1   # The status and conservation of Cape Gannets *Morus capensis*

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22

23   **Abstract**

24   The Cape Gannet *Morus capensis* is one of several seabird species that are endemic to the

25   Benguela upwelling ecosystem (BUS), whose populations recently decreased leading to

26   unfavourable Red List classifications. Application of JARA, a Bayesian state-space tool for IUCN

27   Red List assessment, to updated information on areas occupied by and nest densities of breeding

28   Cape Gannets at their six colonies suggested the species should be classified as Vulnerable.

29   However, the rate of decrease of Cape Gannets in their most recent generation exceeded that of

30   the previous generation, primarily as a result of large decreases at Bird Island, Lambert's Bay,

31   and Malgas Island off South Africa's west coast. Since the 1960s, there has been an ongoing

32   redistribution of the species from northwest to southeast so that c. 70% of the species now occurs

33   at Bird Island, Algoa Bay, on the eastern border of the BUS. Recruitment rather than adult survival

34   may be limiting the present population, although information on demographic parameters and

35   mortality in fisheries is lacking for colonies in the northern BUS. Major present threats to the

36   species include a substantially decreased availability of their preferred prey in the west, heavy

37   mortality of eggs, chicks and fledglings at and around colonies inflicted by Cape Fur Seals

38   *Arctocephalus pusillus* and other seabirds, substantial disturbance at colonies caused by Cape

39   Fur Seals attacking adults ashore, oiling and disease.

40

41   **Keywords:** Bayesian state-space model; Benguela ecosystem; Conservation status; IUCN Red

42   List; Population decline; Seabird conservation.

43

44   **Introduction**

45   The Cape Gannet *Morus capensis* is one of seven seabirds endemic to the Benguela upwelling

46   system off southwest Africa. It has historically bred at ten islands off the coasts of Namibia and

47   South Africa but at only six islands by 1956: Mercury, Ichaboe and Possession in Namibia; Bird

48   at Lambert's Bay (hereafter referred to as Lambert's Bay), Malgas and Bird at Algoa Bay

49   (hereafter referred to as Bird Island, Algoa Bay) in South Africa (Figure 1, Crawford et al. 1983).

50   Although many birds regularly disperse north along the west and east coasts of Africa after

51   breeding (e.g. Broekhuysen et al. 1961, Cyrus and Robson 1980, Klages 1994), the species is

52   not migratory and adults are often present at breeding localities throughout the non-breeding

53   season (Nelson 2005, Pistorius et al. 2015). A number of historical and contemporary pressures

54 from human activities have caused the number of Cape Gannets to decline since the first efforts

55 to estimate their abundance in 1956 (Crawford et al. 2007). For example, Cape Gannets construct

56 their nests from guano, of which they produce substantial quantities at breeding localities (Jarvis

57 1970). Their guano and that of other seabirds was previously harvested at southern African

58 islands and platforms, with much of it being shipped to Europe as a fertilizer (Crawford and

59 Shelton 1978, van Sittert and Crawford 2003). Again, Cape Gannets prefer to feed on two energy-

60 rich forage fish species, sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*, though

61 they may also utilise less nutritious fish species, such as saury *Scomberesox saurus*, and

62 scavenge hake *Merluccius* spp. and other benthic species discarded by demersal trawlers (e.g.

63 Berruti et al. 1993, Dundee 2006; Green et al. 2015, Grémillet et al. 2008, 2019). Sardine and

64 anchovy are the mainstay of the region's industrial purse-seine fisheries (Hutchings et al. 2009)

65 and play a major role in the transfer of energy from lower to higher trophic levels (e.g. Cury et al.

66 2000). However, access to forage fish for the regions' seabirds has changed markedly since the

67 1950s with the collapse of Namibia's sardine stock in the early 1970s (Crawford et al. 1983,

68 Watermeyer et al. 2008, Roux et al. 2013) and a more recent decrease in the availability to

69 seabirds of sardine and anchovy off South Africa's west coast after 2003 (Crawford et al. 2019).

70

71 In the 1950s and 1960s, most Cape Gannets bred in Namibia but by 1978, numbers were shared

72 evenly between Namibia and South Africa (Crawford et al. 1983). Since 1997, > 80% of Cape

73 Gannets bred in South Africa (Crawford et al. 2007). Under the criteria of the International Union

74 for Conservation of Nature (IUCN), in South Africa the Cape Gannet was of Least Concern in

75 1976 (Siegfried et al. 1976) and 1984 (Brooke 1984) but Vulnerable in 2000 (Barnes 2000) and

76 2015 (Hagen 2015). On account of its severe decrease in Namibia, it was there regarded as

77 Critically Endangered in 2015 (Kemper 2015). The global status of the Cape Gannet was Least

78 Concern in 1988, Near Threatened in 1994, Vulnerable in 2000 and Endangered in 2017 (BirdLife

79 International 2019). Its 2017 assessment was based on Bayesian state-space modelling of

80 numbers breeding at the species' six extant colonies between 1956 and 2016, which indicated a

81 decline of c. 52% over three generations of 20.2 years (Birdlife International 2019).

82

83 In this paper we update information on densities of nests, areas occupied by, and generation

84 length of, Cape Gannets. We revisit the generation length calculation, reapply the model used in

85 the 2017 assessment directly to estimates of the area occupied by breeding gannets, and

86 propagate the uncertainty around nesting density in revised estimates of the species' abundance

87 to ascertain whether the classification of Endangered remains applicable. We also review the

88 threats faced by the species and identify interventions needed to secure the species'

89 conservation.

90

91 **Methods**

92 The numbers of nests of Cape Gannets at colonies in breeding seasons were estimated from

93 measurements of the area occupied by breeding birds (in hectares [ha]) from near-vertical aerial

94 photographs, combined with ground-based measures of the densities of nests (Randall and Ross

95 1979, Klages et al. 1992). Aerial photographs were taken in November or December, when most

96 birds were incubating or brooding (Shelton et al. 1982). Cape Gannets may commence breeding

97 in mid-August, first clutches are usually complete by early November and most fledging is

98 complete by the end of March (Staverees et al. 2008). The extent of the area occupied by breeding

99 birds was measured using an Ibas interactive image-analysis system. The photographs were

100 scaled from ground measurements of straight edges, e.g. walls or buildings, near the colonies

101 (Crawford et al. 2007). In certain years (Table S1), when it was not possible to take photographs,

102 the area of a gannet colony was estimated by an observer walking around the colony with a Global

103 Positioning System (GPS) that had a horizontal error of ± 4 m (Crawford et al. 2007). Disturbance

104 to birds was reduced by suspending the GPS from a pole that ensured a 2 m gap between the

105 observer and the gannets. In total, between 1956/57 and 2018/19, estimates of the area occupied

4

106   by breeding birds were available for 27 seasons at Mercury Island, 25 at Ichaboe Island, 23 at

107   Possession Island, 41 at Lambert's Bay, 38 at Malgas Island and 42 at Bird Island, Algoa Bay

108   (Figure 3).

109

110   Measurements of the densities of nests at colonies were undertaken during breeding seasons by

111   placing four poles, each 2 m long, on the surface of the ground, so as to form a square of 4 m^2.

112   The numbers of whole nests and part nests that fell within a square were counted. The overall

113   number of nests in a square was taken to be the number of whole nests plus half the number of

114   part nests (Randall and Ross 1979, Crawford et al. 2007). The number of density measurements

115   made in any season ranged from two at Possession Island in 2002/03 and 2005/06, when the

116   colony was small and it was desired to minimize disturbance, to 30 at Algoa Bay in 2005/06

117   (Crawford et al 2007). Usually 10–25 density measurements were made at a colony in a given

118   breeding season. Density measurements were made at Mercury, Ichaboe and Possession islands

119   in three seasons, at Lambert's Bay in 19 seasons, at Malgas Island in 23 seasons and at Bird

120   Island, Algoa Bay in 11 seasons (Figure 2). Additionally, three published estimates were available

121   for Bird Island, Algoa Bay (Randall and Ross 1979, Batchelor 1982). As information on densities

122   of nests was not available for many seasons, for each locality a mean and SD density were

123   obtained, by giving equal weight to each season for which information existed.

124

125   In addition, in the 2010/11 and 2018/19 seasons, direct counts of the numbers of Cape Gannet

126   nests at the three Namibian colonies were made from aerial photographs (Kemper 2015, MFMR

127   and African Penguin Conservation Project unpubl. data). This method was also applied to the

128   small colony at Possession Island in 2011/12 and 2014/15. We used these eight direct counts of

129   nests to check our model estimates against these cases.

130

131   Generation length (*G*) for Cape Gannets was calculated as:

132
$$G = \frac{A+1}{(1-\phi_a)}$$

133   (1)

134   where A is age of first breeding and ϕ_a is adult survival (Birdlife International 2000). In keeping

135   with the IUCN Red List guidelines, which state "where generation length varies under threat …

136   the more natural, i.e. pre-disturbance, generation length should be used" (IUCN Standards and

137   Petitions Subcommittee 2017), we used A = 4 years and ϕ_a = 0.93 based on Crawford (1999)

138   and the 1990 survival estimates from Distiller et al. (2012).

139

140   To determine the change occurring in the Cape Gannet population over the last 3G years, we

141   used a Bayesian state-space tool for IUCN Red List assessment (Just Another Red List

142   Assessment [JARA], https://github.com/henning-winker/JARA, Winker and Sherley 2019). JARA

143   assumes that the underlying trend in the area occupied (I_t; Figure S1) followed a conventional

144   exponential growth model (e.g. Kéry and Schaub 2012):

145
$$I_{t+1} = I_t \lambda_t$$

146   (2)

147   where λ_t is the growth rate in year t. On the log scale, the state process model was:

148
$$\mu_{t+1,i} = \mu_{t,i} + r_{t,i}$$

149   (3)

150   where $\mu_{t,i} = \log(I_{t,i})$ and $r_{t,i} = \log(\lambda_{t,i})$, the year-to-year rate of change at breeding colony i that

151   is assumed to vary around $\bar{r}_i$ – the underlying mean rate of change for the colony – but with an

152   estimable process variance σ_η^2 that is common to all colonies $r_{t,i} \sim Normal(\bar{r}_i, \sigma_\eta^2)$. The

153   corresponding observation equation is:

154
$$\log(y_{t,i}) = \mu_{t,i} + \epsilon_{t,i}$$

155   (4)

156 where $y_{t,i}$ is the area occupied for year t and $\epsilon_{t,i}$ is the observation residual for year t at breeding

157 colony i. The residual error is assumed to be normally distributed on the log-scale

158 $\varepsilon_{t,i} \sim Normal(0, \sigma_\varepsilon^2)$ as a function of a common observation variance σ_ε^2.

159

160 The estimated posterior of the population size (number of breeding pairs) at each colony became:

161 $$\hat{I}_{t,i} = \exp(\mu_{t,i}) \times \delta_i \times 10{,}000,$$

162 $$\delta_i = gamma(\alpha_i, \beta_i),$$

163 $$\alpha_i = \overline{D}_i^2 / \sigma_{D,i}^2,$$

164 $$\beta_i = \overline{D}_i / \sigma_{D,i}^2$$

165 (5)

166 where δ_i is a colony-specific informative gamma prior for the densities of nests, parameterised

167 via shape (α_i) and rate (β_i) parameters using the observed mean $(\overline{D}_i)$ and SD $(\sigma_{D,i})$ for nesting

168 density (m^2) at each colony. The global population $I_{p,t}$ for year t was computed from the sum of

169 all individual colony trajectory posteriors:

170 $$I_{p,t} = \sum_i \hat{I}_{t,i}$$

171 (6)

172 The percentage change ($C\%$) in numbers at each colony was calculated from the posteriors of

173 the estimated population $(\hat{I}_{t,i})$ as the difference between a three-year average around the final

174 observed data point T, and a three-year average around year $T - (3G)$ (e.g. Figure S2). The year

175 $T + 1$ is always projected to obtain a three-year average around T (to reduce the influence of

176 short-term fluctuations; Froese et al. 2017).

177

178   We implemented JARA in JAGS (v.4.3.0; Plummer 2003) via the "jagsUI" library (v.1.5.1; Kellner

179   2019) for R. The initial for the first modelled count $I_{t=1,i}$ was drawn in log-space from a 'flat' normal

180   distribution with the mean equal to the log of the first observation $y_{t=1,i}$ and a standard deviation

181   of 1000. We used vague normal priors of $Normal(0,1000)$ for $\bar{r}_i$ and inverse gamma priors for

182   both the state and observation process variance of $\sigma^2 \sim 1/gamma(0.001,0.001)$, which is

183   approximately uniform on the log scale (Winker et al. 2018). The model was fitted by running three

184   Monte Carlo Markov chains (MCMC) for 50,000 iterations, with a burn-in of 25,000 and a thinning

185   rate of 5. Convergence was diagnosed using the 'coda' package (Plummer et al. 2006), adopting

186   minimal thresholds of p = 0.05 for Geweke's (1992) diagnostics. Unless otherwise specified, we

187   report medians and 95% Bayesian credible intervals (BCI).

188

189   **Results**

190   *Generation length (G)*

191   Using values of A = 4 years and ϕ_a = 0.93 per annum, we obtained an estimate of G = 18.3 years

192   and 3G = c. 55 years.

193

194   *Nesting densities*

195   Mean (± SD) densities of nests·m^{-2} at the six breeding localities of Cape Gannets were: Mercury

196   Island 3.73 ± 0.57; Ichaboe Island 3.56 ± 0.67; Possession Island 4.39 ± 1.12; Lambert's Bay

197   3.11 ± 0.36; Malgas Island 2.90 ± 0.17; Bird Island, Algoa Bay 3.00 ± 0.276. There was no

198   evidence of a trend in nest densities at any of the three colonies at which densities were obtained

199   in 10 or more seasons (Figure 2).

200

201   *Population count estimates*

202   The state-space model (SSM) estimate for the total number of breeding pairs of Cape Gannets

203   at the six colonies declined from 264,558 (95% BCI: 193,839–365,146) in 1956/57 to 134,775

204   (110,013–166,901) in 2018/19 (Figure S2). In Namibia, estimated numbers declined from c.

205   210,000 pairs, c. 80% of the global population, in 1956/57 to c. 7,000 pairs, or c. 5% of the global

206   population, in 2018/19. Estimated numbers at Mercury Island decreased from c. 9,000 pairs in

207   1956/57 to c. 3,500 pairs in 1969/70, recovered to c. 4,500 pairs in 1978/79 and after 1980

208   fluctuated around c. 2,000 pairs (Figure 3). Cape Gannets occupied much of Ichaboe Island in

209   1956/57 and 1967/68 (Rand 1963, Crawford 1991). In 1956/57, c. 180,000 pairs bred at the island.

210   Estimated numbers declined to c. 50,000 pairs in 1981/82 and fluctuated around this level until

211   the end of the 1980s, then decreased again to a present population of c. 5,000 pairs (Figure 3).

212   The numbers at Possession Island decreased from c. 20,000 pairs in 1956/57 to c. 2,900 pairs

213   from 1980–1992, and then to the present population of c. 130 pairs (Figure 3). Seven of the eight

214   direct counts of nests fell within the 95% credible intervals of the state-space model estimate for

215   the corresponding year and colony (Figure S3).

216

217   In South Africa, fewer than 6,000 pairs bred at Lambert's Bay between 1956/57 and 1978/79. The

218   colony grew to c. 11,000 pairs in 1987/88 and then varied around 10,000 pairs from 1988/89–

219   2003/04. Between c. 5,500 and 7,700 pairs were estimated to have bred there in subsequent

220   years (Figure 3). At Malgas Island, there were about 26,000 pairs between 1956/57 and 1983/84.

221   The colony increased to a peak of c. 52,000 pairs in 1996/97. Since then it decreased in fluctuating

222   fashion to c. 22,000 pairs in 2018/19 (Figure 3). The colony at Bird Island, Algoa Bay grew from

223   c. 22,000 pairs in 1956/57 to c. 95,000 pairs in 2004/05 and subsequently varied around that

224   value (Figure 3).

225

226   *Percentage change (C%) and conservation status*

227 The median *C%* in the global population over the last 3G was estimated as −44.7 (−63.8–−18.9)%

228 (Figure 4), or −1.0% per annum (Figure 5). The median rate of decrease was slower when only

229 the last 2 generations were considered (−0.18% per annum), indicating a period of population

230 stability (Figure 5 and S2). The annual rate of decline appears to have increased again during the

231 most recent generation (−0.97% per annum), though the confidence in this latest estimate was

232 lowest (greatest variance in Figure 5). Overall, the majority (>87%) of the plausible estimates (the

233 posterior probability distribution) for *C%* exceed the decline thresholds for the IUCN threatened

234 categories, with a 56.9% probability that the population meets the A2 criteria for a global

235 classification of Vulnerable (VU; Figure 4) and 31.0% probability of meeting the same criteria for

236 Endangered (EN; Figure 4). Only 0.12% of plausible rates of change were positive.

237

238 **Discussion**

239 *Methodological*Previous estimates gave c. 254,000 and c. 249,000 pairs of Cape Gannets

240 breeding in 1956/57 and 1968/69, respectively (Crawford et al. 2007). Applying the method of

241 Crawford et al. (2007) to the most recent nesting area data suggests c. 135,000 pairs bred in

242 2018/19, a change of c. −46% in the 50 years since 1968/69. This accords well with our SSM

243 estimates, which produced a median decline of −44.7% over the *3G* (54.9 years) prior to

244 2018/2019, from c. 247,000 pairs around 1963/64 to c. 135,000 pairs around 2018/19 (Figure

245 S2). In contrast, densities of nests varied between colonies from 2.9–4.4 m^{-2}, without clear trends

246 at any of the three regularly monitored colonies (Figure 2). This suggests that the area used for

247 nesting expands or contracts in response to increases or decreases in numbers breeding (while

248 nesting density remains relatively constant). Nest sites may be chosen to minimise both

249 aggressive interactions between neighbours (Jarvis 1971) and the loss of eggs and small chicks

250 to predators (de Ponte Machado 2010) as breeding success is higher in the interior of colonies

251 than at their periphery (Staverees et al. 2008, Mullers et al. 2009, Green and Pistorius 2013).

252   Seven of the eight direct counts of nests fell within the 95% credible intervals of the corresponding

253   state-space model estimate (Figure S3). While this gives some credence to our approach for

254   estimating abundance, the direct counts all come from the now relatively small Namibian colonies.

255   Moreover, it is important to emphasize that our results represent modelled population estimates,

256   not direct counts of the number of occupied nests as presented elsewhere (e.g. Kemper 2015).

257

258   It is possible to obtain direct nest counts from aerial photographs, even for the very large gannet

259   colonies (Shelton et al. 1982). While these are likely to be more precise than our estimates, they

260   are more time-consuming to undertake and to date no work has been done to assess the

261   uncertainty associated with that approach. Unmanned aerial vehicles (UAVs or drones) can now

262   be used to census seabird colonies cheaply, accurately and precisely (Hodgson et al. 2018), with

263   minimal disturbance if best-practise guidelines are followed carefully (Brisson-Curadeau et al.

264   2017). Future estimates to census Cape Gannet populations could benefit from using UAV

265   technology to assess the intra-annual variability in colony attendance, to quantify the relative error

266   in using direct counts versus estimates of the area occupied (as applied here), and to calibrate

267   UAV images with aerial photographs from manned aircraft to reduce the cost and increase the

268   frequency of population estimates in future.

269

270   *Conservation status*

271   The most recent IUCN Red List assessment for Cape Gannets reported a −51.5% change in the

272   numbers breeding over 61 years (1956–2017), resulting in a global Red List status of Endangered

273   (Birdlife International 2019). Our revised abundance estimates yielded a lesser decline −44.7%,

274   with the balance of evidence suggesting a global classification of Vulnerable as the most

275   appropriate status. Although the analysis we undertook for the Birdlife International (2019)

276   assessment was also based on a Bayesian SSM model fit, it differed from the analysis reported

277   on in this paper in two keys way. First, that SSM was applied to numbers of breeding pairs that

278   had been calculated without taking into account the uncertainty in the nesting density estimates.

279   In contrast, here we considered both the uncertainty in the nesting density estimates and the

280   estimates of the area occupied by breeding birds in modelling our revised abundance estimates.

281   Greater uncertainty will increase the spread of the posterior probabilities for *%C* across the

282   thresholds for the IUCN threatened categories. Second, we have suggested revising the

283   generation length from 20.2 years (Birdlife International 2019) to 18.3 years based on the results

284   of Crawford (1999) and Distiller et al. (2012). This is the main reason for our more conservative

285   estimate in the median decline of −44.7% versus −51.5%, as the greatest rate of decrease in the

286   Cape Gannet population occurred as a result of large losses of gannets in Namibia in the 1960s

287   and early 1970s (Figure 3 and S2) following the loss of sardine stocks in the Northern Benguela

288   (Roux et al. 2013). With a shorter generation time, these early declines contribute less to the 3G

289   decline estimates in our results than in those used by Birdlife International (2019). Moreover,

290   these losses were ameliorated to some extent by increases at South African colonies in the 1980s

291   and 1990s (Figure 3), initially in the Western Cape as sardine and anchovy recovered in the

292   Southern Benguela, then at Bird Island, Algoa Bay, as these fish shifted eastwards (Roy et al.

293   2007, Coetzee et al. 2008). However, while the current analysis suggests a global Red List status

294   of Vulnerable would be appropriate, it is worth noting that substantial decreases at South Africa's

295   two western colonies in the most recent 1G (since 2000) have again accelerated the rate of

296   decrease (Figure 5).

297

298   *Regional population change*

299   The redistribution of Cape Gannets after 1967/68 in an anti-clockwise direction, from northwest

300   to southeast around the southern African coast, is thought to have resulted from a similar

301   relocation of its main prey species, sardine and anchovy (Crawford et al. 2007, 2015). Sardine off

302   Namibia was depleted through overfishing in the 1960s and 1970s and has not recovered (e.g.

303   Roux et al. 2013). In South Africa, there was a movement of mature sardine and anchovy from its

304   west to south coasts at the end of the 1990s and in the present century sardine has been heavily

305   exploited west of Cape Agulhas (Roy et al. 2007, Coetzee et al. 2008). Additionally, there was a

306   substantial decrease in the epipelagic availability of sardine and anchovy off South Africa's west

307   coast after 2003 (Crawford et al. 2019).

308

309   Cape Gannets likely colonised Halifax and Possession islands in the mid-19th century, possibly

310   due to displacement of birds from Ichaboe Island during intensive harvesting of guano there from

311   1843–1845 (Crawford et al. 1983). However, they did not establish a new colony off South Africa

312   during their recent redistribution. Seal Island in False Bay, where they had previously bred

313   (Crawford et al. 1983), was fully occupied by Cape Fur Seals *Arctocephalus pusillus* at this time

314   (Shaughnessy 1984) and attempts to settle at Robben Island in c. 1968 and Dyer Island in

315   1984/85 (Berruti 1985, Crawford et al. 1986) may have been cut short by disturbance. The result

316   is that >70% of all Cape Gannets now nest at Bird Island, Algoa Bay, at the eastern extremity of

317   their breeding distribution, where the population seems to have reached an asymptote (Figure 3).

318   Gannets at this colony are in poorer condition than those at the smaller South African colonies

319   and have to work harder to find food, probably as a result of intra-specific competition (e.g.

320   Moseley et al. 2012, Rijklief 2016). Outside their breeding season, adult Cape Gannets may

321   disperse > 1,000 km from colonies and juvenile birds may move > 2,000 km (Broekhuysen et al.

322   1961, Klages 1994), but there are no suitable breeding localities for the species in southern Africa

323   east of Bird Island, Algoa Bay.

324

325   *Threats*

326   Present threats to Cape Gannets include scarcity of nutritious prey, mortality in fisheries,

327   predation at or around colonies, disturbance at (see above) or displacement from colonies, oiling,

328   disease and extreme weather events. Each of these pressures is discussed briefly below.

329

330   Although Cape Gannets are able to switch their prey (e.g. Crawford et al. 2014, Grémillet et al.

331   2019), scarcity of good-quality prey is thought to be the main cause of their ongoing population

332   decrease (e.g. Lewis et al. 2006, Pichegru et al. 2007, Cohen et al. 2014, Crawford et al. 2015).

333   The numbers of Cape Gannets breeding in both Namibia and South Africa were significantly

334   related to the biomass of sardine and anchovy (Crawford et al. 2007). In western South Africa,

335   they were also related to the epipelagic availability of these prey species (Crawford et al. 2019).

336   Scarcity of energy-rich prey may decrease the proportion of adult Cape Gannets that breed

337   (Crawford and Dyer 1995) and may have influenced recent variability in numbers of nests at

338   colonies (see Figure 3). It may also reduce breeding success (e.g. Crawford 1999, Grémillet et

339   al. 2008, Cury et al. 2011), inhibit chick growth (Mullers et al. 2009) and nest attendance

340   (Rishworth et al. 2014), increase foraging effort (Grémillet et al. 2016) and negatively impact adult

341   body condition (Cohen et al. 2014). Parents in better body condition spent longer periods at their

342   nests (Rishworth et al. 2014). Faced with scarcity of their natural prey, Cape Gannets exploited

343   fishery waste from trawlers (Tew Kai et al. 2013) but this low-quality resource still results in low

344   adult body condition and reproductive performance (Moseley et al. 2012).

345

346   Considerable numbers of Cape Gannets were killed off southern Africa in demersal-trawl and

347   demersal- and pelagic-longline fisheries at the turn of the recent century (Watkins et al. 2008,

348   Petersen et al. 2009a, 2009b) but numbers killed off South Africa have subsequently been much

349   reduced via mitigation measures (Maree et al. 2014, Rollinson et al. 2017). Many juveniles were

350   exhausted on arrival off Angola and easily killed by fishermen there (Broekhuysen et al. 1961).

351   The extent to which such deliberate killing for food continues is unknown.

352

353   Cape Fur Seals killed an estimated 27,000 fledglings around Malgas Island over the course of

354   three breeding seasons (Makhado et al. 2006) and > 900 gannets around Ichaboe Island in May

355   2000 (du Toit et al. 2004). Fur seals caused cessation of breeding at Hollam's Bird Island between

356   1938 and 1956 by entirely displacing gannets from that locality (Crawford et al. 1983) and, by

357   attacking adults ashore, they also caused the abandonment of the colony at Lambert's Bay in

358   2005/06 (Wolfaardt and Williams 2006) and of c. 10% of the colony at Malgas Island in 2017/18

359   (Dyer et al. 2018). The removal of some damage-causing animals has prevented further losses.

360   At Ichaboe and Bird, Algoa Bay islands, periods of non-attendance by parents caused by poor

361   foraging conditions resulted in many eggs or small chicks being eaten by Kelp Gulls *Larus*

362   *dominicanus* (Mullers and Tinbergen 2009, Rishworth and Pistorius 2015). At Lambert's Bay,

363   between 2009 and 2013, Kelp Gulls ate an average of 13% of eggs laid by Cape Gannets (Saul

364   and Fortuin 2015). At Malgas Island, Kelp Gulls took 10–70% of the colony's egg production

365   between 2012 and 2018 (Pichegru 2017, SANParks unpublished data). In addition, Great White

366   Pelicans *Pelecanus onocrotalus* have eaten gannet chicks at Malgas Island, especially smaller

367   individuals (Pichegru et al. 2007, de Ponte Machado 2010), although active management put in

368   place by South African National Parks since 2008 has drastically reduced their impact.

369

370   Oil-spills are a serious threat to Cape Gannets. In 1979, fish oil killed at least 709 gannets at

371   Lambert's Bay but improvements in fish-offloading techniques lowered this risk (Crawford et al.

372   1983). However, fish oil from vessels processing fish or on-shore factories poses a chronic threat

373   to gannets in Namibia (du Toit and Bartlett 2001, Kemper 2015). In 1983, oil spilt by the *Castillo*

374   *de Bellver* affected > 5,000 Cape Gannets in the vicinity of Saldanha Bay; c. 1,500 were caught,

375   of which 65% were de-oiled and successfully released (Wolfaardt et al. 2009). De-oiled birds had

376   only slightly lower survival rates than un-oiled gannets (Altwegg et al. 2008). Recent harbour

377   developments in Algoa Bay are likely to increase the risk of oil fouling seabirds in that region

378   (Adeniji et al. 2017). This is of concern for Cape Gannets given that 70% of the global population

379   now occurs at Bird Island, Algoa Bay.

380

381   Avian cholera *Pasteurella multocida* killed 172 Cape Gannets at Malgas Island in 1991 and almost

382   400 at Lambert's Bay in 2002 (Crawford et al. 1992, Ward and Williams 2004). In 2018, avian

383   influenza (H5N8) was confirmed in Cape Gannets in South Africa and may have killed > 1,600

384   birds (Khomenko et al. 2018, Roberts 2018). At Lambert's Bay, four heat waves (35–40ºC) killed

385   80 adult gannets attempting to shelter their nests in 1998 and 2000 (Ward and Williams 2004).

386   Storms (heavy rain and strong winds) can also cause shorter nest attendance times and mortality

387   of Cape Gannet chicks (Crawford et al. 1986, Rishworth and Pistorius 2015, Pistorius et al. 2015).

388

389   *Conservation interventions*

390   Assuming an age at first breeding of 4 years, and annual survival of birds aged ≥ 2 years and < 2

391   years of 0.91 and 0.71, respectively (Crawford 1999), an annual production of 0.32 fledglings per

392   pair is required to maintain a (closed) Cape Gannet population in equilibrium (Makhado et al.

393   2006). Long-term averages in breeding success have generally exceeded 0.32 fledglings per pair

394   (e.g. Adams et al. 1992, Staverees et al. 2008, Crawford et al. 2019). In contrast, annual survival

395   of adult Cape Gannets averaged 0.83 at Lambert's Bay, 0.88 at Malgas Island and 0.90 at Bird

396   Island, Algoa Bay from 1990–2009 (Distiller et al. 2012), and mortality immediately after fledging

397   was deemed too high to sustain the population at Malgas Island (Makhado et al. 2006). Although

398   better information on juvenile and immature survival and on demographic parameters at Namibian

399   colonies is required, recruitment rather than adult survival may be limiting the Cape Gannet

400   population (Distiller et al. 2012). In South Africa, adult Cape Gannets buffer their survival in

401   periods of scarcity of sardine and anchovy by switching their diet to include saury or less nutritious

402   hake offal discarded by bottom trawlers (Crawford et al. 2014, Grémillet et al. 2019), but this can

403   have demographic implications through reduced breeding success and lower chick quality (e.g.

404   Grémillet et al. 2008, but cf. Grémillet et al. 2019).

405

406   In order to improve the conservation status of Cape Gannets it will be necessary to maintain the

407   present high rates of adult survival while at the same time increasing recruitment. The major

408   threats to adult survival are mortality caused by fisheries, oiling and outbreaks of disease, which

409   can be countered by requiring fisheries in the Benguela ecosystem to implement best practice

410   by-catch mitigation, by marine spatial planning that minimises the risk of oil spills near colonies,

411   where gannets have their highest densities, and by implementing standard protocols to reduce

412   the possibility of pathogens spreading, e.g. rapid disposal of carcases (e.g. Khomenko et al.

413   2018). Recruitment seems to be mainly limited by insufficient high-quality prey off west southern

414   Africa, and by disturbance and high post-fledging mortality inflicted by Cape Fur Seals around

415   some colonies. Predation mortality at or near colonies can be reduced by removing damage-

416   causing animals (e.g. Makhado et al. 2009).

417

418   Although it would not reverse the changes in the distribution and availability of their main prey

419   species, ecosystem-based management should implement forage thresholds (e.g. Cury et al.

420   2011, Crawford et al. 2019) and marine spatial planning (e.g. Distiller et al. 2012) to ensure

421   sufficient food for Cape Gannets and other seabirds (e.g. Sherley et al. 2017, 2018). In South

422   Africa, there is substantial overlap of areas where gannets feed when breeding and where purse-

423   seiners catch sardine and anchovy (Okes et al. 2009, Pichegru et al. 2009), whereas in Namibia,

424   although some core gannet feeding areas fall within the Namibian Islands' Marine Protected Area

425   (MPA) (Ludynia et al. 2012), an improvement in forage resources for gannets depends on the

426   recovery of the Namibian sardine stock. The new Greater Addo MPA in Algoa Bay, and in

427   particular the eastward extension of the MPA from Bird Island, may benefit Cape Gannets in future

428   as breeding adults generally forage to east of the island, albeit often far outside the bay (Botha

429   and Pistorius 2018). Given a lack of alternative breeding localities in the east, it is particularly

430   important to stabilise the deceasing smaller colonies in the west, where the impact of top-down

431   processes is expected to increase as colony size decreases (Crawford et al. 2018).

432

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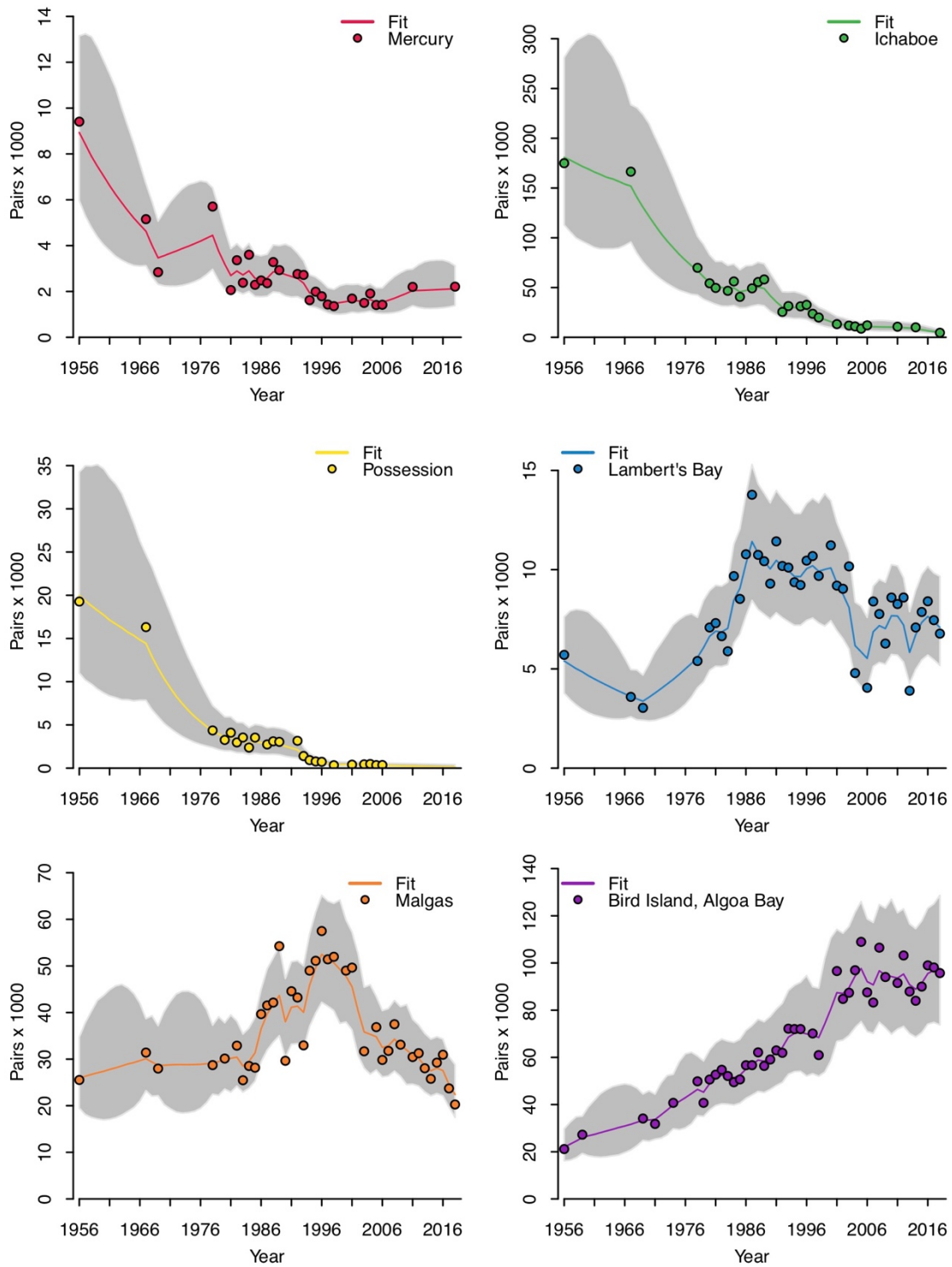700   *Journal of Marine Science* 31: 31–54.

701 **Figures**
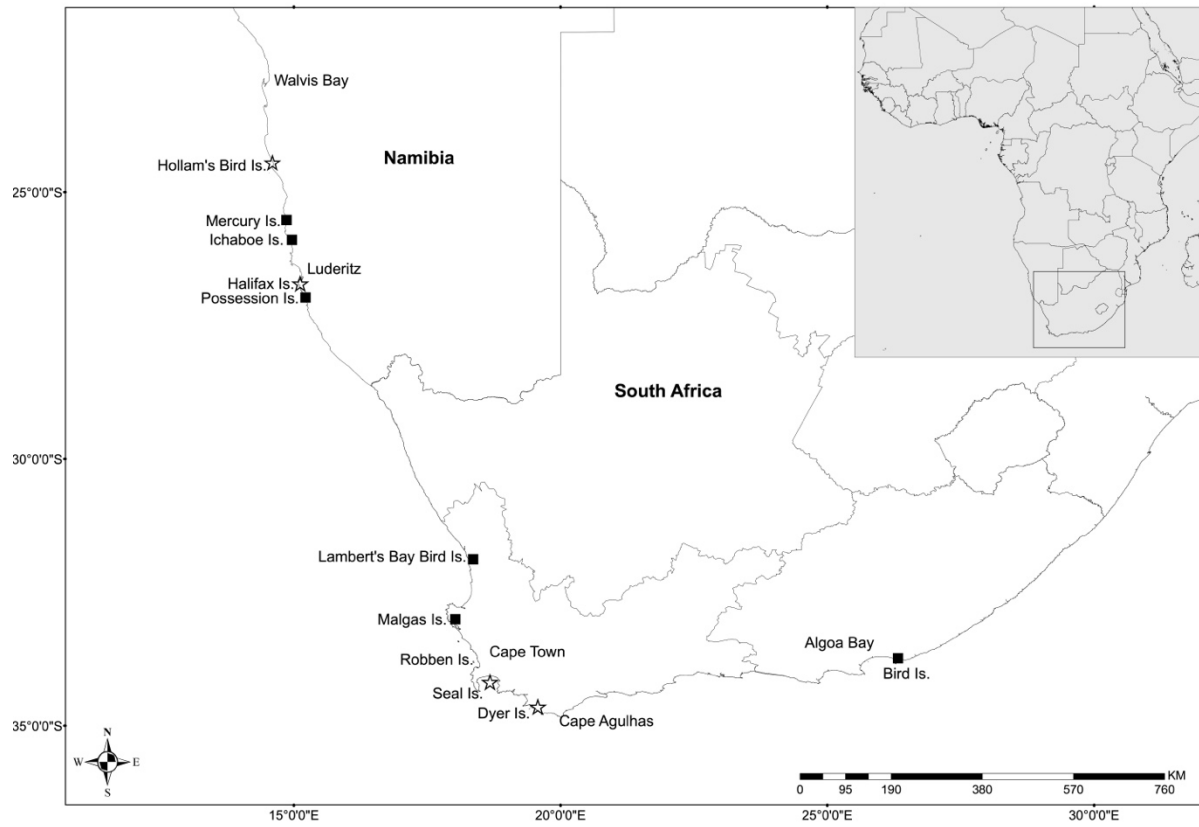
702
703 **Figure 1:** Locations of extant (black squares) and extinct (white stars) colonies of Cape Gannets
704 *Morus capensis* and other southern African localities mentioned in the text.
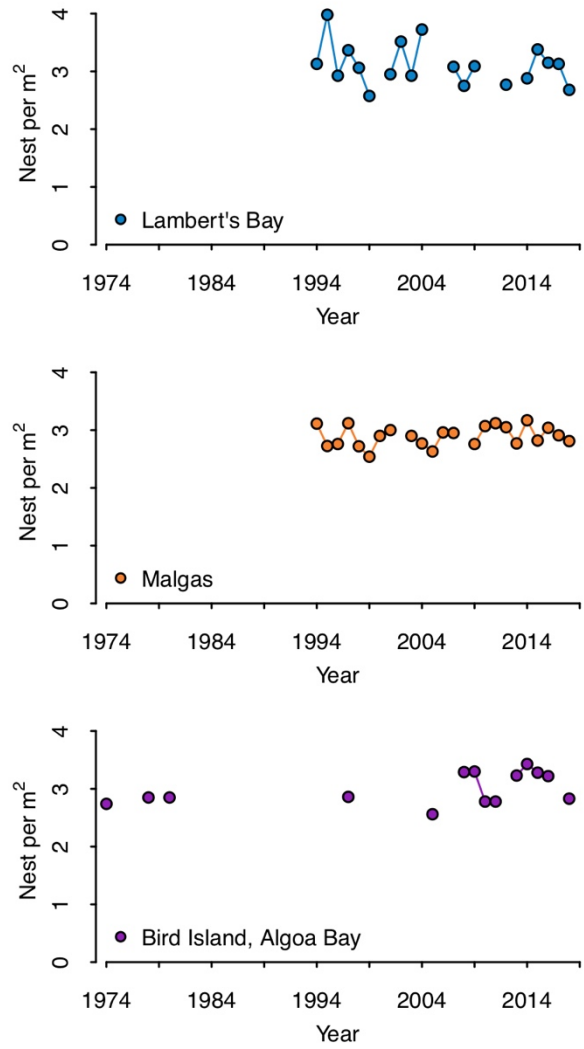
705
706 **Figure 2:** The densities of Cape Gannet *Morus capensis* nests at the three extant South African
707 colonies, 1974–2018.

Figure 3: Bayesian state-space model estimates (coloured lines) and 95% credible intervals (grey polygons) of the number of Cape Gannet *Morus capensis* breeding pairs at the six extant colonies, 1956/57–2018/19. Coloured points show the raw estimated number transformed from the area occupied by breeding gannets in each year and the mean nesting density (see methods for details).
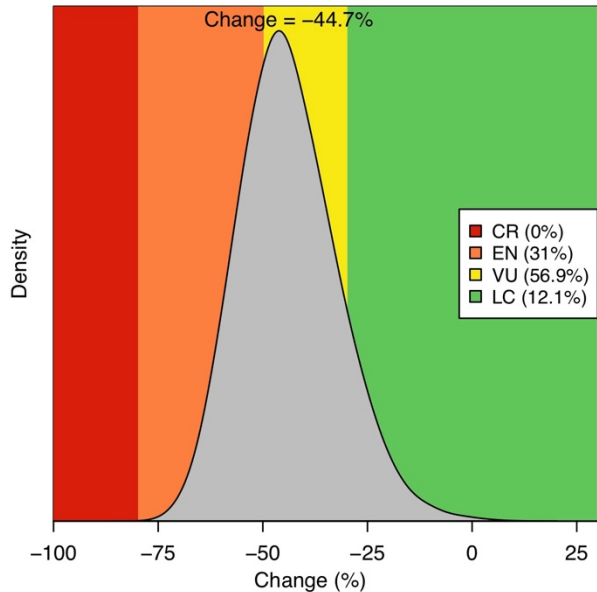
714
715 **Figure 4:** Posterior probability density of the percentage change (*C*%) of the overall population
716 of Cape Gannets *Morus capensis* over three generation lengths (3G). Note that all probabilities
717 are negative and the median rate of change −44.7%.
718
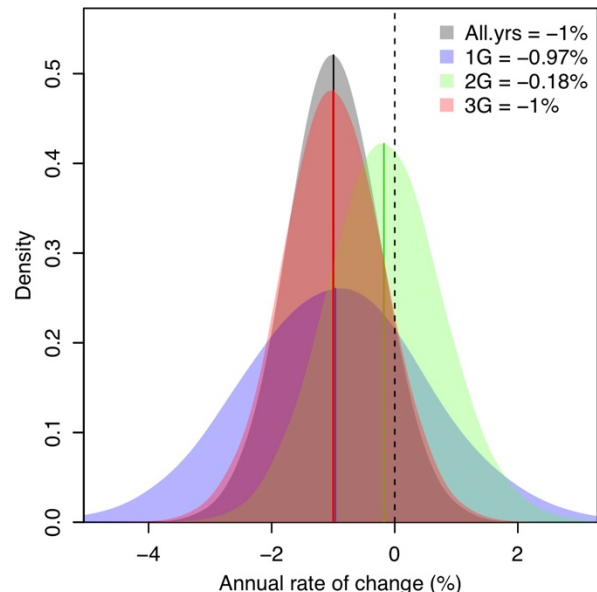
719
720 **Figure 5**: Posterior probability densities for the annual rate of change of the overall population of
721 Cape Gannets *Morus capensis* over the last three generations (3G), the two most recent
722 generations (2G), the years corresponding to the most recent generation (1G) and for all available
723 years (All.yrs). The generation length was G=18.3 years.

Supporting Information

Table S1. Bayesian State-space model estimates of the numbers of Cape Gannets (thousand pairs) that bred at the species' six extant colonies, 1956–2018 based on estimates of areas occupied by breeding Cape Gannets (Figure S1) obtained from aerial photographs or GPS measurements[a] and mean densities of nest at each colony. See main text for methods.

Year	Mercury Is.	Ichaboe Is.	Possession Is.	Lambert's Bay	Malgas Is.	Bird Is., Algoa Bay
1956	8.93	180.77	19.98	5.40	25.93	21.93
1957	8.42	178.04	19.35	5.20	26.33	23.22
1958	7.90	174.92	18.78	5.01	26.72	24.55
1959	7.46	171.75	18.25	4.85	27.06	26.05
1960	7.04	169.05	17.73	4.66	27.38	26.76
1961	6.62	166.04	17.13	4.49	27.79	27.36
1962	6.23	163.61	16.69	4.33	28.13	28.09
1963	5.87	160.82	16.25	4.18	28.54	28.82
1964	5.52	159.16	15.73	4.03	28.96	29.49
1965	5.20	156.65	15.33	3.88	29.26	30.26
1966	4.91	153.95	14.84	3.75	29.68	30.90
1967	4.63	151.97	14.43	3.60	30.09	31.61
1968	4.01	140.75	12.89	3.49	29.37	32.49
1969	3.47	130.73	11.56	3.37	28.69	33.32
1970	3.56	121.57	10.36	3.57	28.68	33.45
1971	3.67	112.67	9.30	3.79	28.77	33.68
1972	3.76	104.23	8.30	4.01	28.83	35.63
1973	3.87	96.71	7.46	4.24	28.83	37.69
1974	3.97	89.93	6.67	4.47	28.82	39.83
1975	4.08	83.31	5.99	4.73	28.84	41.32
1976	4.20	77.41	5.38	5.00	28.88	42.92
1977	4.32	71.99	4.81	5.27	29.02	44.64
1978	4.45	67.01	4.33	5.58	29.06	46.42
1979	3.75	60.73	3.93	6.07	29.49	45.26
1980	3.19	55.23	3.57	6.64	29.87	48.84
1981	2.70	51.48	3.57	6.90	30.18	51.15
1982	2.89	50.05	3.21	6.86	30.43	52.47
1983	2.72	48.64	3.16	7.05	28.51	51.98
1984	2.90	49.59	2.85	8.47	29.50	51.39
1985	2.57	45.64	3.06	9.06	31.34	52.43
1986	2.55	47.06	2.94	10.30	36.49	55.04
1987	2.58	48.55	2.83	11.41	39.71	56.86
1988	2.86	50.48	2.86	10.82	41.71	58.86
1989	2.83	49.03	2.77	10.41	43.64	58.36
1990	2.74	41.84	2.53	10.04	38.02	59.89

						
1991	2.65	35.65	2.33	10.47	41.13	62.26
1992	2.57	30.41	2.14	10.18	41.37	64.21
1993	2.36	30.38	1.44	9.95	40.05	68.57
1994	1.94	29.94	1.03	9.66	45.89	70.20
1995	1.88	29.44	0.81	9.65	49.57	70.60
1996	1.73	27.98	0.68	10.05	52.48	69.96
1997	1.54	23.66	0.54	10.20	51.51	69.41
1998	1.47	20.29	0.43	9.92	50.66	68.38
1999	1.51	17.84	0.42	10.01	49.25	74.19
2000	1.56	15.75	0.41	10.09	47.79	80.54
2001	1.61	13.87	0.41	9.32	45.54	87.43
2002	1.59	12.73	0.41	8.76	40.37	87.08
2003	1.58	11.75	0.42	8.10	35.83	89.55
2004	1.65	10.87	0.41	6.17	35.33	94.43
2005	1.53	10.11	0.37	5.86	34.80	97.64
2006	1.52	10.81	0.34	5.53	32.51	92.12
2007	1.61	10.63	0.32	6.87	32.84	90.73
2008	1.71	10.47	0.29	7.18	34.28	[a]96.69
2009	1.81	10.34	0.27	[a]7.03	33.02	[a]94.81
2010	1.92	10.24	0.25	7.68	31.96	94.24
2011	2.04	10.10	0.23	7.66	30.88	93.61
2012	2.04	9.65	0.21	7.21	30.15	[a]95.31
2013	2.05	9.24	0.19	[a]5.83	28.57	[a]90.79
2014	2.07	8.83	0.18	6.72	27.50	[a]88.88
2015	2.08	7.66	0.16	7.34	28.08	[a]91.46
2016	2.09	6.65	0.15	[a]7.64	27.55	[a]95.51
2017	2.10	5.80	0.14	7.38	[a]24.55	96.93
2018	2.12	5.04	0.13	7.09	22.43	[a]97.52
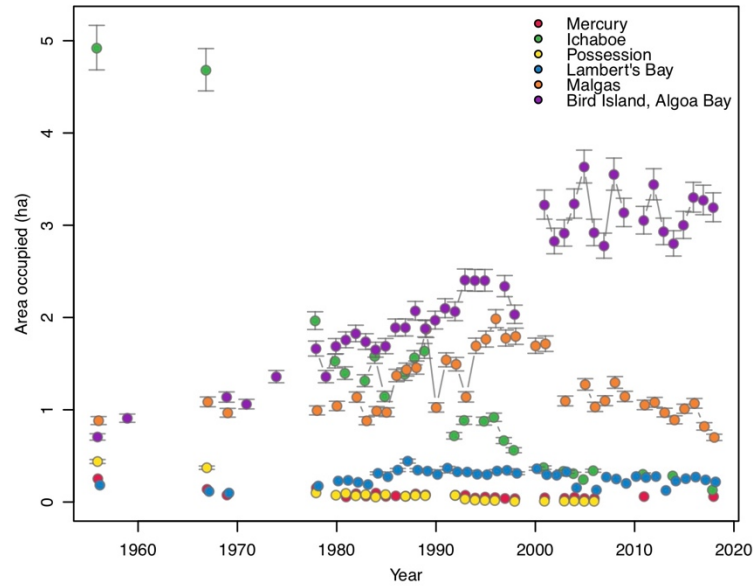
Figure S1: Time series of estimates of the area occupied by breeding Cape Gannets *Morus capensis* at the species' six extant colonies, 1956–2018.
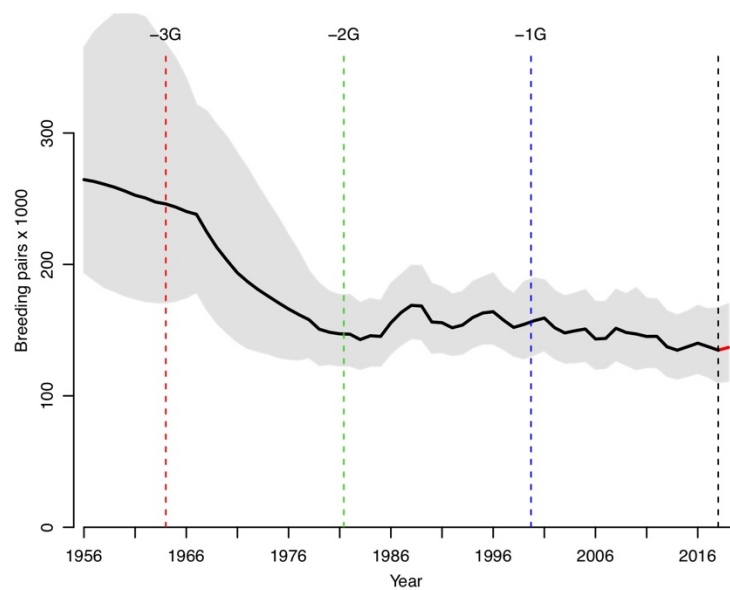

Figure S2: Estimated trajectory (black line) of the total number of breeding pairs of Cape Gannets *Morus capensis* at the species' six extant colonies combined, 1956–2018, from the Bayesian state-space model and 95% Bayesian credible intervals (grey polygon). Vertical dashed lines show the time span from the final observation (2018/19) of 1 generation lengths (−1G; 18.3 years; blue line), 2 generation lengths (−2G; 36.6 years; green line) and (−3G; 54.9 years; red line).
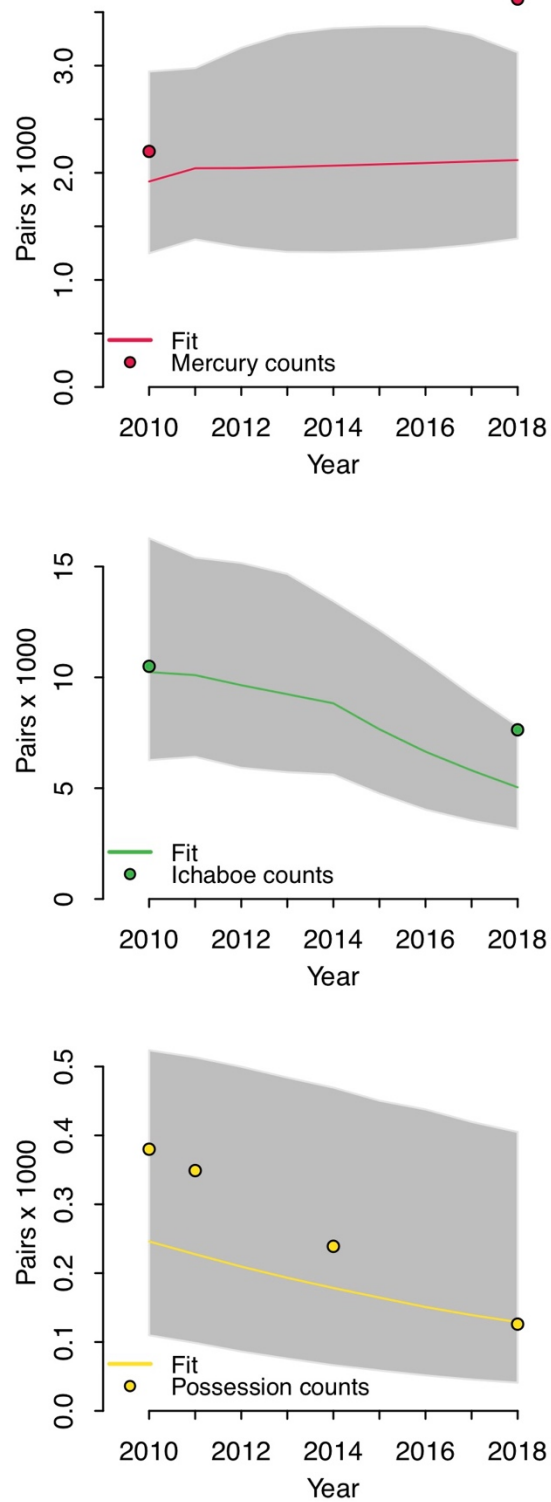
Figure S3: Bayesian state-space model fits (coloured lines) and 95% credible intervals (grey polygons) for the estimated number of Cape Gannet *Morus capensis* breeding pairs at its three Namibian colonies, 2010/11–2018/19, compared against direct counts of the numbers of Cape Gannet nests at these colonies made from aerial photographs (coloured points).