

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

Reynolds, Silas; Hughes, Bernard; Wearn, Colin; Dickey, Roger; Brown, Judith; Weber, Nicola; Weber, Sam; Paiva, Vitor; Ramos, Jaime

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

3

4 **Running head** Bio-indicators and marine ecosystem function

5

6 S. James Reynolds<sup>1,2</sup> | B. John Hughes<sup>1,2</sup> | Colin P. Wearn<sup>3</sup> | Roger C. Dickey<sup>2</sup> | Judith

7 Brown<sup>4</sup> | Nicola Weber<sup>4,5</sup> | Sam B. Weber<sup>4,5</sup> | Vitor H. Paiva<sup>6</sup> | Jaime A. Ramos<sup>6</sup>

8

9 <sup>1</sup>Centre for Ornithology, School of Biosciences, College of Life & Environmental Sciences,  
10 The University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK; <sup>2</sup>The Army  
11 Ornithological Society (AOS), c/o Prince Consort Library, Knollys Road, Aldershot,  
12 Hampshire GU11 1PS, UK; <sup>3</sup>The Royal Air Force Ornithological Society (RAFOS),  
13 Headquarters Air Command, Royal Air Force, High Wycombe, Buckinghamshire HP14 4UE,  
14 UK; <sup>4</sup>Ascension Island Government Conservation and Fisheries Department (AIGCFD),  
15 Georgetown ASCN 1ZZ, Ascension Island; <sup>5</sup>Centre for Ecology and Conservation,  
16 Biosciences, College of Life and Environmental Sciences, University of Exeter, Penryn  
17 Campus, Treliever Road, Penryn, Cornwall TR10 9FE, UK; <sup>6</sup>MARE, Marine and  
18 Environmental Sciences Centre, Department of Life Sciences, University of Coimbra, 3000-  
19 456 Coimbra, Portugal.

20

21 **Correspondence** S. James Reynolds Email: [J.Reynolds.2@bham.ac.uk](mailto:J.Reynolds.2@bham.ac.uk)

22 Telephone: +44 (0)121 414 3639

23

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25 nitrogen-15, *Onychoprion fuscatus*, sooty tern, South Atlantic, stable isotope

## 26 **Abstract**

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

45

## 46 **1 | INTRODUCTION**

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

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

59         Seabirds act as sensitive bio-indicators for the direct and indirect effects of  
60 anthropogenic pressures on the marine environment through the study of their foraging  
61 behaviour, breeding performance and demographics (Furness & Monaghan, 1987). The  
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  
64 environment can be monitored (but see Grémillet & Charmantier, 2010). Phenology and  
65 breeding performance are known to be strongly influenced by oceanic conditions, food  
66 availability and fishing activities in both temperate (Frederiksen, Wanless, Harris, Rothery, &  
67 Wilson, 2004) and tropical (LeCorre, 2001) waters. In the latter case, many foraging seabirds  
68 associate with cetaceans and predatory fish such as tuna (*Thunnus* spp.) that drive prey to the  
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  
71 the presence of such underwater predators (Maxwell & Morgan, 2013; Veit & Harrison,  
72 2017), particularly where foraging occurs over pelagic waters, far from upwelling areas or  
73 other physical oceanographic features that naturally result in large congregations of prey at  
74 the sea surface (Au & Pitman, 1986). Global declines of large predatory fishes since the  
75 middle of the twentieth century as a result of over-fishing, and lack of appropriate

76 management measures (Myers, Baum, Shepherd, Powers, & Peterson, 2007; Juan-Jordá,  
77 Mosqueira, Cooper, Freire, & Dulvy, 2011), may therefore have had significant impacts on  
78 the ecology of tropical oceanic seabirds. Other drivers of global environmental change may  
79 also have impacted on seabird foraging success and demography. For example, ocean  
80 warming has been linked to changes in prey population dynamics (Howells et al., 2017), and  
81 range shifts of both forage fish and pelagic predators in temperate and tropical oceans (e.g.  
82 Perry, Low, Ellis, & Reynolds, 2005; Monllor-Hurtado, Pennino & Sanchez-Lizaso, 2017),  
83 potentially diminishing food availability to seabirds through reductions in both prey  
84 availability and accessibility (e.g. Howells et al., 2017).

85         Studies of contemporary seabird diets, breeding success and population dynamics  
86 have provided valuable data on threats currently facing marine ecosystems. However,  
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  
89 changes to marine food webs have influenced the foraging ecology of the world's most  
90 abundant tropical seabird, the sooty tern (*Onychoprion fuscatus*) at the Atlantic's largest  
91 nesting colony on Ascension Island (Hughes, Martin, Giles, & Reynolds, 2017a). Sooty terns  
92 are long-lived (in some cases >38 years old; Schreiber et al., 2002), pan-tropically distributed  
93 (Schreiber et al., 2002), and near-obligate commensals of tuna and other sub-surface  
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  
96 healthy global population of 21–25 million birds (species account retrieved from  
97 <http://datazone.birdlife.org>). Nevertheless, a number of sizeable populations have declined  
98 markedly (reviewed in Hughes et al., 2017a), including that at Ascension Island. Hughes et  
99 al. (2017a) compared the breeding population size of sooty terns on the island between 1950  
100 and the present day, observing that since 1958, when there were an estimated 3.32 million

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

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

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

126

## 127 **2 | MATERIALS AND METHODS**

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

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

145

### 146 **2.2 | Feather sampling**

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

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

161

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

163 Sooty terns breeding on the island are on migration for at least six months of every sub-  
164 annual cycle (Ashmole, 1963a) and thus cannot be observed directly feeding at sea.

165 Furthermore, no regurgitant samples were available from birds in museum collections.

166 Schreiber et al. (2002) described their diet as containing small (teleost) fish such as halfbeaks

167 (*Oxyporhamphus micropterus*), blue flying fishes (*Exocoetus volitans*), redlip blennies

168 (*Ophioblennius atlanticus*), Simony's frostfishes (*Benthodesmus simonyi*) and hairtails

169 (*Trichiurus* spp.) (Ashmole, 1963a), and squid (Teuthida). Their diet when breeding can be

170 readily reconstructed from regurgitant samples when sooty terns are handled; their

171 regurgitated prey is far less digested than that from other seabird species (Ashmole &

172 Ashmole, 1967). In 2012 during ringing of breeding adults we (i.e. SJR, BJH, CPW and

173 RCD) noted a more catholic diet in birds that rarely regurgitated fish but more often violet

174 sea snails (*Janthina janthina*), megalops (a larval stage) of Sally Lightfoot crabs (*Grapsus*

175 *grapsus*), and locusts (Acrididae spp.) (Figure S1). While regurgitant samples from breeding



176 birds are not truly reflective of their diet during the sub-annual cycle, breeding birds travel  
177 hundreds of kilometres out to sea when foraging (Soanes, Bright, Brodin, Mukhida, & Green,  
178 2015; Neumann, Larose, Brodin, & Feare, 2018; JB, unpubl. data), and thus likely contain  
179 similar prey to those consumed by birds between breeding seasons.

180

#### 181 **2.4 | Stable isotope analysis**

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

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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

208         Since the Industrial Revolution the burning of fossil fuels has a lower  $\delta^{13}\text{C}$  than  
209 background carbon causing an exponentially accelerating decrease of  $\delta^{13}\text{C}$  in the biosphere –  
210 the so-called ‘Suess Effect’ (Keeling, 1979). In addition, the increase in atmospheric  $\text{CO}_2$ ,  
211 and thus aqueous  $\text{CO}_2$ , has increased phytoplankton fractionation, reducing its  $\delta^{13}\text{C}$  values  
212 (Rau, Takahashi, Des Marais, Repeta, & Martin, 1992). Thus, raw  $\delta^{13}\text{C}$  values of sooty tern  
213 feathers were adjusted following Hilton et al. (2006), Jaeger and Cherel (2011), and  
214 Carravieri, Cherel, Jaeger, Churlaud and Bustamante (2016).

215

## 216 **2.5 | Data analyses**

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

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

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

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

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

261

## 262 **3 | RESULTS**

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

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

275

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

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

283

## 284 **3.3 | Isotopic values of prey and reconstructed diets of birds across decades of sampling**

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

298

## 299 **4 | DISCUSSION**

300 Significant declines were found in both the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of contour feathers collected  
301 over the 120-year study period (Figure 2a and b), indicating that the diets of these sooty terns  
302 have changed over a period when breeding population size has declined markedly (Figure 1).  
303 Inferred foraging niches of sooty terns before (1890s–1940s) and after (1970s–2010s) the  
304 population collapse did not overlap, despite widths being similar (Figure 3). Isotopic mixing  
305 models indicated that this was due to a significant decrease in the proportion of teleost fish in  
306 the diet (from 0.62 pre-1950 to 0.26 post-1970) and a corresponding increase in the  
307 proportion of squid (from 0.26 to 0.57), and of marine and terrestrial invertebrates (from 0.06  
308 and 0.04 to 0.08 and 0.11, respectively) (Figure 5).

309         Field observations of breeding sooty terns on Ascension Island also suggest that the  
310 proportion of fish in their diets has declined since the middle of the twentieth century,  
311 decreasing from 0.60 in 1958–1959 (Ashmole & Ashmole, 1967), to 0.50–0.60 in 1972  
312 (Johnston, 1973) and to only 0.17 in 2004 (Hughes, 2014). In 2012 birds were predominantly  
313 feeding on squid and other low energy content foods, reflecting the struggle to locate fish  
314 prey. These observations support our SIA findings (Figure 5) and provide further evidence of  
315 a dietary shift. A similar dietary shift by breeding sooty terns was observed in the Dry  
316 Tortugas (FL, USA) 8,000 km away from Ascension Island: between 1920 and 1941 squid  
317 were absent from diets but they were a common dietary constituent between 1992 and 1994  
318 (Colchero, 2008).

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

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

336

#### 337 **4.1 | What has caused the dietary shift?**

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

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 &  
352 Potthoff, 1972; Potier et al., 2007) with inevitably other fish species also driven to the surface  
353 as they hunt.

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



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

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

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

402

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

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

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

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

434         It is noteworthy that while populations of many pelagic predators have continued to  
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  
437 as might be expected if it was wholly attributable to an environmentally-mediated shift in  
438 diet. Instead, the tern population has apparently stabilised in size (Figure 1). Conservation  
439 measures on the breeding grounds such as the eradication of feral domestic cats from  
440 Ascension Island in 2002 (Ratcliffe et al., 2010) have likely promoted adult and chick  
441 survival and may have offset pressures on food availability. It is also possible that the  
442 population has reached a new, reduced carrying capacity that can be maintained within the  
443 altered marine food web. So-called ‘regime shifts’ between alternative stable states are a  
444 common feature of marine ecosystems (deYoung et al., 2008) and can be triggered by climate  
445 events and over-fishing of top predators resulting in system-wide trophic cascades (Daskalov,  
446 Grishin, Rodionov, & Mihneva, 2007; deYoung et al., 2008). Our results suggest that the  
447 historical sooty tern population decline on Ascension Island may be at least partly explained

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

450

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

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

470

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484

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746 **Tables**

747

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

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

752

753 **Figure captions**

754

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 **FIGURE 2** Box and whisker plots showing (a) carbon ( $\delta^{13}\text{C}$ ) and (b) nitrogen ( $\delta^{15}\text{N}$ ) 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  $\delta^{13}\text{C}$  values are corrected for the ‘Suess Effect’ following Hilton et al.  
766 (2006). Sample sizes of birds are indicated within brackets. In both plots the grey shading  
767 represents the transition between before and after the population collapse of the Ascension  
768 Island sooty tern population (Hughes et al., 2017a)

769

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

776

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

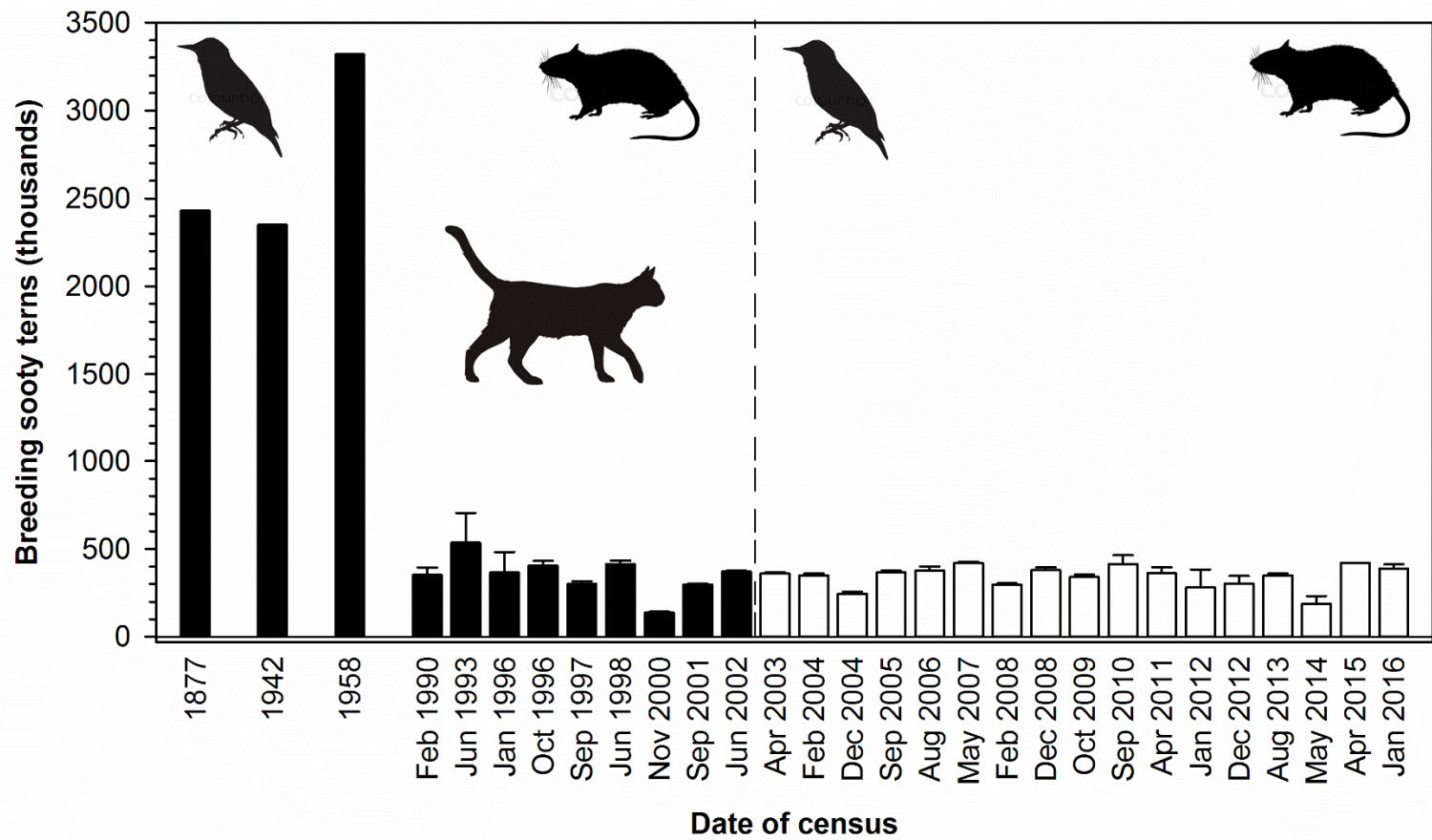
782

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

791

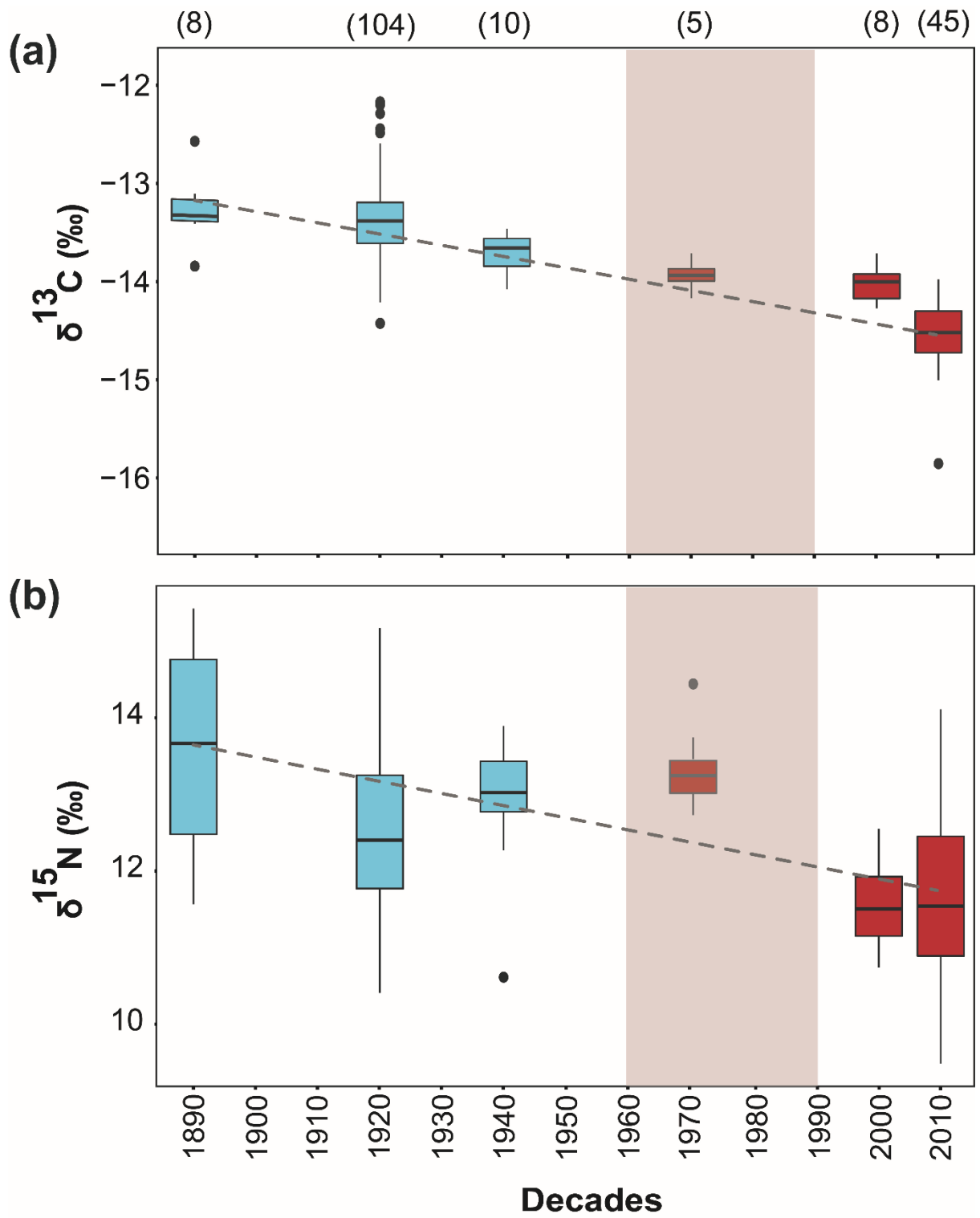
792 **FIGURE 6** (a) Historical trends in tuna catches (in millions of tonnes [t]) in the east tropical  
793 Atlantic Ocean (see <https://www.iccat.int/en/accesingdb.HTM> for further details), and (b)  
794 mean (+ 1 SD) sea surface temperature anomaly (SSTa) within a 1,000 km buffer  
795 surrounding Ascension Island (data retrieved from  
796 <http://www.metoffice.gov.uk/hadobs/hadisst/>). In both plots the grey shading represents the  
797 transition between before and after the population collapse of the Ascension Island sooty tern  
798 population (Hughes et al., 2017a). During the collapse there was a 15-fold increase in  
799 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



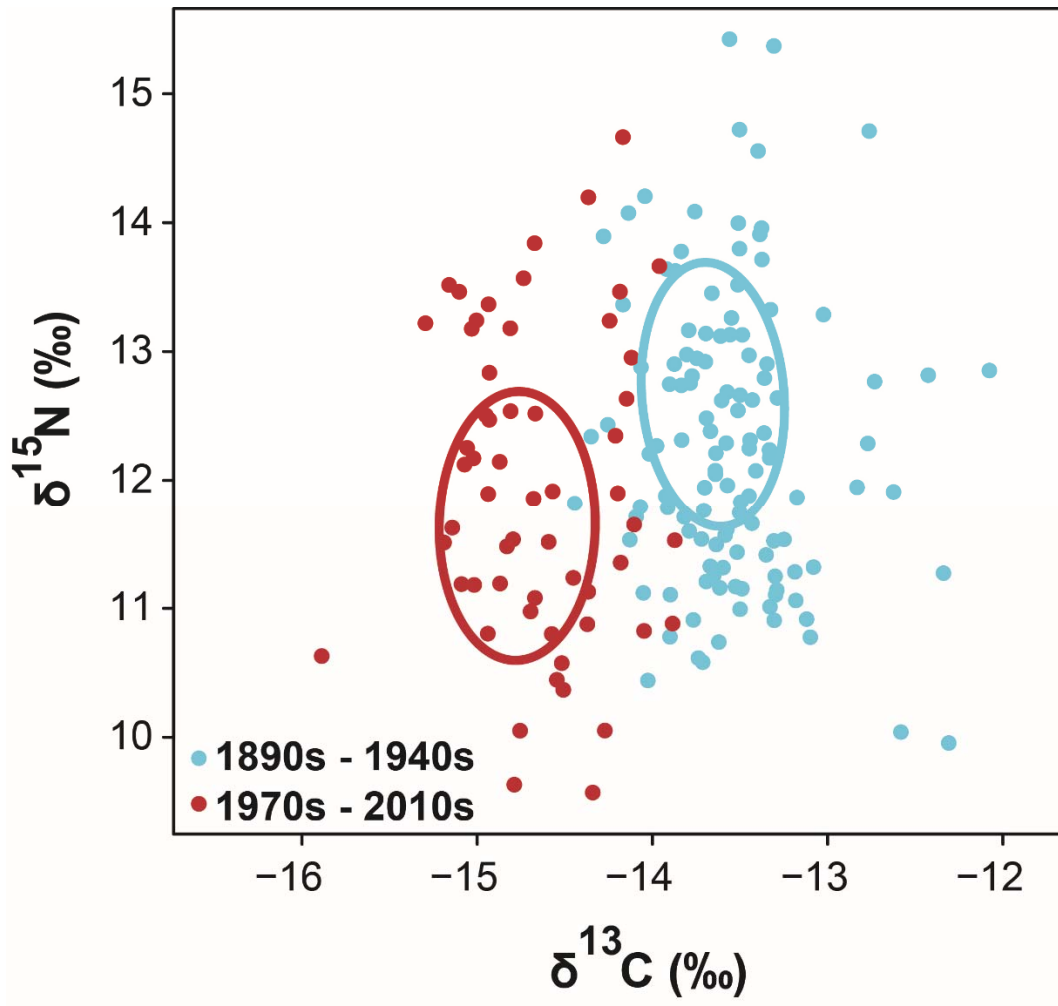
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803 **Figure 1.**



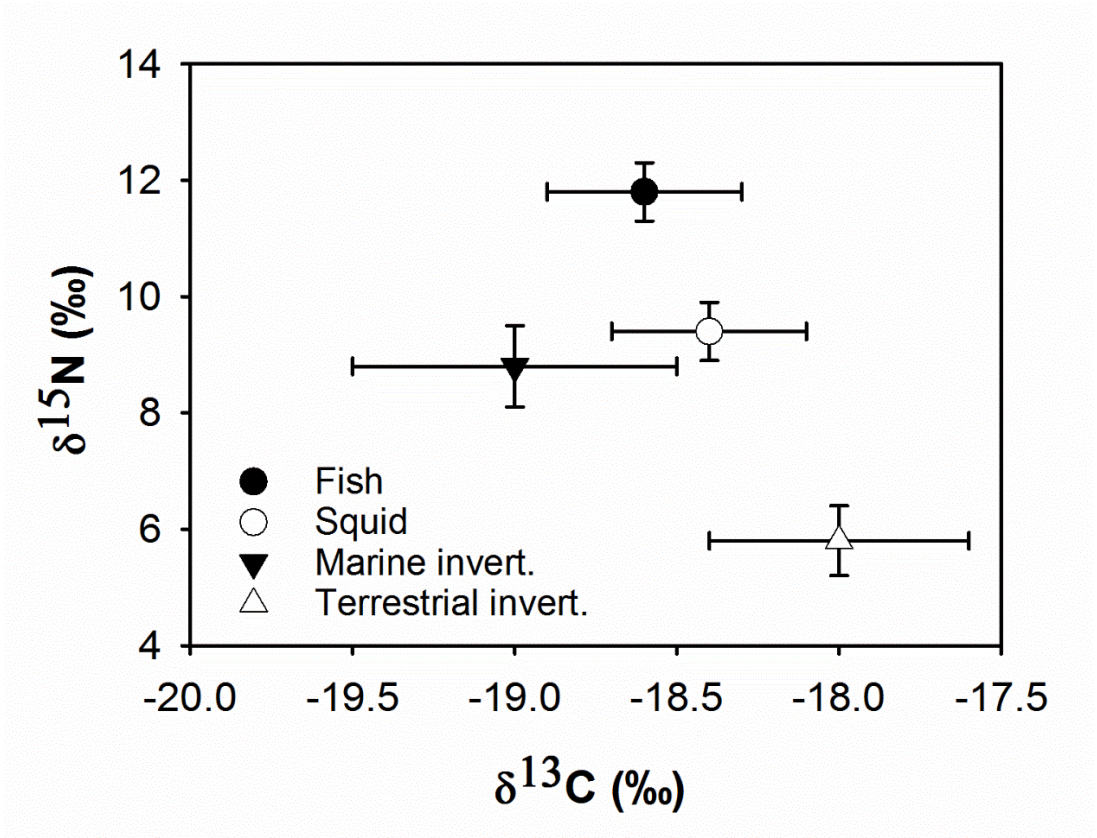
804

805 **Figure 2.**



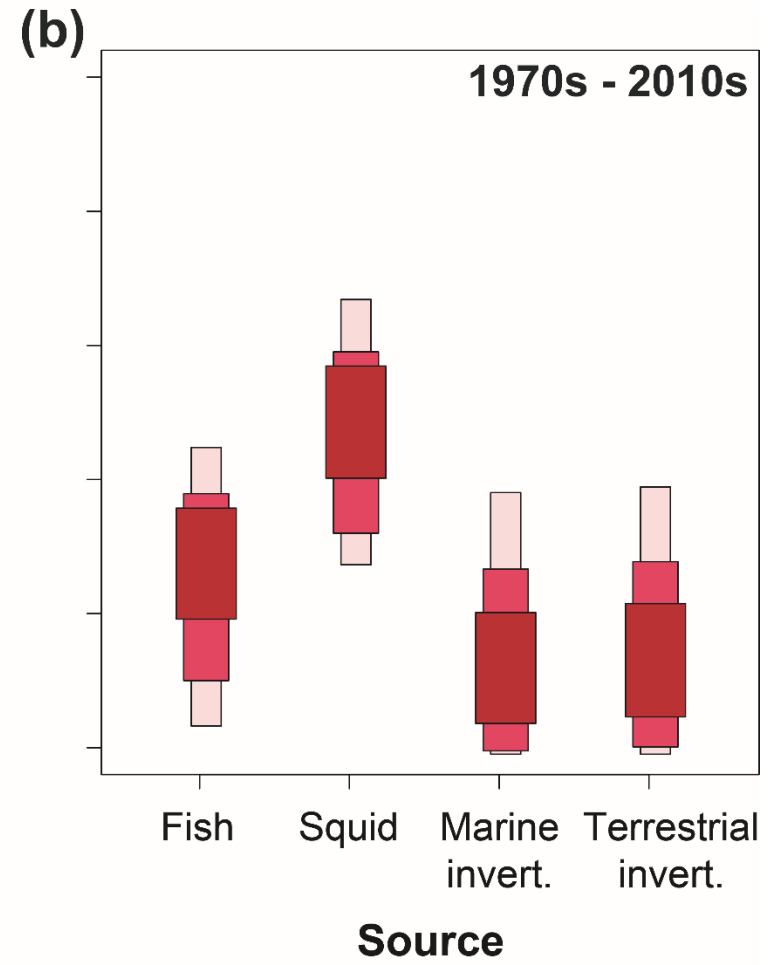
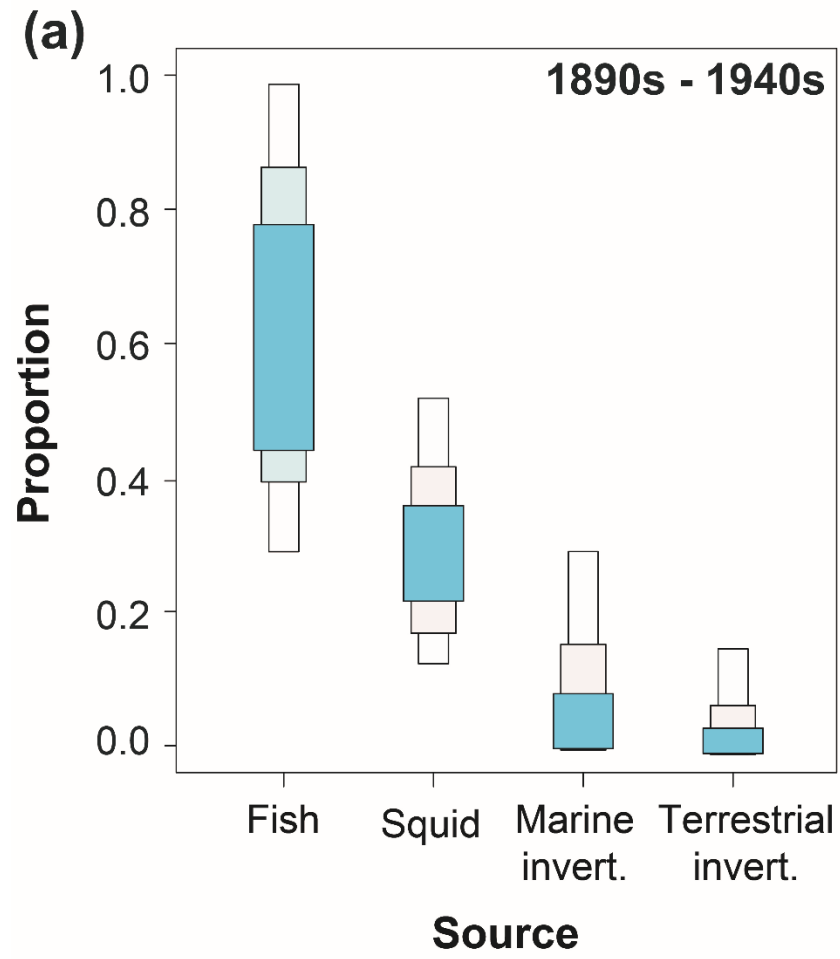
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807 **Figure 3.**



808

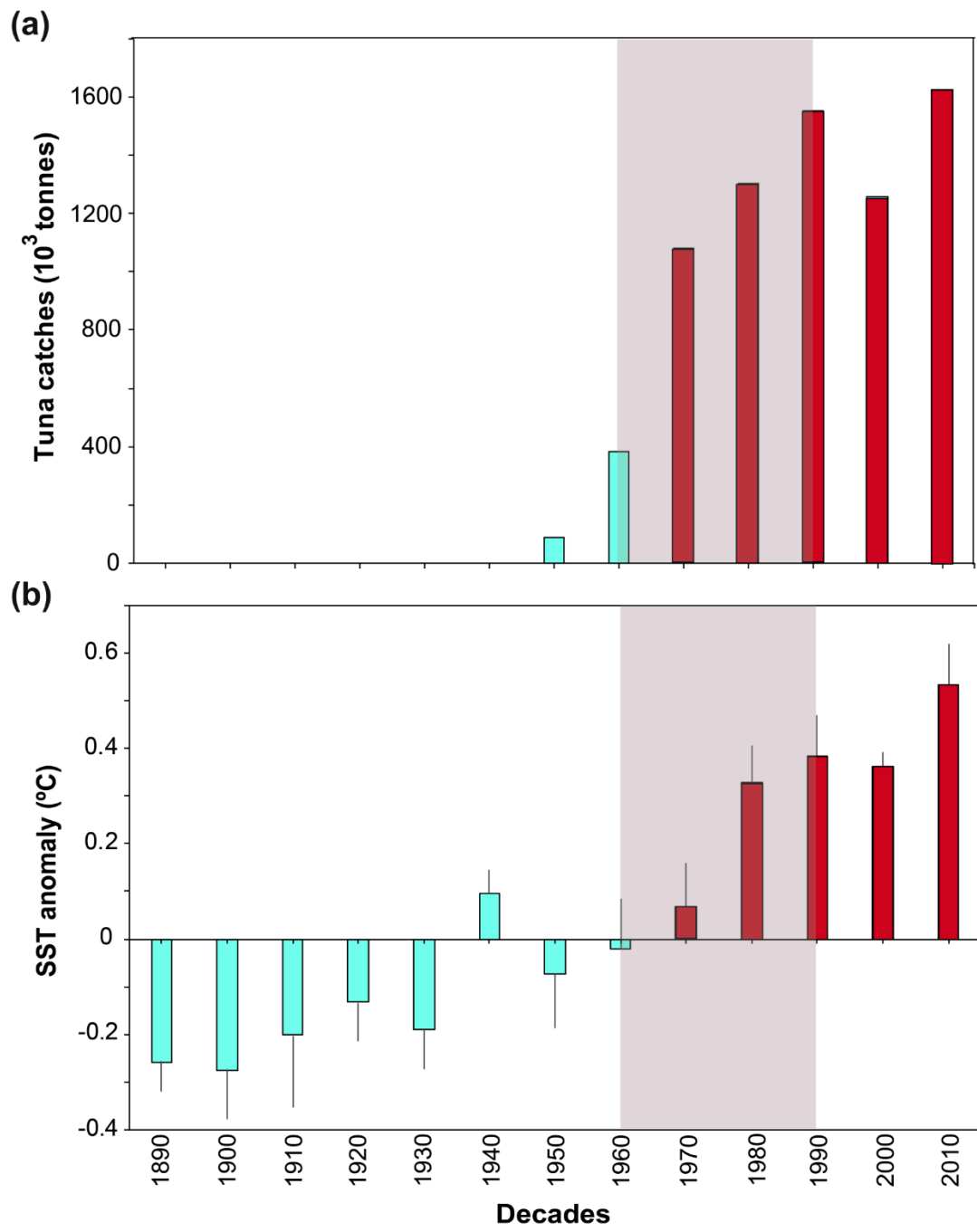
809 **Figure 4.**



810

811 **Figure 5.**





812

813 **Figure 6.**

814

**Supporting information**815 **TABLE S1** Details of museums and their curators who assisted with initial enquiries about

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

817

<b>Name of museum</b>	<b>Location</b>	<b>Name(s) of curator(s)</b>
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

Royal Ontario Museum- Department of Natural History (Ornithology)	Toronto, ON, Canada	Allan Baker and Mark Peck
Smithsonian Institution- Division of Birds	Washington DC, USA	Christina Gebhard, Chris Milensky, and Storrs Olson
Swedish Museum of Natural History	Stockholm, Sweden	Per Ericson and Ulf Johansson
Western Australian Museum	Welshpool, WA, Australia	Ron Johnstone
Zoological Institute	Russian Academy of Sciences, St Petersburg, Russia	Vladimir Loskot

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818

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

831

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

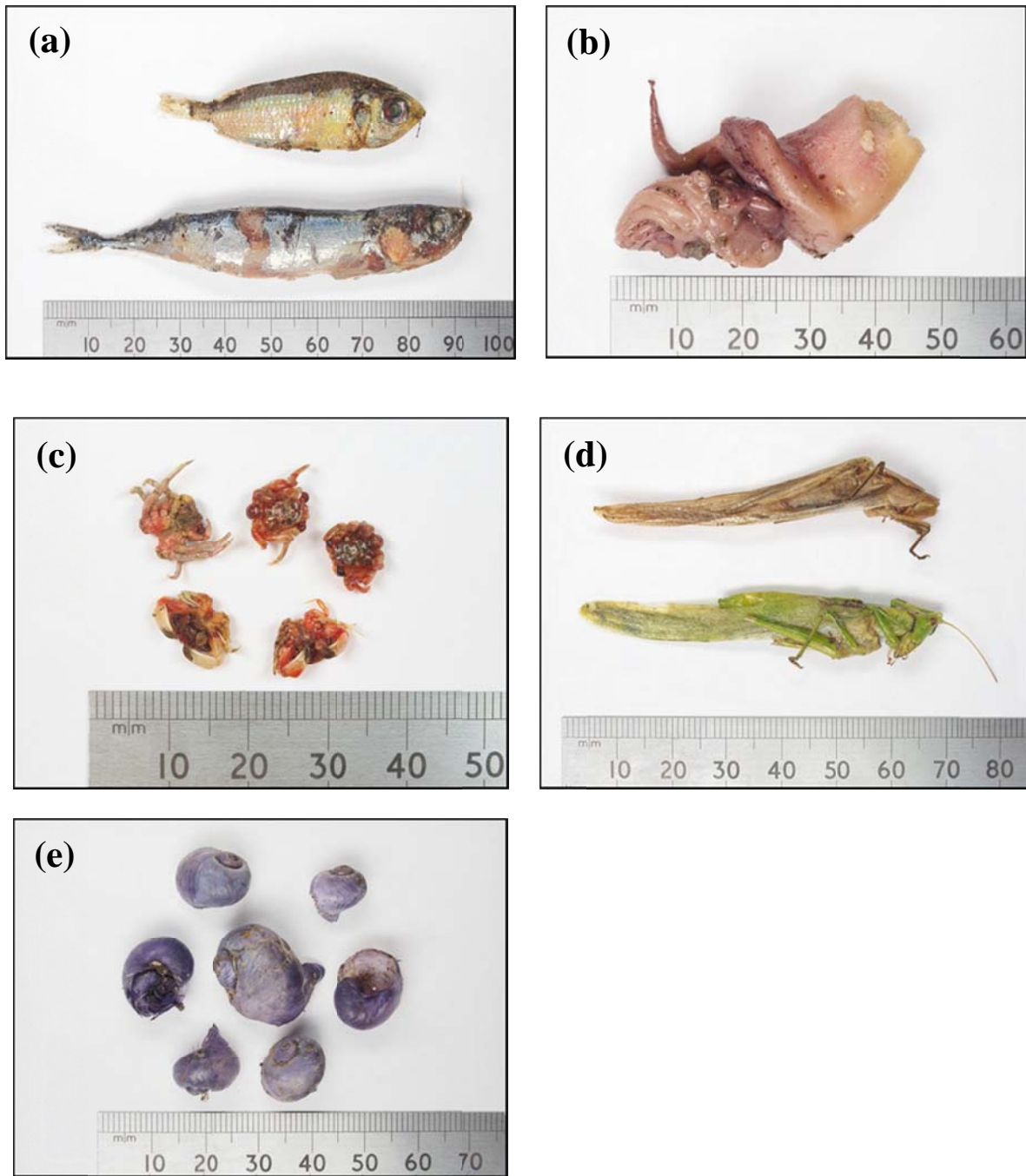
25	Peabody	YPM44874	1920
26	Peabody	YPM44875	1920
27	Peabody	YPM44876	1920
28	Peabody	YPM44877	1920
29	Peabody	YPM44878	1920
30	Peabody	YPM44879	1920
31	Peabody	YPM44888	1920
32	Peabody	YPM44889	1920
33	Peabody	YPM44890	1920
34	Peabody	YPM44891	1920
35	Peabody	YPM44892	1920
36	Peabody	YPM44893	1920
37	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	YPM44907	1920
50	Peabody	YPM44908	1920
51	Peabody	YPM44909	1920
52	Peabody	YPM44921	1920
53	Peabody	YPM44922	1920
54	Peabody	YPM44923	1920
55	Peabody	YPM44924	1920
56	Peabody	YPM44925	1920
57	Peabody	YPM44934	1920
58	Peabody	YPM44935	1920
59	Peabody	YPM44936	1920
60	Peabody	YPM44937	1920
61	Peabody	YPM44938	1920
62	Peabody	YPM44939	1920
63	Peabody	YPM44940	1920
64	Peabody	YPM44941	1920
65	Peabody	YPM44942	1920
66	Peabody	YPM44943	1920
67	Peabody	YPM44944	1920
68	Peabody	YPM44945	1920
69	Peabody	YPM44946	1920
70	Peabody	YPM44947	1920
71	Peabody	YPM44948	1920
72	Peabody	YPM44949	1920
73	Peabody	YPM44950	1920
74	Peabody	YPM44951	1920
75	Peabody	YPM44952	1920
76	Peabody	YPM44953	1920
77	Peabody	YPM44954	1920
78	Peabody	YPM44955	1920
79	Peabody	YPM44956	1920

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	YPM44981	1920
93	Peabody	YPM44982	1920
94	Peabody	YPM44983	1920
95	Peabody	YPM44984	1920
96	Peabody	YPM44985	1920
97	AMNH	269206	1920
98	AMNH	269227	1920
99	AMNH	269226	1920
100	AMNH	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.	UF37533	1970

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/SJR	8Jan2012.9	2010
152	CPW/SJR	8Jan2012.10	2010
153	CPW/SJR	8Jan2012.11	2010
154	CPW/SJR	8Jan2012.12	2010
155	CPW/SJR	8Jan2012.13	2010
156	CPW/SJR	8Jan2012.14	2010
157	CPW/SJR	8Jan2012.15	2010
158	CPW/SJR	8Jan2012.16	2010
159	CPW/SJR	8Jan2012.17	2010
160	CPW/SJR	8Jan2012.18	2010
161	CPW/SJR	8Jan2012.19	2010
162	CPW/SJR	8Jan2012.20	2010
163	CPW/SJR	8Jan2012.21	2010
164	CPW/SJR	8Jan2012.22	2010
165	CPW/SJR	8Jan2012.23	2010
166	CPW/SJR	8Jan2012.24	2010
167	CPW/SJR	8Jan2012.25	2010
168	CPW/SJR	4Dec2012.21	2010
169	CPW/SJR	4Dec2012.22	2010
170	CPW/SJR	4Dec2012.23	2010
171	CPW/SJR	4Dec2012.24	2010
172	CPW/SJR	4Dec2012.25	2010
173	CPW/SJR	4Dec2012.26	2010
174	CPW/SJR	4Dec2012.27	2010
175	CPW/SJR	4Dec2012.28	2010
176	CPW/SJR	4Dec2012.29	2010
177	CPW/SJR	4Dec2012.30	2010
178	CPW/SJR	4Dec2012.31	2010
179	CPW/SJR	4Dec2012.32	2010
180	CPW/SJR	4Dec2012.33	2010
181	CPW/SJR	4Dec2012.34	2010
182	CPW/SJR	4Dec2012.35	2010
183	CPW/SJR	4Dec2012.36	2010
184	CPW/SJR	4Dec2012.37	2010
185	CPW/SJR	4Dec2012.38	2010
186	CPW/SJR	4Dec2012.39	2010
187	CPW/SJR	4Dec2012.40	2010

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





835  
836 **FIGURE S1** Diet items (from regurgitations) of breeding sooty terns on Ascension Island in  
837 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)