird foraging success and demography. For example, ocean warming has been linked to changes in prey population dynamics (Howells et al., 2017), and 80 range shifts of both forage fish and pelagic predators in temperate and tropical oceans (e.g. 81 Perry, Low, Ellis, & Reynolds, 2005; Monllor-Hurtado, Pennino & Sanchez-Lizaso, 2017), 82 potentially diminishing food availability to seabirds through reductions in both prey 83 84 availability and accessibility (e.g. Howells et al., 2017). Studies of contemporary seabird diets, breeding success and population dynamics 85 have provided valuable data on threats currently facing marine ecosystems. However, 86 87 changes to such ecosystems may have occurred that pre-date modern monitoring 88 programmes. Here, we use a historical ecology approach to investigate how long-term changes to marine food webs have influenced the foraging ecology of the world's most 89 90 abundant tropical seabird, the sooty tern (Onychoprion fuscatus) at the Atlantic's largest nesting colony on Ascension Island (Hughes, Martin, Giles, & Reynolds, 2017a). Sooty terns 91 are long-lived (in some cases >38 years old; Schreiber et al., 2002), pan-tropically distributed 92 (Schreiber et al., 2002), and near-obligate commensals of tuna and other sub-surface 93 94 predators (Au & Pitman, 1986), making them ideal indicators of the status of tropical marine 95 ecosystems. The species is currently regarded as of 'Least Concern' by the IUCN owing to a healthy global population of 21–25 million birds (species account retrieved from 96 http://datazone.birdlife.org). Nevertheless, a number of sizeable populations have declined 97 98 markedly (reviewed in Hughes et al., 2017a), including that at Ascension Island. Hughes et al. (2017a) compared the breeding population size of sooty terns on the island between 1950 99 and the present day, observing that since 1958, when there were an estimated 3.32 million 100

birds, it declined by 84% to estimates of 350,000 individuals in 2013. This mirrors the
estimated 69.7% decline in the global seabird population between 1950 and 2010 (inclusive)
calculated by Paleczny, Hammill, Karpouzi and Pauly (2015) based upon data from 3,213
breeding populations of 324 seabird species. Such declines in sooty tern numbers on
Ascension Island are unprecedented; earlier estimates of the population in 1877 and 1942
suggested it contained 2.43 and 2.35 million birds, respectively (Hughes et al., 2017a).

Here, we investigate whether the steep decline in the size of the breeding population 107 of sooty terns on Ascension Island can be related to changes in their diet. Since it is 108 109 impossible to observe birds' foraging behaviour directly at sea, stable isotope analysis (SIA) was used to reconstruct diets from isotopic values of contour feathers grown over many 110 months prior to their collection from each bird. Once formed, feathers are inert metabolically 111 112 and their composition therefore reflects food consumed at the time of growth (Ramos, González-Solís, Croxall, Oro, & Ruiz, 2009). To investigate how diets have changed over 113 decadal scales, we plucked contour feathers from museum specimens of adult breeding sooty 114 terns collected from the island between 1890 and 1972, and from fresh corpses or live birds 115 captured on the colonies between 2006 and 2012. A similar approach has been successfully 116 used in previous studies to reconstruct historical seabird diets (e.g. Hilton et al., 2006; Norris, 117 Arcese, Preikshot, Bertram, & Kyser, 2007; Blight, Hobson, Kyser, & Arcese, 2015). 118

We studied the foraging behaviour and ecology of sooty terns by examining whether their: (i) feather isotopic values change, (ii) isotopic niches overlap, and (iii) diet composition changes either side of their population collapse. We discuss dietary reconstructions from feathers in the context of fundamental changes in marine food webs that have occurred across the same period, in particular the global declines in large predatory fish upon which sooty terns are almost wholly dependent to forage successfully. Finally, we discuss how findings may shape marine conservation initiatives in the future.

#### 127 2 | MATERIALS AND METHODS

#### 128 2.1 | Study area and species, and the seabird community

The study was carried out on Ascension (07°57'S, 14°24'W), a 97 km<sup>2</sup> volcanic island that is 129 isolated in the tropical South Atlantic with its nearest neighbour being the island of St Helena 130 1,300 km to the south-east. The territory contains several Important Bird Areas (IBAs), 131 including the sooty tern nesting grounds at the 'Wideawake Fairs' (IBA SH009) (site 132 description retrieved from http://datazone.birdlife.org), and provides the only breeding 133 134 location for significant numbers of sooty terns in the central, tropical Atlantic Ocean (Hughes et al., 2017a). A detailed account of the breeding biology of sooty terns on the island is 135 provided by Ashmole (1963a). The seabird community on Ascension Island has been heavily 136 137 impacted by predation by invasive species (e.g. domestic cats [Felis silvestris catus]; Hughes, Martin, & Reynolds, 2008; common mynas [Acridotheres tristis]; Hughes, Martin, & 138 Reynolds, 2017b). Declines in the size of seabird populations were so steep that they 139 provoked a seabird restoration project in 2002 by the Royal Society for the Protection of 140 Birds (RSPB) that aimed to promote recovery of former large and diverse seabird populations 141 (Pickup, 1999). It has been partially successful (Ratcliffe et al., 2010) but the sooty tern 142 population has continued to struggle in its recovery (Figure 1), despite the eradication of feral 143 cats (Hughes et al., 2017a). 144

145

# 146 **2.2 | Feather sampling**

Terns typically moult and breed mutually exclusively (Ashmole, 1963b) but only on
Ascension Island do individual sooty terns breed sub-annually (Reynolds, Martin, Dawson,
Wearn, & Hughes, 2014); they start their post-nuptial (basic) moult (when all feathers are
replaced) when still breeding (Ashmole, 1963b). Therefore, contour feathers provide a dietary

record of birds in the latter stages of breeding and on migration. Skins were located by 151 searching museum databases (e.g. https://arctos.database.museum/, http://www.ornisnet.org/, 152 http://www.vertnet.org/), leading to correspondence with museum curators on five continents 153 (Table S1). In total, 187 skins were located (Table S2). SJR either travelled to museums to 154 collect feathers or sent instructions to curators to ensure that sampled feathers were from 155 equivalent breast areas on all specimens. Contour feathers were also obtained from dead birds 156 that had collided with radio masts on Ascension Island and from live birds during ringing on 157 the island (Table S2). For each sample a pair of contour feathers was collected from both the 158 159 left- and right-hand sides of the breast in its mid-zone ~3 cm on either side of the keel ridge. Feathers were stored in a domestic refrigerator prior to SIA. 160

161

# 162 **2.3 | Food sources for diet reconstruction**

Sooty terns breeding on the island are on migration for at least six months of every sub-163 annual cycle (Ashmole, 1963a) and thus cannot be observed directly feeding at sea. 164 Furthermore, no regurgitant samples were available from birds in museum collections. 165 Schreiber et al. (2002) described their diet as containing small (teleost) fish such as halfbeaks 166 (Oxyporhamphus micropterus), blue flying fishes (Exocoetus volitans), redlip blennies 167 (Ophioblennius atlanticus), Simony's frostfishes (Benthodesmus simonyi) and hairtails 168 (Trichiurus spp.) (Ashmole, 1963a), and squid (Teuthida). Their diet when breeding can be 169 170 readily reconstructed from regurgitant samples when sooty terns are handled; their regurgitated prey is far less digested than that from other seabird species (Ashmole & 171 Ashmole, 1967). In 2012 during ringing of breeding adults we (i.e. SJR, BJH, CPW and 172 173 RCD) noted a more catholic diet in birds that rarely regurgitated fish but more often violet sea snails (Janthina janthina), megalops (a larval stage) of Sally Lightfoot crabs (Grapsus 174 grapsus), and locusts (Acrididae spp.) (Figure S1). While regurgitant samples from breeding 175

birds are not truly reflective of their diet during the sub-annual cycle, breeding birds travel
hundreds of kilometres out to sea when foraging (Soanes, Bright, Brodin, Mukhida, & Green,
2015; Neumann, Larose, Brodin, & Feare, 2018; JB, unpubl. data), and thus likely contain
similar prey to those consumed by birds between breeding seasons.

180

# 181 **2.4 | Stable isotope analysis**

We performed SIA on contour feathers for  $\delta^{13}C$  ( $^{13}C/^{12}C$ ) and  $\delta^{15}N$  ( $^{15}N/^{14}N$ ) to estimate the 182 foraging habitat and trophic positioning of birds. Carbon is enriched by ~0.8‰ in coastal or 183 184 benthic areas in relation to offshore or pelagic foraging areas whereas nitrogen is enriched at each successive trophic level by 2–5‰ (Quillfeldt, McGill, & Furness, 2005). Contour 185 feathers retain dietary information of birds in the year of feather collection (Inger & Bearhop, 186 2008) with all feathers of breeding sooty terns on Ascension Island moulted sub-annually 187 (Ashmole, 1963b). To determine  $\delta^{13}$ C and  $\delta^{15}$ N of each of four prey groups (*n* = 15 in each 188 group), we used: (i) muscle of teleost fish species (false halfbeaks [Oxyporhamphus similis], 189 blue flying fishes, redlip blennies and Simony's frostfishes), (ii) squid (Teuthida), (iii) marine 190 invertebrates (Sally Lightfoot crabs and violet sea snails), and (iv) terrestrial invertebrates 191 (locusts), from regurgitations of birds when handled and prey dropped by flying birds at the 192 breeding colonies. Small samples (~10 g) of these prey were dried at 60°C for 48 hours in an 193 oven (Heratherm<sup>TM</sup> General Protocol Oven, Thermo Scientific, Waltham, MA, USA) and 194 then ground into powder using a mixer mill (MM400, Retsch, Leeds, UK). Powder was 195 rinsed five times (10 minutes per rinse) in 2:1 chloroform:methanol (Sigma-Aldrich, St. 196 Louis, MO, USA) to extract lipids prior to SIA (Kojadinovic, Richard, Le Corre, Cosson, & 197 Bustamante, 2008). Because lipid extraction might change the  $\delta^{15}$ N values, separate samples 198 of each of the main prey items were analysed for  $\delta^{13}$ C (subjected to lipid extraction) and  $\delta^{15}$ N 199 (without lipid extraction) values (Kojadinovic et al., 2008). The C:N ratio was used to assess 200

201 the effectiveness of the delipidation process. To remove surface contaminants each feather 202 was washed three times (5 minutes per wash) in a 2:1 chloroform:methanol solution. Feather 203 and dietary samples were then dried at 60°C for 48 hours (as above) with feathers then cut 204 into small fragments. The carbon and nitrogen isotopic composition of samples was 205 determined by mass spectrometry (Thermo Delta VS, ThermoFisher Scientific, Waltham, 206 MA, USA). Replicate measurements of internal laboratory standards (acetanilide) indicated a 207 precision of <0.2‰ for both  $\delta^{13}$ C and  $\delta^{15}$ N.

Since the Industrial Revolution the burning of fossil fuels has a lower  $\delta^{13}$ C than background carbon causing an exponentially accelerating decrease of  $\delta^{13}$ C in the biosphere – the so-called 'Suess Effect' (Keeling, 1979). In addition, the increase in atmospheric CO<sub>2</sub>, and thus aqueous CO<sub>2</sub>, has increased phytoplankton fractionation, reducing its  $\delta^{13}$ C values (Rau, Takahashi, Des Marais, Repeta, & Martin, 1992). Thus, raw  $\delta^{13}$ C values of sooty tern feathers were adjusted following Hilton et al. (2006), Jaeger and Cherel (2011), and Carravieri, Cherel, Jaeger, Churlaud and Bustamante (2016).

215

#### 216 **2.5 | Data analyses**

All statistical analyses were carried out in R (Version 3.01) (R Development Core Team, 217 2016). To test if the trend in  $\delta^{13}$ C and  $\delta^{15}$ N before and after the population collapse differed 218 significantly we ran linear mixed-effect models (LMMs) (lme4 R library; Bates, Mächler, 219 Bolker, & Walker, 2015) to control for uneven sample sizes between decades (i.e. with 220 'decade' included as a random effect). They tested the effect of: (i) decade (1890, 1920, 221 1940, 1970, 2000 and 2010), and (ii) the decade × period (1980–1940 vs. 1970–2010) 222 interaction on the  $\delta^{13}$ C and  $\delta^{15}$ N values. The decade × period interaction was included to test 223 for differences in slopes between the two time periods. We randomly selected 50 values from 224 the 104 samples of the 1920 decade to run the models to ensure that this decade was not over-225

represented in terms of sample size compared to the others. All values are presented as the
mean ± 1 SD unless otherwise stated. Residuals were tested for normality (Q-Q plots) and
homogeneity (Cleveland dotplots) before each statistical test; they were transformed when
required (Zuur, Ieno, & Elphick, 2010). All analyses were performed using an alpha
threshold of .05.

The Stable Isotope Bayesian Ellipses in R (SIBER; Jackson, Inger, Parnell, & 231 Bearhop, 2011) package was used to establish the isotopic niche width of birds, based on 232 isotopic values of feathers before (i.e. between 1890s and 1940s) and after (i.e. between 233 234 1970s and 2010s) the population collapse. The standard ellipse area after small sample size correction (SEA<sub>C</sub>) measure was used to compare estimated isotopic niches between the two 235 periods. This is an ellipse that has 40% probability of containing a subsequently sampled 236 237 datum regardless of sample size. We used the Bayesian estimate of the standard ellipse and its area (SEA<sub>B</sub>) measure to test for differences between the two periods by comparing p (the 238 proportion of ellipses) before with that after the population collapse, for  $10^4$  replicates (see 239 240 Jackson et al., 2011 and Parnell et al., 2013 for further details). All metrics were calculated using *standard.ellipse* and *convexhull* functions from the SIBER R package. 241

Dietary composition of birds was estimated from isotopic values of feathers and their 242 prey using a Bayesian multisource stable isotope mixing model (SIAR; Parnell & Jackson, 243 2011). The proportions of the four main dietary items (fish, squid, marine invertebrates and 244 terrestrial invertebrates) between the two study periods (1890s-1940s and 1970s-2010s) were 245 compared with a Chi-square test. This allowed us to assess the birds' trophic position for the 246 periods of 1890s to 1940s and of 1970s to 2010s. Since there are no diet-blood trophic 247 discrimination factors (TDFs) available for sooty terns, we applied mean enrichment factors 248 generally accepted for seabirds of 1 and 3% to  $\delta^{13}$ C and  $\delta^{15}$ N values, respectively, between 249 each prey group and feathers (Caut, Angulo, & Courchamp, 2009; Kelly, 2000). A SD of ± 250

1.0% was taken into account, considering potential differences in fractionation factors among 251 species. To test the robustness of this approach we: (i) ran a sensitivity analysis (after Inger et 252 al., 2006) that revealed model outputs varied by a maximum of 4% when TDFs varied by 1– 253 2‰ for  $\delta^{13}$ C and 3–5‰ for  $\delta^{15}$ N values, and (ii) used the discrimination estimation (DEsiR) 254 functions in the Stable Isotope Discrimination Estimation in R (SIDER; Healy et al., 2017) 255 package to estimate TDF values for sooty terns. It compares isotopic values of our study 256 species with those of others in a large database of reported TDF values and, based on 257 phylogenetic relatedness, it uses Bayesian imputation methods to calculate the most likely 258 TDF values. It estimated modal values of 1.1% and 2.8% for  $\delta^{13}$ C and  $\delta^{15}$ N, respectively, a 259 deviation of only  $\sim 1.1\%$  from the TDFs we chose. Therefore, it validated our approach. 260

261

#### 262 **3 | RESULTS**

#### 263 **3.1** | Temporal trends in isotopic values

There were significant temporal trends in both carbon and nitrogen isotopic values of feathers 264 across the decades from 1890 to 2010. Carbon isotopic values of feathers from the 2010s 265 were significantly lower than those of feathers collected from birds in the 1970 and 2000 266 decades which, in turn, were lower than those of feathers from museum skins collected 267 between the 1890s and 1940s (Figure 2a; Table 1). The nitrogen isotopic values of feathers 268 from birds sampled in the field in the 2000 and 2010 decades were significantly lower than 269 270 those in feathers of museum specimens collected in the 1920s and 1940s which, in turn, were lower than those from the 1890s (Figure 2b; Table 1). Moreover, the decrease in the slope of 271 models for both carbon and nitrogen isotopic values was steeper for the 1970-2010 period of 272 decades following the population collapse compared to the 1890–1940 period of decades 273 preceding it, as shown by the significantly negative decade × period interaction (Table 1). 274 275

#### 276 **3.2** | Isotopic niche widths

The isotopic niche widths of birds reconstructed from isotopic values of feathers collected in decades before (1890s–1940s) and after (1970s–2010s) the population collapse were similar (SEA<sub>C</sub>: before – 0.97; after – 0.88; SEA<sub>B</sub>: *p* value = .43; see **Materials and methods** for further details). There was no overlap in these isotopic niches between these periods although the niches of birds decreased both in  $\delta^{13}$ C and  $\delta^{15}$ N values from the former to the latter period (Figure 3).

283

# 284 3.3 | Isotopic values of prey and reconstructed diets of birds across decades of sampling The mean $\delta^{13}$ C and $\delta^{15}$ N values differed between prev categories – fish, squid, marine 285 invertebrates and terrestrial invertebrates (Figure 4). The C:N mass ratios for fish (3.01), 286 287 squid (2.87), marine (3.12) and terrestrial invertebrates (2.77) were similar indicating the delipidation treatment (Materials and methods) was equally as effective across all prey 288 samples. According to dietary estimates provided by the isotopic mixing models, birds 289 underwent a dietary shift between the decades in the 1890s-1940s period, when they fed 290 significantly more on fish prey (mean relative contributions: fish -0.62; squid -0.26), and 291 those in the 1970s–2010s period, when they fed significantly more on squid (fish -0.26; 292 squid – 0.57; Chi-square test: $\chi^2_3 = 28.30$ , p value < .001) (Figure 5). Moreover, 293 accompanying a more squid-dominated diet were marine and terrestrial invertebrates that 294 constituted greater proportions of birds' diets in the 1970s-2010s period (marine 295 invertebrates -0.08; terrestrial invertebrates -0.11) compared with the 1890s–1940s period 296 (marine invertebrates -0.06; terrestrial invertebrates -0.04) (Figure 5). 297 298

299 4 | DISCUSSION

Significant declines were found in both the  $\delta^{13}$ C and  $\delta^{15}$ N values of contour feathers collected 300 over the 120-year study period (Figure 2a and b), indicating that the diets of these sooty terns 301 have changed over a period when breeding population size has declined markedly (Figure 1). 302 303 Inferred foraging niches of sooty terns before (1890s-1940s) and after (1970s-2010s) the population collapse did not overlap, despite widths being similar (Figure 3). Isotopic mixing 304 models indicated that this was due to a significant decrease in the proportion of teleost fish in 305 the diet (from 0.62 pre-1950 to 0.26 post-1970) and a corresponding increase in the 306 proportion of squid (from 0.26 to 0.57), and of marine and terrestrial invertebrates (from 0.06 307 308 and 0.04 to 0.08 and 0.11, respectively) (Figure 5). Field observations of breeding sooty terns on Ascension Island also suggest that the 309 proportion of fish in their diets has declined since the middle of the twentieth century, 310 311 decreasing from 0.60 in 1958–1959 (Ashmole & Ashmole, 1967), to 0.50–0.60 in 1972 (Johnston, 1973) and to only 0.17 in 2004 (Hughes, 2014). In 2012 birds were predominantly 312

feeding on squid and other low energy content foods, reflecting the struggle to locate fish

prey. These observations support our SIA findings (Figure 5) and provide further evidence of

a dietary shift. A similar dietary shift by breeding sooty terns was observed in the Dry

Tortugas (FL, USA) 8,000 km away from Ascension Island: between 1920 and 1941 squid

were absent from diets but they were a common dietary constituent between 1992 and 1994(Colchero, 2008).

We worked with museum skins primarily because they extended the study beyond the period for which reliable field observations of sooty terns on Ascension Island were available. However, the number of years for which feathers were available for analysis (*n* = 11) was necessarily restricted to those when museum collectors and field ornithologists made visits to the island. Unfortunately, a lack of prey specimens in museums collected contemporaneously with these visits also results in an unavoidable temporal mismatch

between dietary samples and feathers used in our SIA (a known limitation when using 325 isotopic mixing models; Inger & Bearhop, 2008). Stable isotope analysis lends itself well to 326 dietary reconstruction of seabirds using museum specimens (Barrett et al., 2007), but without 327 328 access to historical prey too, it is difficult to know whether the isotopic prey composition remained constant over the period of study (Bond & Jones, 2010). Some caution is therefore 329 required when interpreting our results. Although we acknowledge that temporal and spatial 330 changes in the stable isotopic values at the base of the food webs could partly explain the 331 changes we found in isotopic values of feathers, there is evidence to suggest that processes 332 333 driving the distribution of carbon and nitrogen stable isotope values are temporally stable over relatively large spatial scales (e.g. MacKenzie, Longmore, Preece, Lucas, & Trueman, 334 2014). 335

336

337 4.1 | What has caused the dietary shift?

The middle part of the twentieth century, during which the dietary shift apparently occurred, 338 marked the beginning of a period of major change in the world's oceans with the expansion 339 of industrialised fishing and an acceleration of anthropogenic climate change dramatically 340 altering marine food webs (Estes et al., 2011). Shifts in diet from predominantly fish to a 341 greater dependence on less nutritious prey such as squid have been reported regularly in 342 seabird species over the past 50 years, and have often been attributed to the direct depletion 343 344 of forage fish by fisheries (see Kowalczyk, Chiaradia, Preston, & Reina, 2014 and references therein). In the case of sooty terns, no commercial fisheries exist for the small, pelagic 345 species typically found in their diet. However, the rapid growth of commercial fisheries for 346 tuna and other large-bodied, predatory species since the 1960s may have caused a similar 347 effect on prey availability through the disruption of foraging associations on which terns 348 depend to locate and catch fish at the surface (Au & Pitman, 1986; Veit & Harrison, 2017). 349

350 While many large predatory fish are opportunistic foragers (Cherel, Sabatié, Potier, Marsac,

351 & Ménard, 2007), a large proportion of their diet can comprise fish species (e.g. Dragovich &

Potthoff, 1972; Potier et al., 2007) with inevitably other fish species also driven to the surfaceas they hunt.

According to some estimates, the abundance of large pelagic fish in tropical 354 international waters has declined by ~90% over a 50-year period (Safina, 2003), including 355 substantial reductions in the biomass of surface-schooling tunas such as yellowfin (Thunnus 356 albacares) and skipjack (Katsuwonus pelamis) in the Atlantic (Cullis-Suzuki & Pauly, 2010; 357 358 Juan-Jordá et al., 2011). Total nominal catches of these species in the eastern tropical Atlantic (ETROP), where sooty terns from Ascension Island are known to forage extensively (SJR, 359 unpublished data), increased 15-fold since the 1940s, when 0.10 M tonnes were landed, to the 360 361 1970s when 1.67 M tonnes were extracted. A peak of 2.04 M tonnes was landed during the 2000s (International Commission for the Conservation of Atlantic Tunas [ICCAT]; 362 https://www.iccat.int/en/accesingdb.HTM; Figure 6a). Note that data for the 2010s were only 363 364 available to 2014. With fewer sub-surface predators to associate with, terns may have had to rely more heavily on alternative modes such as feeding at night when squid rise to the top of 365 the water column (Ashmole & Ashmole, 1967), or exploiting less mobile prey from lower 366 trophic levels (e.g. invertebrates), as indicated by declines in  $\delta^{15}$ N values of feathers (Figures 367 2b and 3). In addition to reducing the availability of fish prey, declining predator populations 368 369 may have increased availability of alternative food items that are now more common in the diet of sooty terns (e.g. see Emslie, Polito, & Patterson, 2013). For example, global 370 populations of cephalopods have increased dramatically in the past 60 years (Doubleday et 371 al., 2016) with the loss of their major predators, resulting in foraging terns perhaps now 372 encountering squid far more frequently. 373

The availability of fish prey to adult seabirds may also be strongly influenced by 374 ocean warming and associated environmental change that can significantly impact their 375 foraging success (e.g. Howells et al., 2017). In the case of sooty terns, changes in diet 376 377 composition could be mediated through shifts in the range and behaviour of forage fish (Perry et al., 2005), and of the pelagic predators they associate with (e.g. Kitagawa et al., 2000; 378 Hazen et al., 2013). Mean annual sea surface temperature anomaly (SSTa) in the waters 379 surrounding Ascension Island increased by ~0.80°C from the 1890s to the 2010s, with the 380 biggest increase (by  $\sim 0.55^{\circ}$ C) occurring between the 1970s and the 2010s (UK 381 382 Meterological Office Hadley [HadISST1]; http://www.metoffice.gov.uk/hadobs/hadisst/; Rayner et al., 2003; Figure 6b). It is possible that changes in the distribution or behaviour of 383 forage fish and large marine predators may therefore have occurred as a result of ocean 384 warming, particularly in the last 40 years. There appears to be a strong relationship between 385 declining  $\delta^{15}$ N isotopic values of feathers (Figure 2b) and increasing SSTa (Figure 6b) that 386 suggests that birds are responding to changes in prey availability and accessibility in warming 387 388 foraging areas through changes in diet. However, given the high mobility of sooty terns and their extensive foraging range during inter-breeding periods (Schreiber et al., 2002; SJR, 389 unpublished data), it seems likely that they would have been able to track any regional shifts 390 in distributions of prey or feeding associates. 391

Given the timescales involved, unravelling the precise causes of the observed dietary
shift is likely to be challenging. Applying a similar 'historical ecology' approach (e.g. Wu,
Liu, Fu, Xu, Li, & Li, 2017) using SIA to other species in Ascension Island's seabird
community that are less dependent on 'facilitated foraging' (Maxwell & Morgan, 2013) (e.g.
noddies [*Anous* spp.] and tropicbirds [*Phaethon* spp.]) may help to determine the extent to
which observed changes have been driven by the disruption of feeding associations as
opposed to more general changes in prey availability (Gagne, Hyrenbach, Hagemann, & Van

Houtan, 2018). Nevertheless, it is apparent that a fundamental shift in the diet of sooty terns
at Ascension Island has occurred over the past 60 years which most likely has its roots within
anthropogenic disturbances to marine food webs over the same period.

402

#### 403 **4.2** | Can the dietary shift explain population decline?

Undoubtedly invasive species have impacted on the breeding success and demographics of 404 405 sooty terns on the island (Stonehouse, 1962; Hughes et al., 2017b; Hughes, Dickey, & Reynolds, In press). Domestic cats, black rats (Rattus rattus) and common mynas were all 406 407 introduced to Ascension Island during the eighteenth and nineteenth centuries and depredate incubating adults, chicks and eggs (cats were later eradicated in 2001–2004). However, none 408 of these introductions was coincidental with the apparent population decline of sooty terns 409 410 (Figure 1), nor is there evidence that populations of these species reached critical levels at around that time. Rats were reported as being highly abundant on the island in 1725 411 (Ritsema, 2006) but were rarely seen in low-lying areas in the mid-twentieth century 412 (Ashmole, 1963a and other reports), perhaps due to the influence of cats which had been 413 introduced in 1815 to control their numbers. Predation by cats was also a persistent threat to 414 seabirds throughout the nineteenth century during which time many of the island's resident, 415 ground-nesting species were eradicated from the mainland (Stonehouse, 1962). As such, 416 invasive species do not satisfactorily explain the reported collapse in sooty tern numbers 417 418 during the middle part of the twentieth century and nor is it straightforward to estimate their relative impacts. 419

The link between diet and breeding success has been well established in numerous seabird species (e.g. see Kowalczyk et al., 2014 and references therein), particularly with regard to the lipid/energetic content (Wanless, Harris, Redman, & Speakman, 2005). With reduced teleost fish consumption, terns have had to rely on an increasingly low quality diet of

squid and invertebrates which is considerably lower in lipid and may often fail to meet 424 energetic demands of breeding. Limited data are available on the breeding success of sooty 425 terns prior to their population collapse but years of low productivity have occurred (Ashmole, 426 427 1963a) and years of high breeding success still occur now (Hughes, 2014). Variation in food availability and breeding success is typical in seabirds, and most of these long-lived species 428 are able to survive recruitment gaps or occasional breeding failures linked to environmental 429 stochasticity. However, Cury et al. (2011) identified a threshold in prey availability 430 (corresponding to  $\sim^{1}/_{3}$  of maximum biomass) beyond which seabird breeding success is 431 432 consistently compromised, potentially precipitating population collapses such as those experienced on Ascension Island and elsewhere. 433

It is noteworthy that while populations of many pelagic predators have continued to 434 435 decline in recent decades (Cullis-Suzuki & Pauly, 2010) and ocean warming has continued to 436 accelerate, this trend has not been paralleled by a sustained decline in numbers of sooty terns as might be expected if it was wholly attributable to an environmentally-mediated shift in 437 diet. Instead, the tern population has apparently stabilised in size (Figure 1). Conservation 438 measures on the breeding grounds such as the eradication of feral domestic cats from 439 Ascension Island in 2002 (Ratcliffe et al., 2010) have likely promoted adult and chick 440 survival and may have offset pressures on food availability. It is also possible that the 441 population has reached a new, reduced carrying capacity that can be maintained within the 442 443 altered marine food web. So-called 'regime shifts' between alternative stable states are a common feature of marine ecosystems (deYoung et al., 2008) and can be triggered by climate 444 events and over-fishing of top predators resulting in system-wide trophic cascades (Daskalov, 445 Grishin, Rodionov, & Mihneva, 2007; deYoung et al., 2008). Our results suggest that the 446 historical sooty tern population decline on Ascension Island may be at least partly explained 447

by a fundamental change in diet over the same period driven by ecosystem-wide changesaffecting the tropical Atlantic (Ostrom et al., 2017).

450

#### 451 **4.3** | Implications for marine conservation

Seabirds represent key bio-indicators of marine ecosystem status (Furness & Greenwood, 452 1993), and sooty terns are no exception. Their steep population decline over approximately 453 the last 30 years on Ascension Island is mirrored to a lesser extent elsewhere in their range 454 (reviewed in Hughes et al., 2017a). These declines are indicative of a widespread and 455 456 consistent pressure on the ecology of the species as evidenced in the long-term dietary shift in our dataset. Indeed, similar long-term dietary shifts have been reported in various seabirds 457 (e.g. Hilton et al., 2006; Wiley et al., 2013), often associated with population decline (e.g. 458 459 Hilton et al., 2006), suggesting that our findings are symptomatic of wider pressures impacting marine ecosystems. The close correspondence between historical shifts in the diet 460 and population status of sooty terns, and the expansion of industrial fisheries into the areas 461 462 where they forage serves to highlight further the potentially cascading impacts of predatory fish depletion for marine ecosystem function and adds further urgency to the need to secure 463 sustainable fisheries for these species. The announcement of a large-scale marine reserve to 464 be designated in the waters surrounding Ascension Island by 2019 may go some way to 465 improving the status of our study population. However, given the wide distribution and 466 467 considerable mobility of both sooty terns and of the species with which they associate, it is likely that ocean-scale solutions will be needed to reinstate past food webs and reverse 468 historical declines. 469

470

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# 746 Tables

747

- **TABLE 1** Summary table of linear mixed-effect models (LMMs) explaining trends in carbon ( $\delta^{13}$ C) and nitrogen ( $\delta^{15}$ N) isotopic values of feathers from sooty terns sampled from decades within two periods before (1890s–1940s) and after (1970s–2010s) their population collapse
- 751 on Ascension Island in the South Atlantic

	Estimate	SE	$F_{(5,120)}$	p value
$\delta^{13}C$				
Decade	-0.43	0.13	4.19	.04
Decade × Period	-0.14	0.07	7.50	.01
$\delta^{15}N$				
Decade	-0.38	0.19	11.32	.002
Decade × Period	-0.10	0.03	6.16	.02

#### 753 **Figure captions**

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768

755	FIGURE 1 Estimated numbers (+ 95% confidence limits) of sooty terns breeding on
756	Ascension Island in the South Atlantic from 29 censuses that took place before (three
757	predators; filled bars) and after (two predators; open bars) the cat eradication programme.
758	Note that spaces have been inserted between the bars on the left to highlight the irregularity
759	of censuses. Note also that the sub-annual breeding cycle results in birds breeding twice in
760	1996, 2004, 2008 and 2012 when two censuses took place
761	
762	<b>FIGURE 2</b> Box and whisker plots showing (a) carbon ( $\delta^{13}$ C) and (b) nitrogen ( $\delta^{15}$ N) isotopic
763	values (median, 25–75% inter-quartile range, non-outlier range and outliers) of feathers from
764	sooty terns breeding on Ascension Island in the South Atlantic in different decades (see text
765	for further details). The $\delta^{13}$ C values are corrected for the 'Suess Effect' following Hilton et al.

769

Island sooty tern population (Hughes et al., 2017a)

(2006). Sample sizes of birds are indicated within brackets. In both plots the grey shading

represents the transition between before and after the population collapse of the Ascension

**FIGURE 3** Bivariate plots of  $\delta^{15}$ N against  $\delta^{13}$ C demonstrating the isotopic niche areas 770 reconstructed from SIA of feathers from sooty terns breeding on Ascension Island in the 771 South Atlantic in decades before (1890s–1940s) and after (1970s–2010s) their population 772 collapse (Hughes et al., 2017a). The Standard Ellipse Areas corrected for small sample size 773 (SEA<sub>C</sub>s) are represented by the solid lines (see Parnell et al., 2013 for more details on these 774 metrics of isotopic niche width based on SIA) 775

776

FIGURE 4 Stable isotope bi-plot of carbon-nitrogen (mean ± 1 SD) showing the isotopic
values of the four main prey groups in the diet of sooty terns from Ascension Island in the
South Atlantic: teleost fish species (false halfbeaks, blue flying fishes, redlip blennies and
Simony's frostfishes), squid (Teuthida), marine invertebrates (Sally Lightfoot crabs and
violet sea snails), and terrestrial invertebrates (locust species) (see Figure S1)

782

FIGURE 5 Estimated contributions of each of the four prey groups (teleost fish species [false 783 halfbeaks, blue flying fishes, redlip blennies and Simony's frostfishes], squid [Teuthida], 784 785 marine invertebrates [Sally Lightfoot crabs and violet sea snails], and terrestrial invertebrates [locust species]; see Figure S1) to the diet of sooty terns breeding on Ascension Island in the 786 South Atlantic in decades (a) before (1890s-1940s) and (b) after (1970s-2010s) their 787 788 population collapse (Hughes et al., 2017a). Contributions are presented by dietary proportions as calculated with SIAR (95, 75 and 50% credibility intervals) using  $\delta^{13}$ C and  $\delta^{15}$ N values of 789 adult contour feathers and of their main prey 790

791

**FIGURE 6** (a) Historical trends in tuna catches (in millions of tonnes [t]) in the east tropical

793 Atlantic Ocean (see https://www.iccat.int/en/accesingdb.HTM for further details), and (b)

mean (+ 1 SD) sea surface temperature anomaly (SSTa) within a 1,000 km buffer

surrounding Ascension Island (data retrieved from

http://www.metoffice.gov.uk/hadobs/hadisst/). In both plots the grey shading represents the

transition between before and after the population collapse of the Ascension Island sooty tern

population (Hughes et al., 2017a). During the collapse there was a 15-fold increase in

skipjack and yellowfin tuna catches for the eastern tropical Atlantic region in the 1970s and a

800 five-fold increase in the average SSTa until the 2010s

801



**Figure 1.** 



**Figure 2.** 





**Figure 4.** 



**Figure 5.** 







# Supporting information

**TABLE S1** Details of museums and their curators who assisted with initial enquiries about

- specimens of sooty tern skins collected from Ascension Island in the South Atlantic

Name of museum	Location	Name(s) of curator(s)
American Museum of Natural History	New York, NY, USA	Mary LeCroy, Merle Okada, Paul Sweet, and Tom Trombone
Australian Museum	Sydney, NSW, Australia	Walter Boles
Bombay Natural History Society	Mumbai, India	Rahul Khot
Conner Museum	Washington State University, Pullman, WA, USA	Kelly Cassidy
Delaware Museum of Natural History	Wilmington, DE, USA	Jean Woods
Denver Museum of Nature & Science	Denver, CO, USA	Jeff Stephenson
Florida Museum of Natural History	Gainesville, FL, USA	Dave Johnston and Tom Webber
Great North Museum-Hancock Collection	Newcastle upon Tyne, UK	Dan Gordon
Fundación Miguel Lillo	Tucumán, Argentina	Ada Echevarria
Instituto Nacional de Pesquisas da Amazônia	Manaus, Brasil	Mario Cohn-Haft
Museum of Comparative Zoology	Harvard Museum, Boston, MA, USA	Alison Pirie and Jeremiah Trimble
Museum of Natural Science	Jackson, MS, USA	Nick Winstead
Museum of Natural Science	Louisiana State University, Baton Rouge, LA, USA	Steve Cardiff and James van Remsen
National Museum of Ireland- Natural History Division	Dublin, Ireland	Nigel Monaghan
National Museum of Natural History-Collection of Birds	Paris, France	Jérôme Fuchs and Marie Portas
National Museums Liverpool	Liverpool, UK	Tony Parker
National Museums Scotland	Edinburgh, UK	Bob McGowan
Natural History Museum- Bird Group	Tring, UK	Mark Adams and Robert Prys-Jones
Natural History Museum of Denmark	Copenhagen, Denmark	Jon Fjeldså
Natural History Museum of Los Angeles County	Los Angeles, CA, USA	Kimball Garrett
Natural History Museum- University of Oslo	Oslo, Norway	Jan Lifjeld
Oxford University Museum of Natural History	Oxford, UK	Malgosia Nowak-Kemp
Peabody Museum of Natural History	Yale University, New Haven, CT, USA	Rick Prum and Kristof Zyskowski
Royal Museum for Central Africa	Tervuren, Belgium	Alain Reygel

Toronto, ON, Canada	Allan Baker and Mark Peck
Washington DC, USA	Christina Gebhard, Chris Milensky, and Storrs Olson
Stockholm, Sweden	Per Ericson and Ulf Johansson
Welshpool, WA, Australia	Ron Johnstone
Russian Academy of Sciences, St Petersburg, Russia	Vladimir Loskot
	Toronto, ON, Canada Washington DC, USA Stockholm, Sweden Welshpool, WA, Australia Russian Academy of Sciences, St Petersburg, Russia

TABLE S2 Details of contour feathers of sooty terns breeding on Ascension Island in the 819 South Atlantic between the 1890s and the 2010s. Sources: AMNH - American Museum of 820 Natural History, New York, NY, USA; BJH – B. John Hughes; CPW – Colin P. Wearn; Flor. 821 Mus. Nat. Hist. - Florida Museum of Natural History, Gainesville, FL, USA; Hancock -822 Great North Museum-Hancock Collection, Newcastle upon Tyne, UK; Mus. Nat. Sci. LSU -823 Museum of Natural Science, Louisiana State University, Baton Rouge, LA, USA; Nat. Mus. 824 Liverpool - National Museums Liverpool, Liverpool, UK; Nat. Mus. Scotland - National 825 Museums Scotland, Edinburgh, UK; NHM Tring - Natural History Museum-Bird Group, 826 827 Tring, UK; NMNH Paris – National Museum of Natural History-Collection of Birds, Paris, France; Peabody – Peabody Museum of Natural History, Yale University, New Haven, CT, 828 USA; SJR - S. James Reynolds; and Smithsonian - Smithsonian Institution-Division of 829 830 Birds, Washington DC, USA

Sample			
number	Source	Catalogue number	Decade of collection
1	Hancock	B020.71	1890
2	Nat. Mus. Scotland	NMS.Z.1956.3 (3161)	1890
3	NHM Tring	2012.102.1	1890
4*	NHM Tring	1880.11.18.707	-
5	Smithsonian	USNM118379	1890
6	Smithsonian	USNM118380	1890
7	Smithsonian	USNM118381	1890
8	NHM Tring	1894.10.28.7	1890
9	NHM Tring	1899.1.4.19	1890
10*	NHM Tring	1899.1.4.20	-
11*	NMNH Paris	_	-
12*	Nat. Mus. Liverpool	_	-
13*	NHM Tring	1922.12.6.49	_
14*	NHM Tring	1922.12.6.50	-
15	Peabody	YPM44863	1920
16	Peabody	YPM44864	1920
17	Peabody	YPM44865	1920
18	Peabody	YPM44866	1920
19	Peabody	YPM44868	1920
20	Peabody	YPM44869	1920
21	Peabody	YPM44870	1920
22	Peabody	YPM44871	1920
23	Peabody	YPM44872	1920
24	Peabody	YPM44873	1920

25	Peabody	YPM44874	1920
26	Peabody	YPM44875	1920
27	Peabody	YPM44876	1920
28	Peabody	YPM44877	1920
29	Peabody	YPM44878	1920
30	Peabody	YPM44879	1920
31	Peabody	YPM44888	1920
32	Peabody	YPM44889	1920
33	Peabody	YPM44890	1920
34	Peabody	YPM44891	1920
35	Peabody	YPM44892	1920
36	Peabody	YPM44893	1920
37	Peabody	YPM44894	1920
38	Peabody	YPM44895	1920
39	Peabody	YPM44896	1920
40	Peabody	YPM44897	1920
41	Peabody	YPM44898	1920
42	Peabody	YPM44899	1920
43	Peabody	YPM44901	1920
44	Peabody	YPM44902	1920
45	Peabody	YPM44903	1920
46	Peabody	YPM44904	1920
47	Peabody	YPM44905	1920
48	Peabody	YPM44906	1920
49	Peabody	VPM44907	1920
50	Peabody	VPM44908	1920
51	Peabody	VPM44909	1920
52	Peabody	VPM44921	1920
53	Peabody	VPM44922	1920
54	Peabody	VPM44922	1920
55	Peabody	VPM44924	1920
56	Peabody	VPM44925	1920
57	Peabody	VPM44934	1920
58	Peabody	VPM44935	1920
59	Peabody	VPM44936	1920
60	Peabody	VPM44937	1920
61	Peabody	VPM44938	1920
62	Peabody	VPM44939	1920
63	Peabody	VPM44940	1920
64	Peabody	VPM44941	1920
65	Peabody	VPM44942	1920
66	Peabody	VPM44943	1920
67	Peabody		1920
68	Peabody	VPM44945	1920
60	Peabody	VPM44945	1920
70	Peabody	VPM44940	1920
70	Peabody	VPM//0/8	1920
72	Peabody	VPM44949	1920
73	Peabody	VPM//050	1920
7/	Peabody	VPM//051	1920
75	Peabody	VPM//052	1920
76	Peabody	VPM//053	1920
70	Peabody	VDM44955	1920
78	Peabody	VPM44955	1920
70	Peabody	VPM//056	1920
17	i cauduy		1/40

80	Peabody	YPM44967	1920
81	Peabody	YPM44968	1920
82	Peabody	YPM44969	1920
83	Peabody	YPM44970	1920
84	Peabody	YPM44971	1920
85	Peabody	YPM44972	1920
86	Peabody	YPM44973	1920
87	Peabody	YPM44974	1920
88	Peabody	YPM44975	1920
89	Peabody	YPM44976	1920
90	Peabody	YPM44977	1920
91	Peabody	YPM44978	1920
92	Peabody	VPM44981	1920
93	Peabody	VPM44982	1920
94	Peabody	VPM44983	1920
95	Peabody	VPM//08/	1920
95	Pashody	VDM44085	1920
90		260206	1920
97		269200	1920
98		209227	1920
99		209220	1920
100	AMINH	269225	1920
101	AMNH	269224	1920
102	AMNH	269223	1920
103	AMNH	269222	1920
104	AMNH	269221	1920
105	AMNH	269220	1920
106	AMNH	269219	1920
107	AMNH	269218	1920
108	AMNH	269217	1920
109	AMNH	269216	1920
110	AMNH	269215	1920
111	AMNH	269214	1920
112	AMNH	269213	1920
113	AMNH	269212	1920
114	AMNH	269211	1920
115	AMNH	269210	1920
116	AMNH	269209	1920
117	AMNH	269208	1920
118	AMNH	269207	1920
119	AMNH	308427	1940
120	AMNH	308426	1940
121	AMNH	308425	1940
122	AMNH	308424	1940
123	AMNH	308423	1940
124	AMNH	308422	1940
125	AMNH	308421	1940
126	AMNH	308428	1940
127	AMNH	308429	1940
128*	Mus. Nat. Sci. LSU	LSUMZ73125	
129	NHM Tring	1962.42.2	1940
130	Smithsonian	USNM534287	1970
131	Smithsonian	USNM534285	1970
132	Smithsonian	USNM534286	1970
133	Smithsonian	USNM534288	1970
134	Flor Mus Nat Hist	LIF37533	1970
131	1 101. 11100. 1 (ut. 1110t.	0157555	1770

135	BJH	09Aug2006.1	2000
136	BJH	09Aug2006.2	2000
137	BJH	09Aug2006.3	2000
138	BJH	09Aug2006.4	2000
139	BJH	09Aug2006.5	2000
140	BJH	09Aug2006.6	2000
141	BJH	09Aug2006.7	2000
142	BJH	09Aug2006.8	2000
143	CPW/SJR	8Jan2012.1	2010
144	CPW/SJR	8Jan2012.2	2010
145	CPW/SJR	8Jan2012.3	2010
146	CPW/SJR	8Jan2012.4	2010
147	CPW/SJR	8Jan2012.5	2010
148	CPW/SJR	8Jan2012 6	2010
149	CPW/SJR	8Jan2012.7	2010
150	CPW/SJR	8Jan2012 8	2010
151	CPW/SIR	8Jan2012.9	2010
152	CPW/SIR	8Ian2012.10	2010
152	CPW/SIR	8Ian2012 11	2010
154	CPW/SIR	8Ian2012 12	2010
155	CPW/SIR	8 Jan 2012 13	2010
156	CPW/SIR	8Jan2012.15	2010
157	CPW/SIR	8 Jan 2012 15	2010
158	CPW/SIR	8Ian2012.16	2010
150	CPW/SIR	8 Jan 2012 17	2010
160	CPW/SIR	8 Jan 2012 18	2010
161	CPW/SIR	8Jan2012.10	2010
162	CPW/SIR	8 Jan 2012 20	2010
163	CPW/SIR	8Jan2012.20	2010
164	CDW/SIR	8 Jan 2012 22	2010
165	CPW/SIR	8 Jan 2012 23	2010
166	CPW/SIR	8 Jan 2012 24	2010
167	CDW/SIR	8 Jan 2012 25	2010
168	CDW/SIR	4Dec2012.23	2010
160	CDW/SIR	4Dec2012.21 4Dec2012.21	2010
109	CDW/SJR	4Dec2012.22	2010
170	CPW/SJR	4Dec2012.23	2010
171	CPW/SJR	4Dec2012.24	2010
172	CPW/SJR	4Dec2012.23	2010
173	CPW/SJR	4Dec2012.20	2010
1/4	CPW/SJR	4Dec2012.27	2010
1/5	CPW/SJK	4Dec2012.28	2010
1/0	CPW/SJK	4Dec2012.29	2010
1//	CPW/SJK	4Dec2012.30	2010
1/8	CPW/SJK	4Dec2012.31	2010
1/9	CPW/SJK	4Dec2012.32	2010
180	CPW/SJK	4Dec2012.33	2010
181		4Dec2012.34	2010
182	CPW/SJK	4Dec2012.35	2010
183	CPW/SJK	4Dec2012.36	2010
184	CPW/SJK	4Dec2012.37	2010
185	CPW/SJK	4Dec2012.38	2010
186	CPW/SJR	4Dec2012.39	2010
18/	CPW/SJK	4Dec2012.40	2010

- \*Samples omitted from subsequent statistical analyses as they yielded outlying  $\delta^{13}$ C and  $\delta^{15}$ N
- values even after processing multiple replicates through stable isotope analysis (SIA)



**FIGURE S1** Diet items (from regurgitations) of breeding sooty terns on Ascension Island in

- the South Atlantic collected during ringing in December 2012. (a) Teleost fish, (b) squid
- 838 (Teuthida), (c) megalops of Sally Lightfoot crabs, (d) locusts, and (e) violet sea snails.
- 839 (Photos: N. Day)