Quantifying climate change impacts emphasises the importance of managing regional threats in an endangered species

Thomas Mattern[1,2,*], Stefan Meyer[1], Ursula Ellenberg[2], David M. Houston[3],

John T. Darby[4], Melanie Young[1], Yolanda van Heezik[1], Philip J. Seddon[1]

[1] Department of Zoology, PO Box 56, University of Otago, Dunedin, NZ

[2] Department of Ecology, Environment and Evolution, La Trobe University, Melbourne, Australia

[3] Science and Policy Group, Department of Conservation, Private Bag 68 908, Newton, Auckland, NZ

[4] Otago Museum, PO Box 6202, Dunedin, NZ

* corresponding author: (email) t.mattern@eudyptes.net, (phone) +64 27 6003036

Abstract

As a global issue the effects of climate change are difficult to manage on a region scale. However, more often than not it is only one of many problems that need to be addressed in species conservation. Non-climatic factors – especially those of anthropogenic origins – play equally if not more important roles with regards to population developments of species and often provide much better toeholds for conservation activities. We examined the population trends of the endangered Yellow-eyed penguin (*Megadyptes antipodes*) in New Zealand using monitoring data dating back to the 1980s. We developed a Bayesian population model incorporating various climatic factors to assess the relative influence of climate change on the penguin numbers over the past 30 years. Sea surface temperature (SST) proved to be the dominating factor influencing survival of both adult birds and fledglings. Increasing SST since the mid-1990s went along with a reduction in survival rates and population decline. The population model showed that 33% of the variation in population numbers could be explained by SST alone, significantly increasing pressure on the penguin population. Consequently, the population becomes less resilient to non-climate related impacts, such as fisheries interactions, habitat degradation and human disturbance. But their exact contribution towards population trends is extremely difficult to assess principally due to the absence of quantifiable data. This potentially creates an analysis bias towards climate variables, effectively distracting from non-climate factors that can be managed on a regional scale to ensure the viability of the population.

Keywords

1. Introduction

Climate change significantly alters the phenology and distribution of the world's fauna and flora (Parmesan 2006). In particular, species with spatially limited distributions suffer from climate-related change in their habitats which can drive range shifts (e.g. Grémillet and Boulinier 2009; Sekercioglu et al. 2008), range restrictions (Sexton et al. 2009) or, in the worst case, extinction (Thomas et al. 2004). Current climate predictions suggest that the pressure on ecosystems will continue to increase (Stocker 2014), especially affecting species that occupy fragmented habitats. The spatial segregation of suitable habitat might preclude range shift adjustments and increase the risk of local extinctions (Opdam and Wascher 2004).

For species conservation, this creates a daunting scenario. With resources for conservation often limited, the inevitability of climate change could be used as an argument against taking action to conserve species at locations that could be predicted to become sub-optimal due to environmental change (Sitas et al. 2009). However, more often than not, cumulative anthropogenic impacts (e.g. habitat destruction, pollution, resource competition, accidental mortality) significantly add to – or even exceed – the impact of climate-related environmental change (Parmesan and Yohe 2003; Trathan et al. 2015). While climate change is a global issue that is difficult to tackle on a regional scale, addressing local-scale anthropogenic factors could enhance species resilience to environmental change.

The New Zealand endemic Yellow-eyed penguin (YEP, *Megadyptes antipodes*) illustrates the complexity of this issue. YEP is a species of significant cultural and economic value for New Zealand (Seddon et al. 2013a). Particularly the tourism industry of the Otago Peninsula benefits from the presence of the birds with the annual contribution per breeding pair to the local economy estimated to range around NZ$250,000 (Tisdell 2007). Ensuring the survival of the species is therefore not only a matter of ethical considerations, but also of economic importance.

With an estimated 1,700 breeding pairs it is one of the rarest penguin species world-wide (Garcia Borboroglu and Boersma 2013). Compared to other penguins, the YEP's distributional

60   range is fairly limited. About 60% of the species' population is thought to inhabit the sub-

61   Antarctic Auckland and Campbell Islands, while the remaining ∼40% breed along the south-

62   eastern coastline of New Zealand's South Island (Seddon et al. 2013a). Genetic analyses revealed

63   that there is virtually no gene flow between the sub-Antarctic and mainland YEP populations

64   (Boessenkool et al. 2009b).

65   While little is known about the sub-Antarctic populations, mainland YEPs have received

66   considerable scientific attention. The first comprehensive studies of breeding biology and

67   population dynamics were carried out in the first half of the 20th century by Lance Richdale

68   (Richdale 1949, 1951, 1957). Interest in the species waned after Richdale's retirement from

69   active research, but was rekindled in the late 1970s (Darby 1985b). Regular monitoring of some

70   breeding sites commenced in the early 1980s, and was expanded and intensified following a

71   catastrophic die-off affected breeding adult penguins on the Otago Peninsula in the austral

72   summer of 1989-90 (Efford et al. 1996). Parts of the population have been monitored without

73   interruption since 1982 resulting in a data set spanning more than three decades (Ellenberg and

74   Mattern 2012). Numbers of breeding pairs have been subject to considerable inter-annual

75   fluctuations making it difficult to identify long-term trends (Seddon et al. 2013a). Yet, a recent

76   review of available information revealed that a steady decline of the population might have been

77   masked by more intensive monitoring in the past decades (Ellenberg and Mattern 2012).

78   Most New Zealand penguin species including YEPs are believed to have undergone significant

79   population declines in the past century, with climate change suspected to be playing a major role

80   (e.g. Peacock et al. 2000, Cunningham and Moors 1994). At the same time, penguin populations

81   are exposed to numerous anthropogenic threats (Trathan et al. 2015). Climatic variables and

82   anthropogenic influences create a complex mix of factors that make it challenging to decipher

83   the causation of population developments.

84   Using population data recorded between 1982 and 2015 from one of the YEP's mainland

85   strongholds, we set out to develop a population model that integrates observed population

86   changes with key climatic variables. While climate data is readily available as continuous data

87   sets, data on anthropogenic factors is often sparse or of low temporal and spatial resolution

88   which inhibits quantitative analysis. We assess to which extent population trends can be

89   attributed to climate change and discuss the importance of other, more manageable threats for

90   the long-term viability of the mainland YEP population.

2. Methods

2.1 Species information

93   The IUCN Red list classifies Yellow-eyed penguins as "Endangered" (BirdLife International

94   2012), and they are listed as "Nationally Vulnerable" under the New Zealand Threat

95   Classification System (Robertson et al. 2013). The three main subpopulations are estimated to

96   range between 520-570 breeding pairs (Auckland Islands), 350-540 pairs on Campbell Island,

97   and 580-780 pairs along New Zealand's south-eastern coastlines and Stewart Island (Seddon et

98   al. 2013b). On the mainland, the Otago Peninsula represents the species' stronghold where

99   numbers of breeding pairs in the past three decades have been as high as 385 in 1996, but have

100   steadily declined over the last 20 years to only 108 pairs in 2011 (Ellenberg and Mattern 2012).

101   Yellow-eyed penguins breed in the austral summer (September-February) so that their annual

102   breeding period spans the turn of the calendar year. Socialising and courtship in July marks the

103   onset of a new breeding season that ends in March/April with annual moult and subsequent

104   replenishing of resources in preparation for the next breeding season (Seddon et al. 2013a).

105   Hence, we used austral year (i.e. July to June) to calculate means and for summarising annual

106   statistics of demographic and environmental parameters.

2.2 Study sites

108   The Otago Peninsula penguin population has received considerable scientific attention in the

109   past century, with Richdale conducting his seminal population research between 1936 and 1954

110   (Richdale 1949, 1951, 1957), followed by a string of projects from the 1980s onwards

111   addressing many aspects of the Yellow-eyed penguin's biology including phylogeny (e.g.

112   Boessenkool et al. 2009a), breeding biology (e.g. Darby and Seddon 1990), diet (e.g. van Heezik

113   1990), foraging ecology (e.g. Mattern et al. 2007), and conservation (e.g. Ellenberg et al. 2007).

114   While Richdale conducted most of his work at Kumo Kumo Whero Bay, most of the recent

115   research was carried out at the Boulder Beach complex (Fig 1) which, as a result, has the longest

116   ongoing population monitoring program and the most reliable data set available (Ellenberg and

117   Mattern 2012).

2.3 Population monitoring & Yellow-eyed penguin database (YEPDB)

119   Flipper banding of Yellow-eyed penguins commenced at Boulder Beach in the 1970s and by the

120   mid-1980s the majority of the local population was marked. Annual nest searches were

121   conducted to determine number of breeders and repeated nest checks provided information on

122   identity and reproductive success (Darby 1985a). After a catastrophic adult die-off during the

123   1989 breeding season (Gill and Darby 1993), monitoring was intensified to include 60% of the

124   known South Island breeding sites (Seddon et al. 2013b). The Yellow-eyed penguin database

125   (YEPDB) was created in the early 1990s (Efford et al. 1994) and is maintained by the New

126   Zealand Department of Conservation (DOC) which also oversees the YEP monitoring program.

127   At the time of writing, the database contained banding records for 13,788 penguins (date range:

128   1973-2013), and 9,006 nest records (range: 1979-2014). It also holds information on incidental

129   penguin recoveries or sightings outside the breeding season; however, these recovery data are

130   patchy and were deemed too unreliable for analysis.

2.4 Data

2.4.1 Demographic data

133   Nearly one third of all banding records (n=3,733) and nest records (n=2,342) originate from

134   Boulder Beach (Fig 1) providing consistent, uninterrupted monitoring data for our analyses.

135   While monitoring commenced in the late 1970s, first complete data sets are available from 1982

136   onwards, although for the first season there are only records of six nests.

137   Data were extracted from YEPDB as a series of SQL queries. Population numbers were retrieved

138   from the table holding nest records. Number of breeding adults is number of nests times two;

139   number of fledglings is the sum of chicks fledged from all nests, and number of new breeders

140   represents the sum of all adults that were recorded for the first time as breeders. Where

141   possible we determined age of breeding birds per year by querying their banding details; age is

142   unknown for birds banded as adults (ca. 15% of all banded birds).

143   To estimate demographic parameters, we first extracted ID numbers for individuals banded at

144   the Boulder Beach complex since 1982. Secondly, we identified the years in which each bird was

145   recorded as a breeding adult in the nest record table. Finally, we compiled the information from

146   both database queries into a table where each column represented a nest year and rows

147   comprised encounter histories for each individual. Birds had to miss out at least two consecutive

148   breeding seasons before being defined as dead or senescent. In a small number of cases a bird

149   was not recorded as a breeder for three or more consecutive years before remerging as a nest

150   occupant, but this applied to fewer than 1% of all birds.

151   ***2.4.2 Environmental data***

152   We obtained monthly averages for selected climatic variables deemed likely to have an influence

153   on demographic parameters (Table 1). The National Climate Database (CliFlo,

154   http://cliflo.niwa.co.nz) has kept records from weather stations in Dunedin and the Otago

155   Peninsula continuously since the early 20th century. Austral annual means were calculated for

156   each parameter (i.e. July – June) as well as for the months March to May, which covers the

157   penguins' annual moult and post-moult periods. During this time birds are particularly

158   susceptible to environmental perturbations due the increased energy requirements for feather

159   replacement (Croxall 1982). Data on local sea surface temperatures (SST) were obtained from

160   the Portobello Marine Laboratory (University of Otago) which holds a near continuous time

161   series of daily measurements dating back to January 1953. We calculated the monthly SST

162   anomaly by subtracting monthly means from the average value calculated from all monthly

163   means ranging from January 1953 to December 2014; annual SST anomaly is the mean of

164   monthly SST anomalies for the corresponding year. To examine for potential lag effects of SST

165   anomaly on prey availability (see Beentjes and Renwick 2001), we also examined SST anomalies

166   shifted backwards in time by one and two years.

2.5 Population model

168   We estimated adult survival and fledgling survival by developing a Bayesian mark-recapture

169   (MR) model that incorporated effects of climate parameters. Chicks are only banded shortly

170   before fledging, so that the MR model could not consider hatchlings that died before they were

171   marked (i.e. chick survival). Hence, fledgling survival was adjusted by incorporating the

172   proportion of chicks fledged to chicks hatched. We modelled survival in any year as a random

173   process ranging around a mean of zero within the bounds of a total temporal variance. This

174   allowed us to determine the relative importance of each climate covariate in terms of percentage

175   of total variance explained (Grosbois et al. 2008). For models with covariates explaining at least

176   20% of the total variance, we estimated posterior model probabilities using Gibbs Variable

177   Selection (GVS, Tevacchia et al. 2016)

178   Subsequently, we modelled YEP population dynamics via a female-only model assuming a birth-

179   pulse population (Tang and Chen 2002). The effect of environmental factors on the population

180   growth rate was examined by using fixed survival rates (means) within the population model,

181   allowing it to approximate the deterministic population growth rate between 1982 and 2014.

182   Similarly, we estimated the population growth rate by changing mean survival rates

183   corresponding to low SSTs that were measured from 1982 to 1996, and high SSTs characteristic

184   for the time period from 1997 to 2015. Finally, we projected future populations by running a

185   series of stochastic projections that used a range of survival rate estimates (i.e. omitting years

186   with increasing uncertainty in estimate validity) and predicted trends in influential

187   environmental factors.

188   Detailed descriptions of all modelling procedures are provided as Electronic Supplementary

189   Material (ESM1).

2.6 Comparison with historic population trends

Richdale (1957) provides comprehensive data on penguin demography allowing it to draw comparisons between historic and contemporary penguin numbers. We inferred population parameters from three tables. Table 67 (p147) provides direct information about the number of eggs laid and chicks fledged. Using number of eggs, we inferred the number of nests for the reported years by assuming only two-egg clutches were present. In table 72 (p154), Richdale reports the percentage of surviving breeders of both sexes for each year, adjusted to the fractional format by dividing the reported values by 100. Finally, table 62 (p138) provides clues about annual recruitment, which was calculated as proportion of new breeders each year. We omitted Richdale's data for the 1936 season and for the seasons following 1949, as he noted less frequent monitoring and incomplete data sets for the initial and the latter years of his study (Richdale 1957).

3. Results

3.1 Observed penguin numbers

Numbers of adult breeders at Boulder Beach fluctuated considerably between 1982 and 2015 (Fig 2). Immigration of birds that had been banded outside Boulder Beach was a rare occurrence throughout the study period (mean proportion of immigrants per year 1982-2015: 2.7±2.2%). If birds banded as breeders are considered to come from elsewhere, the median immigration is similar (2.0%) although three years (1991, 2010 and 2012) would stand out where unbanded adults made up 11, 10 and 8% of the breeding population, respectively. An apparent rise in penguin numbers at the beginning of the monitoring period (i.e. 1982-1985) reflects increasing monitoring effort. Reduced monitoring effort may explain the drop in numbers after 1985-86; two areas were not monitored in several years (A1: 1986-1989; Highcliff: 1989). Both areas account for 46±4% of penguin counts (1990-2015), so that true penguin numbers in 1989 were likely higher than the database would suggest. Breeder numbers in the two areas monitored in 1989 (Midsection; Double Bay) dropped by 62% in the following season (1989: 74 birds, 1990:

216   28 birds) when the population was affected by a catastrophic adult die-off. The population

217   recovered between 1990 and 1996 to reach levels comparable to those observed in 1985. The

218   1996 season had the highest numbers of breeders recorded at Boulder Beach (n=242) and

219   represents a turning point for the population. Subsequently penguin numbers reached a low of

220   104 breeders in 2002, with losses compounded by another adult die-off event occurring in the

221   2001 season. Between 2002 and 2012 the population fluctuated between 100 and 150 breeders

222   without any apparent trend before another drastic decline in numbers began in the years

223   following a third adult die-off event at the end of the 2012 season. The steepest drop in numbers

224   (41%) recorded since 1989 occurred between 2013 (128 breeders) and 2014 (76 breeders). In

225   2015, only 58 breeding penguins were recorded, which translates to a 76% decline in numbers

226   since 1996.

227   Number of chicks that fledged each year generally followed the trends observed for adults (Fig.

228   2). However, significant variation between 2003 and 2010 reflects a series of years with poor

229   breeding success followed by better reproductive output in the following year. Numbers of new

230   breeders showed a similar albeit weakened pattern delayed by 5 years: starting in 2004,

231   numbers of new breeders seem to mimic those of fledglings beginning in 1999.

232   Age of breeding birds ranged between 8.4 years (1984) and 14.9 years (1990, mean: 12±1.4

233   years, Fig. 3). Between 1990 and 2015 the average age of returning breeders showed a slightly

234   decreasing trend from around 14 to 11 years (Pearson correlation ρ=-0.307, t_{24}=-1.5781,

235   p=0.13). At the same time, average age of new breeders dropped significantly from more than 10

236   years in the 1990s to only 4 years in 2015 (ρ=-0.796, t_{24}=-1.5781, p<0.001). The average age of

237   new breeders increased steeply after both the 1989 and 2001 adult die-offs (Fig 3) indicating a

238   substantial pool of older non-breeders ready to recruit following the disappearance of

239   established breeders. No such spike is apparent after the 2012 die-off suggesting that the pool of

240   older recruits has dried up over the last decade.

3.2 Demographic estimates from the mark-recapture model

The MR model without covariate revealed a fledgling survival rate of 0.12 (95%, Credible Interval: 0.08, 0.19) in chicks (Table 2). The survival of adults was 0.87 (95%, CrI: 0.83, 0.90). Throughout the study period (1982-2014), fledgling survival varied 2.56 times more than adult survival (95%, CrI: 1.03, 6.45) (Table 2).

Years with increased wind activity had a positive effect on fledgling survival, whereas the effect of higher than normal SST was negative; both covariates explained 33.2% of the variance (Table 3a). Similarly, SST anomaly in the previous year and during the first three months after fledging had an effect on survival, explaining 16.5% and 24.8% of the variance. Furthermore, years with increased SST had a negative effect on fledgling survival, explaining between 12 and 15% of the variance (Table 3a).

In adults, SST had the greatest effect on the survival rate, explaining 36.8% of the variance (Table 3b). The relationship of adult survival and SST becomes apparent when the deviation of annual adult survival from the median survival rate is plotted against SST anomaly (Fig 4). In periods with cooler than usual SST, adult survival was high (e.g.1990-1996), whereas warm periods were characterized by lower adult survival. The same was true for air temperature. Warmer years were associated with reduced adult survival; air temperature-related covariates explained 34.4% of the variation in adult survival (Table 3b).

Refitting the MR model with the two most influential explanatory covariates each for fledging and adult survival, and subsequent assessment of posterior model probability, ranked highest the model where both chick and adult survival were fitted to the single covariate SST anomaly (Table 4).

3.3 Predictions for the adult female population

Using year-specific survival rates from the MR model generates predictions of numbers of adults that were similar to those determined during monitoring. For most years, the observation-based

266   number of adult female YEPs and the 95% credible intervals for the predicted number of adult

267   female YEPs overlapped (Fig 5).

268   Based on a deterministic model (i.e. without temporal variance in survival rates) the population

269   growth rate was 1.02 (95% CrI 0.98, 1.06) per year throughout the entire study period. For the

270   time period when SST was below average (1982 to 1996, Fig. 4) the population showed an

271   increasing trend with a growth rate of 1.038 (95% CrI 0.99, 1.080, Fig 6). However, from 1996

272   onwards an ongoing period of mainly warmer than normal SST went along with a growth rate of

273   0.94 (95% CrI 0.90, 0.98) indicating a population decline (Fig 6).

274   3.4 Future projections

275   Based on projections of increasing SST at a rate of 0.02°C per year in the next decades (Oliver et

276   al. 2014), the penguin population at Boulder Beach will continue to decline. Stochastic

277   simulations using the most reliable estimates for adult survival (1982-2012) suggest that the

278   number of adult female penguins will drop below 10 individuals by 2048 (Fig 5a). If the recent

279   poor breeding years 2013-2015 are included this negative trend gets progressively worse (Fig

280   5b-d). Including adult survival rates estimated for 2015, the mean projection predicts YEPs to be

281   locally extinct by 2043.

282   4. Discussion

283   Numbers of Yellow-eyed penguins at Boulder Beach have declined since 1996 (Figs 5&6). The

284   local population seemed to experience a reprieve from this decline in the first decade of the new

285   millennium, despite unfavourable climatic conditions at that time. This might have been driven

286   by a temporary reduction in other, non-climate negative impacts, the nature of which remain

287   unclear due to a lack of data.

288   The ages of breeding penguins provide some explanation about the underlying mechanics of the

289   population decline. In the years following the 1989 and 2001 adult die-offs, the average age of

290   new breeders recruited into the population was substantially higher than in the years prior to

291   the events. All of these birds were locally banded individuals, which suggests that there was a

292   pool of older, previously unpaired birds which replaced experienced breeders that had died

293   during the event. After the 2012 die-off, the mean age of new breeders reached an historic low

294   (4.1 years, Fig 3). Hence, old breeders that had lost their partner now paired up with younger

295   penguins indicating that the pool of older bachelors available to replace lost birds had

296   disappeared. This is supported by the number of recruits reflecting the marked variation in

297   fledgling numbers with a 5-year-lag (Fig 2). It appears that since the turn of the century,

298   penguins recruit into the breeding population at the earliest possible opportunity. This likely has

299   negative effects on breeding performance since in seabirds age is an important determinant for

300   foraging success (e.g. Daunt et al. 2007; Zimmer et al. 2011) and subsequently reproductive

301   success (e.g. Limmer and Becker 2009; Nisbet and Dann 2009). The decline in the mean age of

302   new breeders in recent years indicates that more inexperienced birds are recruiting as breeders,

303   and possibly explains the overall deteriorating reproductive success.

304   When the 2012 die-off of adult breeding birds occurred, penguin numbers were less than 60% of

305   what they had been in the mid-1990s (Fig 2). While the penguin population showed a

306   remarkably recovery after the 1989 event this did not happen following 2012; instead numbers

307   have continued to decline. The most apparent differences following the two die-offs are the

308   trends in ocean temperatures with a cooler-than-normal period in the first half of the 1990s

309   whereas SST has been almost continuously higher than the 1953-2014 average since the late

310   1990s (Fig 4).

4.1 Sea surface temperature effects

312   Sea surface temperature explained 33% of the variation in observed population trends. Hence,

313   SST is an important driver of penguin numbers. Years with warmer than usual SST result in

314   reduced adult survival, whereas the reverse is true when SST is cooler.

315   Variation in SST likely influences the abundance and quality of YEP prey. In Little penguins

316   (*Eudyptula minor*) breeding on the Otago Peninsula, climatic fluctuations – and connected to

317   this, ocean temperatures – were found to affect prey composition (Perriman et al. 2000). Little

318   penguins are generalist foragers that take a variety of pelagic prey (Dann 2013), most likely a

319   beneficial trait in relation to climate related change in resource abundance (Thuiller et al. 2005).

320   YEPs on the other hand, are principally benthic foragers (Mattern et al. 2007) that feed

321   predominantly on demersal species (e.g. Browne et al. 2011; Moore and Wakelin 1997; van

322   Heezik 1990). Although this specialisation reduces competition for pelagic prey with the

323   abundant marine avifauna in New Zealand (Mattern et al. 2007), it comes at the cost of reduced

324   behavioural flexibility to respond to changes in prey distribution or abundance (e.g. Browne et

325   al. 2011; Mattern et al. 2013).

326   Temperature affects the annual biomass of many fish species in New Zealand (Beentjes and

327   Renwick 2001). Warmer than normal conditions negatively affect spawning in fish, reducing

328   subsequent recruitment (e.g. Takasuka et al. 2008). Abundance of the demersal red cod

329   (*Pseudophycis bacchus*), historically an important prey species for YEP from Boulder Beach

330   (Moore and Wakelin 1997; van Heezik 1990), shows a strong correlation to SST fluctuations,

331   albeit with a lag of 14 months (Beentjes and Renwick 2001). At Boulder Beach, a reduction in

332   body mass of breeding YEPs in 1985 when compared to 1984 was associated with lower

333   quantities of red cod taken (van Heezik and Davis 1990). 1983 featured cooler than normal SST

334   (mean monthly SST anomaly: -0.73), while 1984 temperatures were above average (SST

335   anomaly: 0.17). As such the lagged correlation between SST and red cod abundance reported by

336   Beentjes & Renwick (2001) also seems to be manifested in penguin body condition. This

337   explains the relative importance of the corresponding covariate (i.e. sst_anomaly_minus1year)

338   for survival rates (Table 3a&b) and corresponds to findings of a previous analysis of climate

339   variables on YEP numbers (Peacock et al. 2000).

340   However, model selection showed an even stronger direct SST effect (Table 4). Ocean

341   temperatures play an important role in the spatial distribution of fish populations (Beentjes et

342   al. 2002). Warmer than usual SST are often an indication of increased stratification of the water

343   column where a layer of warmer water sits on top of cooler water. This disrupts the benthic-

344   pelagic coupling, i.e. mixing processes that regulate nutrient flow between benthos and surface

345   waters (Jones et al. 2014). Land run-off has been identified as a major source of nutrients for the

346   South Otago continental shelf, which results in higher near-surface nutrient concentrations

347   (Hawke 1989), so that vertical mixing is likely of crucial importance for benthic productivity and

348   subsequent prey abundance in the penguins' home ranges. Penguin foraging conditions are

349   likely compromised under stratified, warm-water conditions.

350   The three major die-offs of adult penguins (seasons 1989-90, 2001-02, and 2012-13) all

351   occurred in years with higher than normal SST suggesting that stratification might have more

352   severe impacts than can be explained by the disruption of nutrient fluxes alone.

4.2 SST and relevance of die-off events

354   Die-off events do not seem to be related to prey availability. Body condition of adult penguins

355   did not indicate malnutrition (Gill and Darby 1993). The cause of mortality could not be

356   identified although necropsies after the 2012 die-off indicated it to be toxin related (Department

357   of Conservation, unpublished data). Harmful algal blooms (HAB) were suspected (Gill and Darby

358   1993), yet water samples taken along a transect through the penguin's known foraging ranges

359   found no evidence for the presence of harmful algae (unpubl. data). Moreover, it seems unlikely

360   that a HAB would selectively affect only one seabird species; no other unexplained seabird

361   deaths occurred during either of the die-offs. That only bottom foraging YEPs were affected

362   suggests that the distribution of a toxin was probably limited to the near-seafloor region.

363   Stratification and the disruption of vertical mixing potentially would contribute to a

364   concentration of toxic components at the sea floor. While the origin or exact nature of the toxin

365   is unclear, it could be related to technical malfunctions that occurred at the time at Dunedin's

366   sewage treatment plant, which discharges at the seafloor about 1.5 km from the shore and ca. 5

367   km upstream from Boulder Beach.

368   Although the cause of die-off events remains a matter of speculation, their relevance for

369   population trends is closely tied to prevalent environmental conditions following these events.

370   The 1989 die-off, which removed about 50% of penguins from the breeding population (Efford

371   et al. 1996) was followed by a six year period of population recovery, likely aided by cooler than

372   normal SST (Fig. 4). The next die-off event occurred at Boulder Beach in 2001 (Alvin Setiawan,

373   pers. comm.) and reduced the local population by nearly 40%. Following this event, the

374   population showed no sign of recovery during a prolonged period of warmer-than-normal SST

375   that began in 1998 and prevails until today. The associated reduced adult survival explains the

376   lack of recovery in the penguin population (Fig 4). Consequently, the 2012 die-off had a

377   cumulative effect, further reducing the population to its lowest level on record.

378   With projected SST increases over the next decades it seems doubtful that marine conditions

379   supporting the recovery of YEPs will occur in the future. Hence, future die-off events will be

380   increasingly critical for penguin numbers. However, sea surface temperatures only explained

381   about one third of the variation in survival rates. This means that other factors also play

382   important roles for population dynamics.

383   **4.3 Other climate factors**

384   Daily minimum air temperature (Table 3b) is a proxy for prevailing temperature regimes, where

385   a higher average minimum temperature indicates warmer years. Air temperature could simply

386   be a covariate of SST and affect penguin survival through the mechanisms suggested above. In

387   addition, air temperatures recorded during the moult (March-May) negatively affected adult

388   survival probably as a result of hyperthermia (Table 3b). Little penguins in Australia suffer

389   increased adult mortality when exposed to higher temperatures when moulting (Ganendran et

390   al. 2015).

391   Frequency of days with strong winds had a positive influence on fledgling survival (Table 3a).

392   Wind aids oceanic mixing processes and thereby can become a driver for foraging success in

393   penguins (Dehnhard et al. 2013). Wind generally acts as an antagonist to SST-related

394   stratification effects, creating enhanced foraging conditions for penguins thereby increasing the

395   survival chances of inexperienced fledglings.

396   **4.4 Non-climate factors**

397   In this study we were able to use comprehensive climate data to test the influence of a wide

398   range of factors on the population developments of Yellow-eyed penguins from Boulder Beach,

399   and show that climate change is likely to have a detrimental impact on the YEP population.

400   However, there are many other environmental parameters known to have a substantial

401   influence on reproductive success and survival in YEPs, but which could not be included in our

402   models due to the lack of adequate or inconsistent data. These factors are likely responsible for

403   the remaining variation in survival rates.

404   ***4.4.1 Fisheries interactions***

405   Potential impacts of incidental bycatch in gill net fisheries (Darby and Dawson 2000) and

406   alteration of the penguins' benthic foraging habitat by bottom fishing activities (Ellenberg and

407   Mattern 2012; Mattern et al. 2013) could not be quantified because data on gill net fisheries

408   supplied by the Ministry of Primary Industries (NZ Ministry Of Primary Industries, Official

409   Information Act Request OIA12-397) proved to be spatially coarse and temporally limited, with

410   approximate locations of gill net fishing events specified only from 2006 onwards. Provided data

411   on bottom fishing effort only covered the years 2000-2012 and originated from vessels

412   operating outside the penguins' ranges (OIA12-460).

413   The impact of single fisheries interactions might have a much greater effect on penguin numbers

414   than annual fishing statistics would suggest. There are reports of multiple YEP killed in a single

415   gill net haul (Ellenberg and Mattern 2012) and reported bycatch incidents in gill net fisheries

416   have been as high as 12 cases per year, many of which affected YEPs from the Otago Peninsula

417   (Darby and Dawson 2000). The lack of independent observer coverage on gill nets operating

418   within the YEP foraging grounds prevents reliable quantification of bycatch mortality. Yet it

419   stands to reason that incidental fisheries mortality is an important factor affecting survival rates

420   and, hence, population trends.

421   Impacts of bottom fishing activities on YEP survival are even more difficult to quantify. Bottom

422   trawling and dredge fisheries can substantially alter the benthic environment, reducing

423   biodiversity, and prey abundance and quality for YEPs. Low quality prey were brought ashore by

424   YEPs on Stewart Island, which had home ranges that apparently avoided the vast areas of

425   potential habitat subject to intensive oyster dredging (Browne et al. 2011; Ellenberg and

426   Mattern 2012). On the Otago Peninsula, some penguins forage along straight-line paths

427   following bottom trawl scrape marks, searching for scavenging prey that appears to be

428   inadequate food for young chicks (Mattern et al. 2013).

429   ***4.4.2 Disease outbreaks***

430   In the past decade several breeding seasons saw the occurrence of diphtheritic stomatitis, a

431   secondary infection negatively affecting chick survival (Houston 2005). We could not test the

432   effects of such disease outbreaks on population trends, because the YEP database does not

433   facilitate quantitative storage of disease-related data. Diphtheritic stomatitis only affects chicks

434   which generally survive when older than 2 weeks. So the disease is unlikely to have a lasting

435   effect on population trends as it does not affect adults which are critical for the maintenance of a

436   stable population (Benton and Grant 1999). Although YEPs are subject to exposure to avian

437   malaria parasites (Graczyk et al. 1995), observed infections are too low to suggest that avian

438   malaria represents a significant problem for the species (Sturrock and Tompkins 2007).

439   ***4.4.3 Predators***

440   Introduced terrestrial predators are one of the biggest challenges for native wildlife in New

441   Zealand (Wilson 2004). Mustelids, dogs, and to a lesser extent cats and rats can have a

442   significant impact on YEP (e.g. Alterio et al. 1998; Ratz and Murphy 1999), but it is very difficult

443   to quantify these effects because direct evidence of predation is sparse (e.g. King et al. 2012).

444   Predation by the native NZ sea lion (*Phocarctos hookeri*) has to date been limited to two female

445   sea lions that were active between 1997 and 2005 (Lalas et al. 2007) that have since died (Jim

446   Fyfe, pers. com.). More recently, a number of YEPs have been reported with injuries that were

447   speculated to have been inflicted by barracouta (*Thyrsites atun*). Considering that barracouta are

448   smaller than adult YEPs (mean body lengths – barracouta: 55 cm, Fishbase.org 2016; YEPs: 65

449   cm, Seddon et al. 2013a) such injuries are at best an accidental consequence of penguins and fish

450   targeting the same prey patch. Some external injuries might be the result of interactions with

451   humans; in Australia, Little penguins (*Eudyptula minor*) have been injured and killed by water

452   craft such as jet skis (Cannell et al. 2016), a recreational activity that has also been observed in

453   the penguin landing zone at Boulder Beach (pers. obs).

454   *4.4.4 Human disturbance*

455   The significance of human impacts in the form of deforestation of breeding habitat, capture by

456   collectors, egging, and shooting of adults on the YEP population was highlighted early by

457   Richdale (1952). While these impacts are no longer an issue, unregulated tourism has become

458   the main type of human disturbance at some Yellow-eyed penguin colonies and is reflected in

459   reduced breeding performance and a steady decline of local penguin numbers (e.g. Ellenberg et

460   al. 2009; Ellenberg et al. 2007; McClung et al. 2004).

4.5 Conservation implications

462   Stochastic simulations of future population trends for Yellow-eyed penguins at Boulder Beach,

463   which are likely representative of the entire Otago Peninsula, suggest that the population will

464   continue to decline (Fig 5). Global ocean temperatures are rising (Stocker 2014); projections for

465   the Tasman region until 2060 predict an increase in SST of up to 2°C (Oliver et al. 2014), hence

466   future climatic conditions will not be favorable for a recovery of the YEP population. However,

467   climate change-related pressure on YEP can likely be offset through control of the other more

468   manageable factors negatively affecting population trends. This has already been demonstrated:

469   positive YEP population growth during the 1940s, at a time when SST was strongly increasing in

470   the Pacific to levels comparable to those recorded in the 1990s (Guan and Nigam 2008), was

471   attributed to a reduction in human disturbances such as conversion of breeding habitat to farm

472   land, establishment of road networks, road traffic and random acts of violence (Richdale 1957).

473   During World War II, when resources were directed towards the war effort 'man's destructive

474   agencies were practically negligible' (Richdale 1957, p157).

475   While climate change is a global phenomenon that is both inevitable and quantifiable, it is

476   important to bear in mind its impact on species population trends relative to other more

477   regional factors, such as, in the case of penguins, fisheries, pollution, habitat destruction,

478   introduced terrestrial predators, and human disturbance (Trathan et al. 2015). Managing local

479   and regional factors can mitigate the increasing pressure that climate change will impose on

480   populations of some vulnerable species.

481   The virtual absence of quantifiable data to examine the effects of non-climatic factors makes it

482   difficult to provide fact-based management recommendations and puts a potentially

483   overbearing emphasis on climate change. However, these principally anthropogenic factors

484   likely also explain significant portions of the variation in survival rates, so that the focus should

485   be on improving our understanding and management of these impacts to enhance this species'

486   resilience to climate change.

5. Acknowledgements

6. References

491   Alterio, N., Moller, H., Ratz, H., 1998. Movements and habitat use of feral house cats Felis catus,

492   stoats Mustela erminea and ferrets Mustela furo, in grassland surrounding yellow-eyed

493   penguin Megadyptes antipodes breeding areas in spring. Biological Conservation 83, 187-

494   194.

495   Beentjes, M., Bull, B., Hurst, R., Bagley, N., 2002. Demersal fish assemblages along the continental

496   shelf and upper slope of the east coast of the South Island, New Zealand. New Zealand

497   Journal of Marine and Freshwater Research 36, 197-223.

498   Beentjes, M., Renwick, J., 2001. The relationship between red cod, *Pseudophycis bachus*,

499   recruitment and environmental variables in New Zealand. Environmental Biology of

500   Fishes 61, 315-328.

501   Benton, T.G., Grant, A., 1999. Elasticity analysis as an important tool in evolutionary and

502   population ecology. Trends in Ecology & Evolution 14, 467-471.

503   BirdLife International, 2012. Medayptes antipodes, In The IUCN Red List of Threatened Species

504   2012. p. e.T22697800A40186242.

505   Boessenkool, S., Austin, J.J., Worthy, T.H., Scofield, P., Cooper, A., Seddon, P.J., Waters, J.M., 2009a.

506   Relict or colonizer? Extinction and range expansion of penguins in southern New Zealand.

507   Boessenkool, S., Star, B., Waters, J.M., Seddon, P.J., 2009b. Multilocus assignment analyses reveal

508   multiple units and rare migration events in the recently expanded yellow-eyed penguin

509   (Megadyptes antipodes). Molecular ecology 18, 2390-2400.

510   Browne, T., Lalas, C., Mattern, T., Van Heezik, Y., 2011. Chick starvation in yellow-eyed penguins:

511   Evidence for poor diet quality and selective provisioning of chicks from conventional diet

512   analysis and stable isotopes. Austral Ecology 36, 99-108.

513   Cannell, B.L., Campbell, K., Fitzgerald, L., Lewis, J.A., Baran, I.J., Stephens, N.S., 2016.

514   Anthropogenic trauma is the most prevalent cause of mortality in Little Penguins,

515   *Eudyptula minor*, in Perth, Western Australia. Emu 116, 52-61.

516   Croxall, J., 1982. Energy costs of incubation and moult in petrels and penguins. The Journal of

517   Animal Ecology, 177-194.

518   Dann, P., 1991. Distribution, Population Trends and Factors Influencing the Population Size of

519   Little Penguins <I>Eudyptula minor</I> on Phillip Island, Victoria. Emu 91, 263-272.

520   Dann, P., 2013. Little Penguin (*Eudyptula minor*), In Penguins: Natural History and Conservation.

521   eds P. Garcia Borboroglu, P.D. Boersma, pp. 304-319. University of Washington Press,

522   Seattle & London.

523   Darby, J., 1985a. The great hoiho count. Forest and Bird, 16-18.

524   Darby, J., 1985b. The great yellow-eyed penguin count. Forest & Bird 16, 16-18.

525   Darby, J., Seddon, P., 1990. Breedig biology of Yellow-eyed Penguins (*Megadyptes antipodes*), In

526   Penguin Biology. eds L. Davis, J. Darby, pp. 45-62. Academic Press, San Diego.

527   Darby, J.T., Dawson, S.M., 2000. Bycatch of yellow-eyed penguins (Megadyptes antipodes) in

528   gillnets in New Zealand waters 1979–1997. Biological Conservation 93, 327-332.

529   Daunt, F., Wanless, S., Harris, M., Money, L., Monaghan, P., 2007. Older and wiser: improvements

530   in breeding success are linked to better foraging performance in European shags.

531   Functional Ecology 21, 561-567.

532   Dehnhard, N., Ludynia, K., Poisbleau, M., Demongin, L., Quillfeldt, P., 2013. Good Days, Bad Days:

533   Wind as a Driver of Foraging Success in a Flightless Seabird, the Southern Rockhopper

534   Penguin. PloS one 8, e79487.

535   Efford, M., Spencer, N., Darby, J., 1994. A relational database for Yellow-eyed penguin banding

536   and breeding records. Landcare Research, Dunedin, New Zealand, unpublished report.

537   Efford, M., Spencer, N., Darby, J., 1996. Population studies of Yellow-eyed penguins - 1994-94

538   progress report. Department of Conservation, Wellington.

539   Ellenberg, U., Mattern, T., 2012. Yellow-eyed penguin - review of population information, In

540   Conservation Services Programme Reports. p. 144. Department of Conservation,

541   Wellington, New Zealand.

542   Ellenberg, U., Mattern, T., Seddon, P.J., 2009. Habituation potential of yellow-eyed penguins

543   depends on sex, character and previous experience with humans. Animal Behaviour 77,

544   289-296.

545   Ellenberg, U., Setiawan, A.N., Cree, A., Houston, D.M., Seddon, P.J., 2007. Elevated hormonal stress

546   response and reduced reproductive output in Yellow-eyed penguins exposed to

547   unregulated tourism. General and comparative endocrinology 152, 54-63.

548   Fishbase.org, 2016. Thyrsites atun (Euphrasen, 1791) Snoek, In Fishbase.org.

549   Ganendran, L.B., Sidhu, L.A., Catchpole, E.A., Chambers, L.E., Dann, P., 2015. Effects of ambient air

550   temperature, humidity and rainfall on annual survival of adult little penguins Eudyptula

551   minor in southeastern Australia. International Journal of Biometeorology, 1-9.

552 Garcia Borboroglu, P., Boersma, P., 2013. Penguins: Natural History and Conservation. University
553   of Washington Press.

554 Gill, J., Darby, J., 1993. Deaths in yellow-eyed penguins (Megadyptes antipodes) on the Otago
555   Peninsula during the summer of 1990. New Zealand Veterinary Journal 41, 39-42.

556 Graczyk, T.K., Cranfield, M.R., Brossy, J.J., Cockrem, J., Jouventin, P., Seddon, P., 1995. Detection of
557   avian malaria infections in wild and captive penguins. JOURNAL-HELMINTHOLOGICAL
558   SOCIETY WASHINGTON 62, 135-142.

559 Grémillet, D., Boulinier, T., 2009. Spatial ecology and conservation of seabirds facing global
560   climate change: a review. Marine Ecology Progress Series 391, 121-137.

561 Grosbois, V., Gimenez, O., Gaillard, J.M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.,
562   Weimerskirch, H., 2008. Assessing the impact of climate variation on survival in vertebrate
563   populations. Biological Reviews 83, 357-399.

564 Guan, B., Nigam, S., 2008. Pacific Sea Surface Temperatures in the Twentieth Century: An
565   Evolution-Centric Analysis of Variability and Trend. Journal of Climate 21, 2790-2809.

566 Hawke, D., 1989. Hydrology and near-surface nutrient distribution along the South Otago
567   continental shelf, New Zealand, in summer and winter 1986. New Zealand Journal of
568   Marine and Freshwater Research 23, 411-420.

569 Houston, D.M., 2005. Diphtheritic stomatitis in yellow-eyed penguins, In Oamaru Penguin
570   Symposium 2005. ed. A. Hocken, p. 267. New Zealand Journal of Zoology, Oamaru, New
571   Zealand.

572 Jones, D.O.B., Yool, A., Wei, C.-L., Henson, S.A., Ruhl, H.A., Watson, R.A., Gehlen, M., 2014. Global
573   reductions in seafloor biomass in response to climate change. Global Change Biology 20,
574   1861-1872.

575   King, S., Harper, G., Wright, J., McInnes, J., van der Lubbe, J., Dobbins, M., Murray, S., 2012. Site-
576   specific reproductive failure and decline of a population of the Endangered yellow-eyed
577   penguin: a case for foraging habitat quality. Marine Ecology Progress Series 467, 233.

578   Lalas, C., Ratz, H., McEwan, K., McConkey, S.D., 2007. Predation by New Zealand sea lions
579   (Phocarctos hookeri) as a threat to the viability of yellow-eyed penguins (Megadyptes
580   antipodes) at Otago Peninsula, New Zealand. Biological Conservation 135, 235-246.

581   Limmer, B., Becker, P.H., 2009. Improvement in chick provisioning with parental experience in a
582   seabird. Animal Behaviour 77, 1095-1101.

583   Mattern, T., Ellenberg, U., Houston, D.M., Davis, L.S., 2007. Consistent foraging routes and benthic
584   foraging behaviour in yellow-eyed penguins. Marine Ecology Progress Series 343, 295-
585   306.

586   Mattern, T., Ellenberg, U., Houston, D.M., Lamare, M., Davis, L.S., van Heezik, Y., Seddon, P.J., 2013.
587   Straight line foraging in yellow-eyed penguins: new insights into cascading fisheries
588   effects and orientation capabilities of marine predators. PloS one 8, e84381.

589   McClung, M.R., Seddon, P.J., Massaro, M., Setiawan, A., 2004. Nature-based tourism impacts on
590   yellow-eyed penguins Megadyptes antipodes: does unregulated visitor access affect
591   fledging weight and juvenile survival? Biological Conservation 119, 279-285.

592   Moore, P., 1999. Foraging range of the Yellow-eyed Penguin Megadyptes antipodes. Marine
593   Ornithology 27, 49-58.

594   Moore, P., Wakelin, M., 1997. Diet of the yellow-eyed penguin Megadyptes antipodes, South
595   Island, New Zealand, 1991-1993. Marine Ornithology 25, 17-29.

596   Moore, P.J., 2001. Historical records of yellow-eyed penguin (Megadyptes antipodes) in southern
597   New Zealand. Notornis 48, 145-156.

598 Nisbet, I.C., Dann, P., 2009. Reproductive performance of little penguins Eudyptula minor in

599   relation to year, age, pair-bond duration, breeding date and individual quality. Journal of

600   Avian Biology 40, 296-308.

601 Oliver, E., Wotherspoon, S., Chamberlain, M., Holbrook, N., 2014. Projected Tasman Sea Extremes

602   in Sea Surface Temperature through the Twenty-First Century. Journal of Climate 27,

603   1980-1998.

604 Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape

605   and biogeographical scale levels in research and conservation. Biological Conservation

606   117, 285-297.

607 Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annual

608   Review of Ecology, Evolution, and Systematics, 637-669.

609 Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across

610   natural systems. Nature 421, 37-42.

611 Peacock, L., Paulin, M., Darby, J.T., 2000. Investigations into the climate influence on population

612   dynamics of yellow-eyed penguins Megadyptes antipodes. New Zealand Journal of Zoology

613   27, 317-325.

614 Perriman, L., Houston, D., Steen, H., Johannesen, E., 2000. Climate fluctuation effects on breeding

615   of blue penguins (*Eudyptula minor*). New Zealand Journal of Zoology 27, 261-267.

616 Ratz, H., Murphy, B., 1999. Effects of habitat and introduced mammalian predators on the

617   breeding success of Yellow-eyed Penguins Megadyptes antipodes, South Island, New

618   Zealand. Pacific Conservation Biology 5, 16-27.

619 Richdale, L.E., 1949. A study of a group of penguins of known age. Otago Daily Times and Witness

620   Newspapers Company.

621 Richdale, L.E., 1951. Sexual behavior in penguins.

622 Richdale, L.E., 1957. A population study of penguins. Clarendon Press.

623   Robertson, H.A., Dowding, J.E., Elliott, G.P., Hitchmough, R.A., Miskelly, C.M., O'Donnell, C.F.J.,

624   Powlesland, R.G., Sagar, P.M., Scofield, P.R., Taylor, G.A, 2013. Conservation status of New

625   Zealand birds, 2012. New Zealand Threat Classification Series 4. Department of

626   Conservation, Wellington, New Zealand, 22p.

627   Seddon, P., Ellenberg, U., van Heezik, Y., 2013a. Yellow-eyed penguin (*Megadyptes antipodes*), In

628   Penguins: Natural History and Conservation. eds P. Garcia Borboroglu, P. Boersma, pp. 91-

629   110. University of Washington Press, Seattle & London.

630   Seddon, P.J., Ellenberg, U., van Heezik, Y., 2013b. Yellow-Eyed Penguin (Megadyptes antipodes).

631   Penguins: Natural History and Conservation, 97-100.

632   Sekercioglu, C.H., Schneider, S.H., Fay, J.P., Loarie, S.R., 2008. Climate change, elevational range

633   shifts, and bird extinctions. Conservation Biology 22, 140-150.

634   Sexton, J.P., McIntyre, P.J., Angert, A.L., Rice, K.J., 2009. Evolution and ecology of species range

635   limits.

636   Sitas, N., Baillie, J.E.M., Isaac, N.J.B., 2009. What are we saving? Developing a standardized

637   approach for conservation action. Animal Conservation 12, 231-237.

638   Stocker, T.F., 2014. Climate change 2013: the physical science basis: Working Group I

639   contribution to the Fifth assessment report of the Intergovernmental Panel on Climate

640   Change. Cambridge University Press.

641   Sturrock, H.J.W., Tompkins, D.M., 2007. Avian malaria (Plasmodium spp) in yellow-eyed

642   penguins: Investigating the cause of high seroprevalence but low observed infection. New

643   Zealand Veterinary Journal 55, 158-160.

644   Takasuka, A., Oozeki, Y., Kubota, H., 2008. Multi-species regime shifts reflected in spawning

645   temperature optima of small pelagic fish in the western North Pacific. Marine Ecology

646   Progress Series 360, 211-217.

647   Tang, S., Chen, L., 2002. Density-dependent birth rate, birth pulses and their population dynamic

648   consequences. Journal of Mathematical Biology 44, 185-199.

649   Tavecchia, G., Tenan, S., Pradel, R., Igual, J.M., Genovart, M., Oro, D., 2016. Climate-driven vital

650   rates do not always mean climate-drievn population. Global Change Biology, doi:

651   10.1111/gcb.13330

652   Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus,

653   B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S.,

654   Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L., Williams,

655   S.E., 2004. Extinction risk from climate change. Nature 427, 145-148.

656   Thuiller, W., Lavorel, S., Araújo, M., 2005. Niche properties and geographical extent as predictors

657   of species sensitivity to climate change. Global Ecology and Biogeography 14, 347-357.

658   Trathan, P.N., García-Borboroglu, P., Boersma, D., Bost, C.A., Crawford, R.J., Crossin, G.T.,

659   Cuthbert, R.J., Dann, P., Davis, L.S., De La Puente, S., 2015. Pollution, habitat loss, fishing,

660   and climate change as critical threats to penguins. Conservation Biology 29, 31-41.

661   van Heezik, Y., 1990. Seasonal, geographical, and age-related variations in the diet of the yellow-

662   eyed penguin (Megadyptes antipodes). New Zealand Journal of Zoology 17, 201-212.

663   van Heezik, Y., Davis, L., 1990. Effects of food variability on growth rates, fledging sizes and

664   reproductive success in the Yellow-eyed Penguin *Megadyptes antipodes.* Ibis 132, 354-365.

665   Whittington, P.A., Randall, R.M., Crawford, R.J.M., Wolfaardt, A.C., Klages, N.T.W., Randall, B.M.,

666   Bartlett, P.A., Chesselet, Y.J., Jones, R., 2005. Patterns of immigration to and emigration

667   from breeding colonies by African penguins. African Journal of Marine Science 27, 205-

668   213.

669   Wilson, K.-J., 2004. Flight of the Huia: Ecology and conservation of New Zealand's frogs, reptiles,

670   birds and mammals. Canterbury University Press Christchurch.

671   Zimmer, I., Ropert-Coudert, Y., Kato, A., Ancel, A., Chiaradia, A., 2011. Does Foraging Performance

672   Change with Age in Female Little Penguins (*Eudyptula minor*)? PloS one 6, e16098.

673
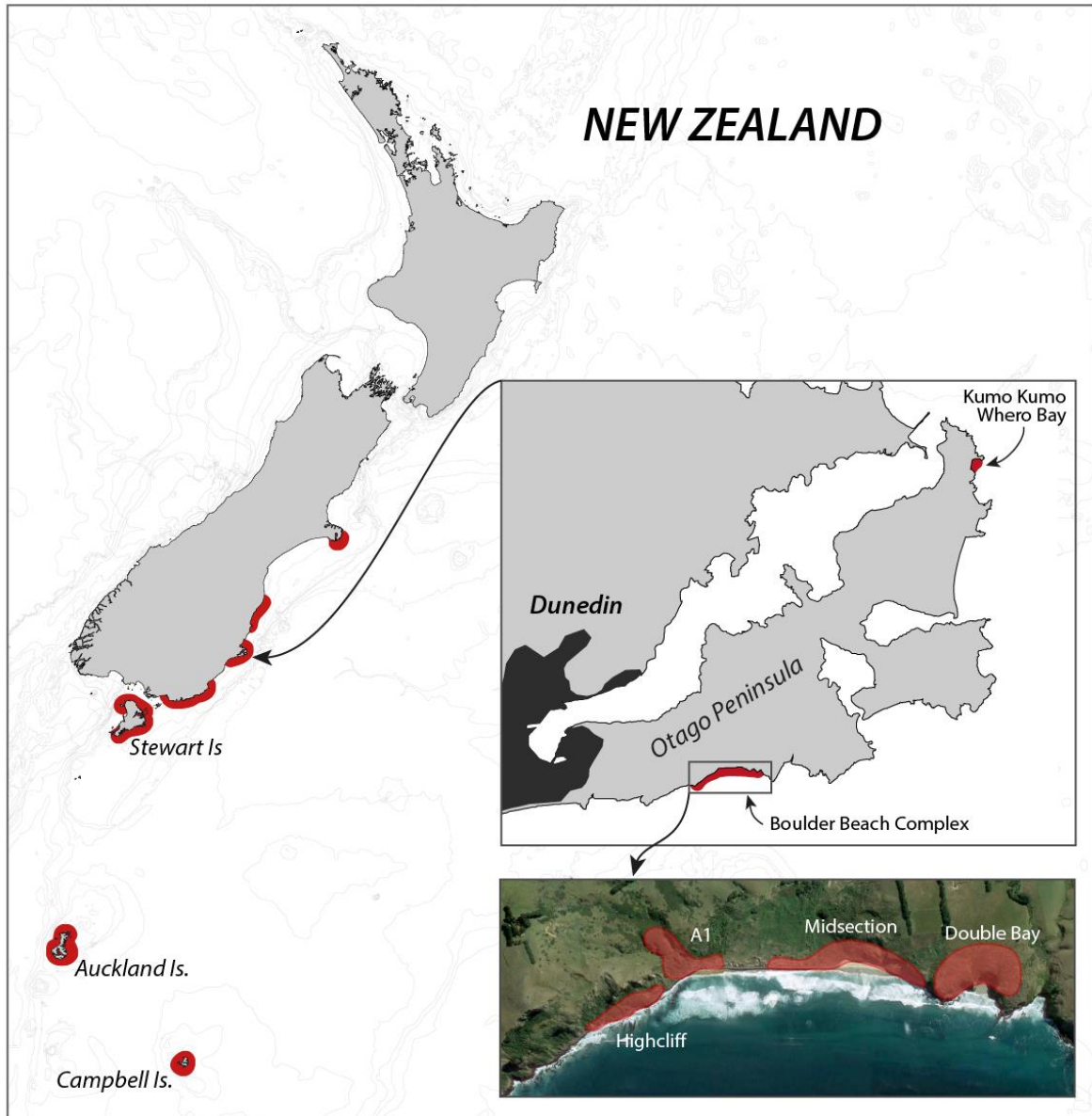
Figure 1. Overview of the breeding range of Yellow-eyed penguins, detail of the Otago Peninsula with and aerial view of the Boulder Beach Complex (henceforth Boulder Beach) with outlines indicating the locations of the four main monitoring plots
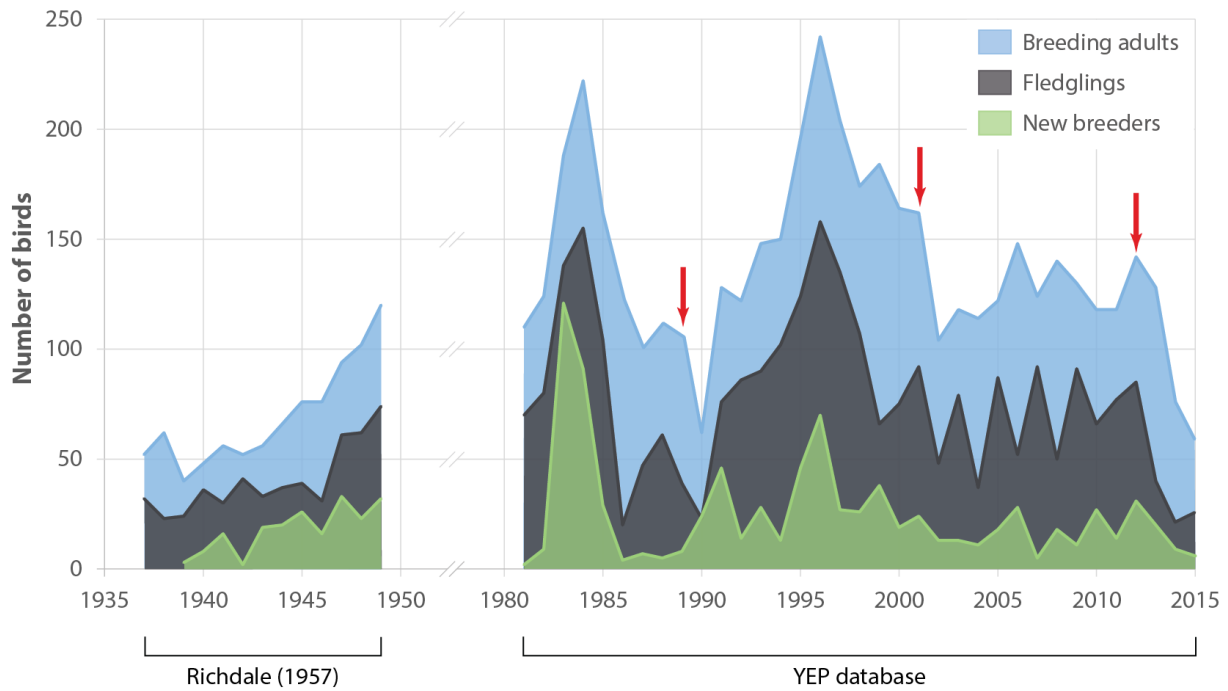
Figure 2. Observed penguin numbers at Kumo Kumo Whero 1937-1948 (from data published in Richdale 1957, see Methods for details) and at the Boulder Beach complex 1982-2015 as extracted from the Yellow-eyed penguin database. 'New breeders' represents the portion of all 'breeding adults' that were recorded as breeders for the first time. Red arrows indicate years with observed die-off events affecting adult breeders. Note that as some sections of the Boulder Beach complex were not monitored in all years, data for the years 1986-1989 were adjusted by adding the mean proportion these areas contributed to the total count in all other years.

685
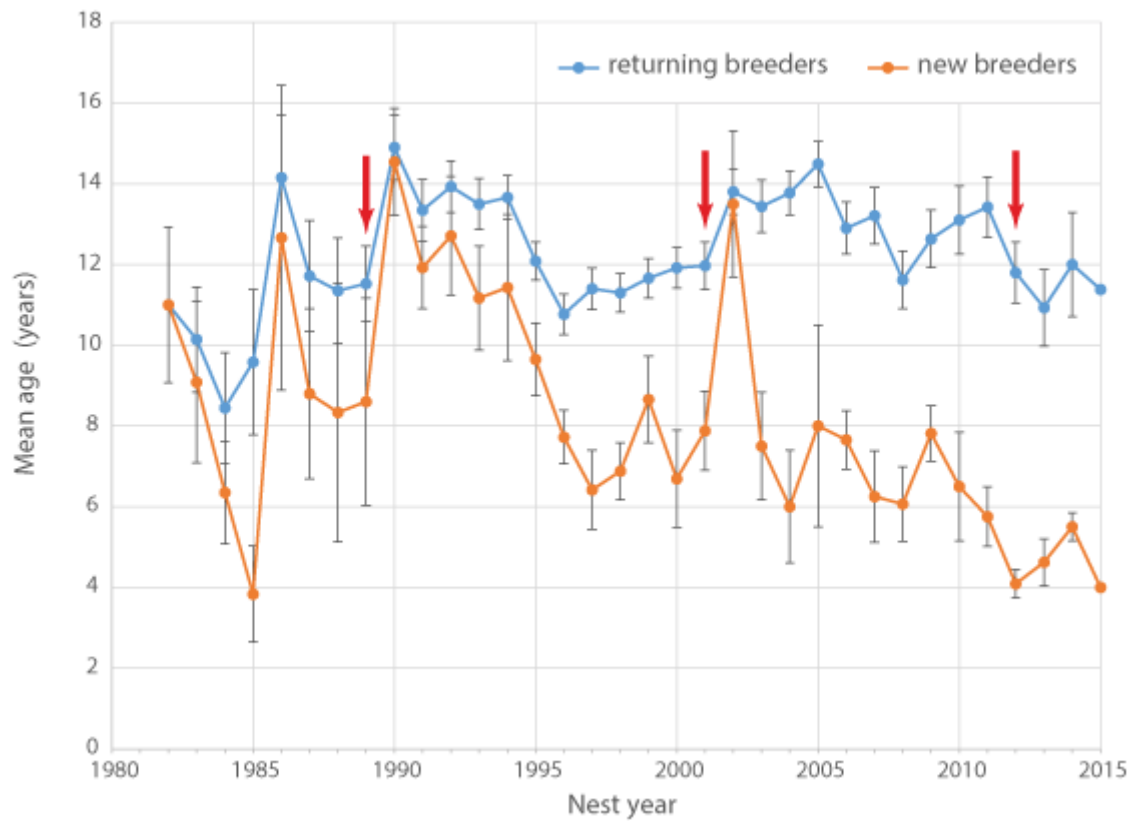
Figure 3. Average age of breeding Yellow-eyed penguins active at Boulder Beach between 1982

and 2015. Red arrows indicate years with observed die-off events affecting adult breeders.
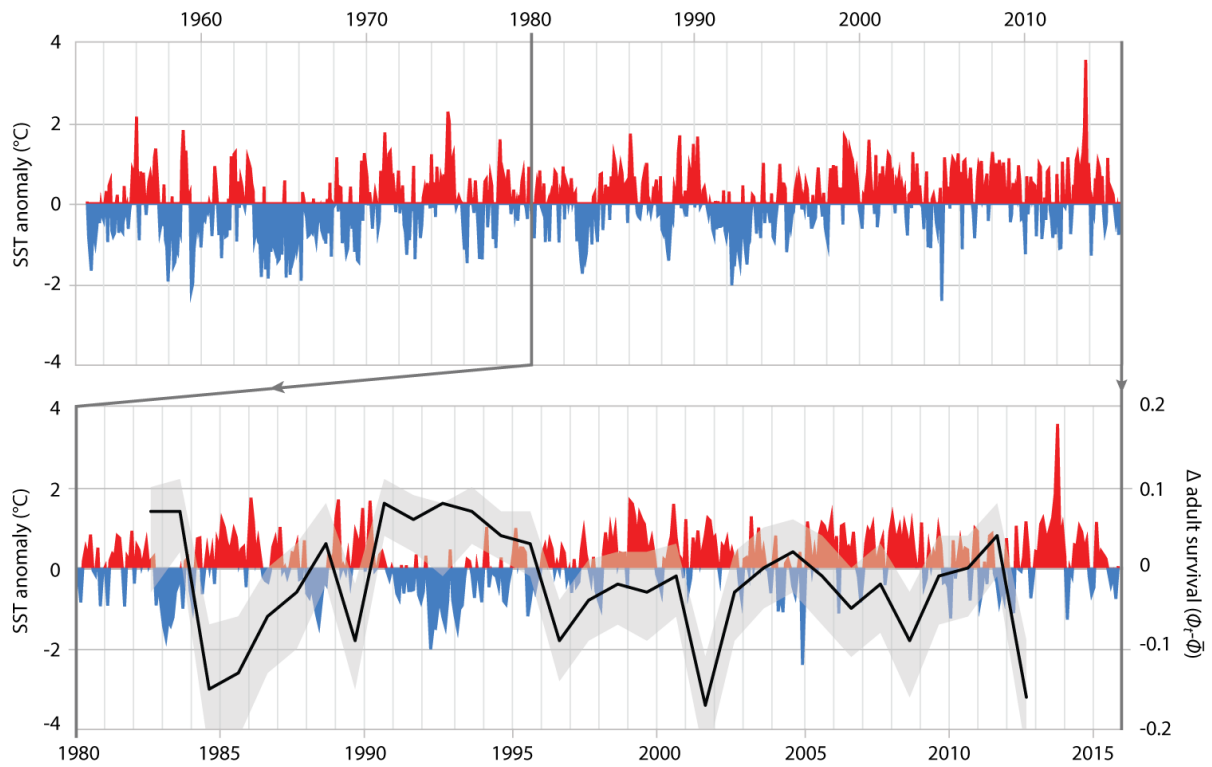
Figure 4. Top graph: Local Sea Surface Temperature anomalies recorded at Portobello Marine Lab, Otago Peninsula, between 1953 and 2016. Bottom graph: detail of SST anomalies 1980-2016 and associated deviance (black line: mean; grey area: 95% credible interval) in survival of adult Yellow-eyed penguins as determined from a MR recapture model.

693
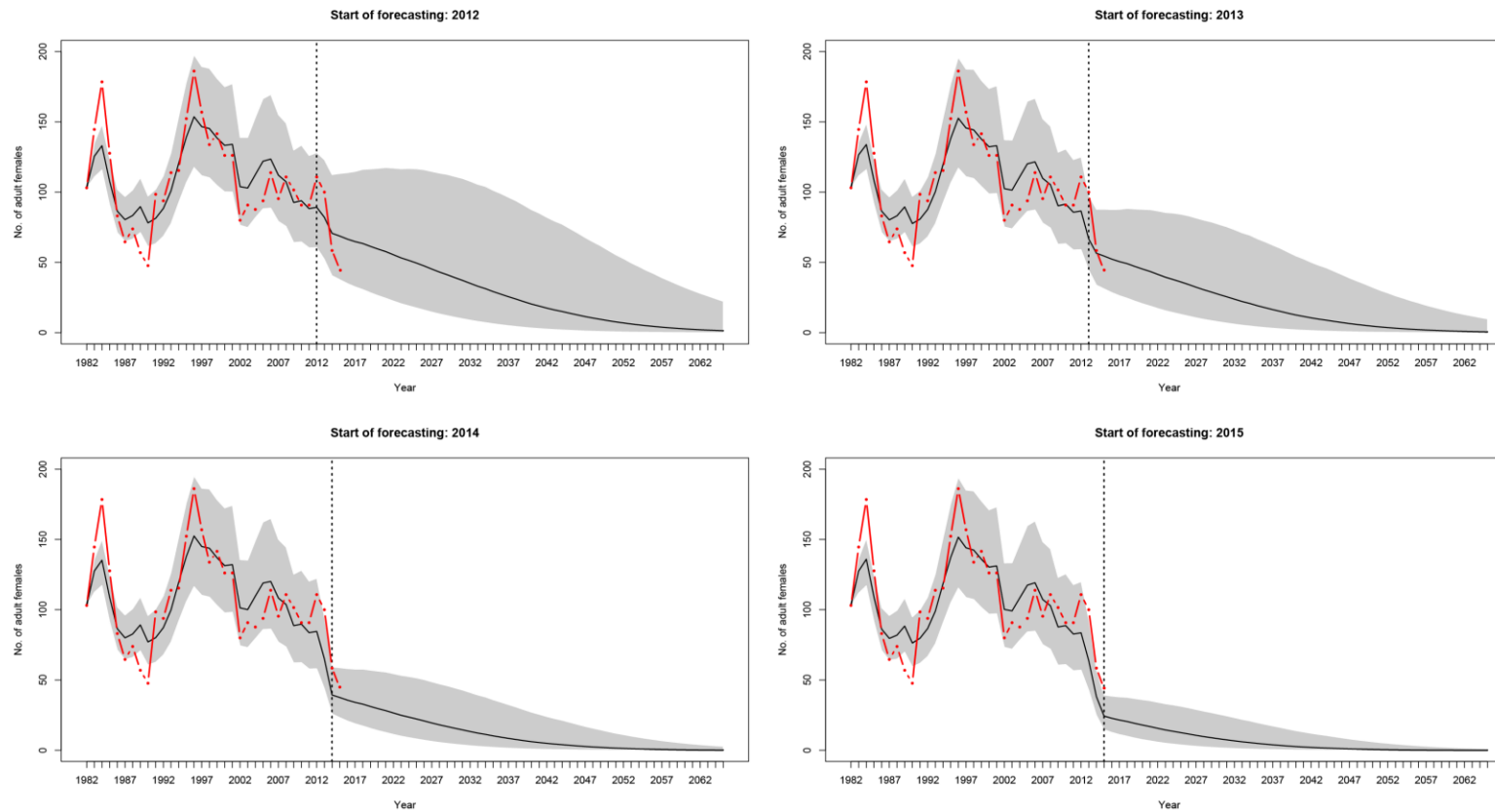
Figure 5. Population projections for Yellow-eyed penguins at Boulder Beach, Otago Peninsula. The graphs show the observed (red line) and estimated (black line) number of female penguins, and associated 95% credible interval (grey area), as derived from the population model. The dashed vertical line indicates the last year used to parameterise the MR model and the starting year of the simulation. It is important to note that after 2012 survival rate estimates get increasingly unreliable because these are based on data about individual absence from breeding rather than from reported mortalities (see 'Methods').

699
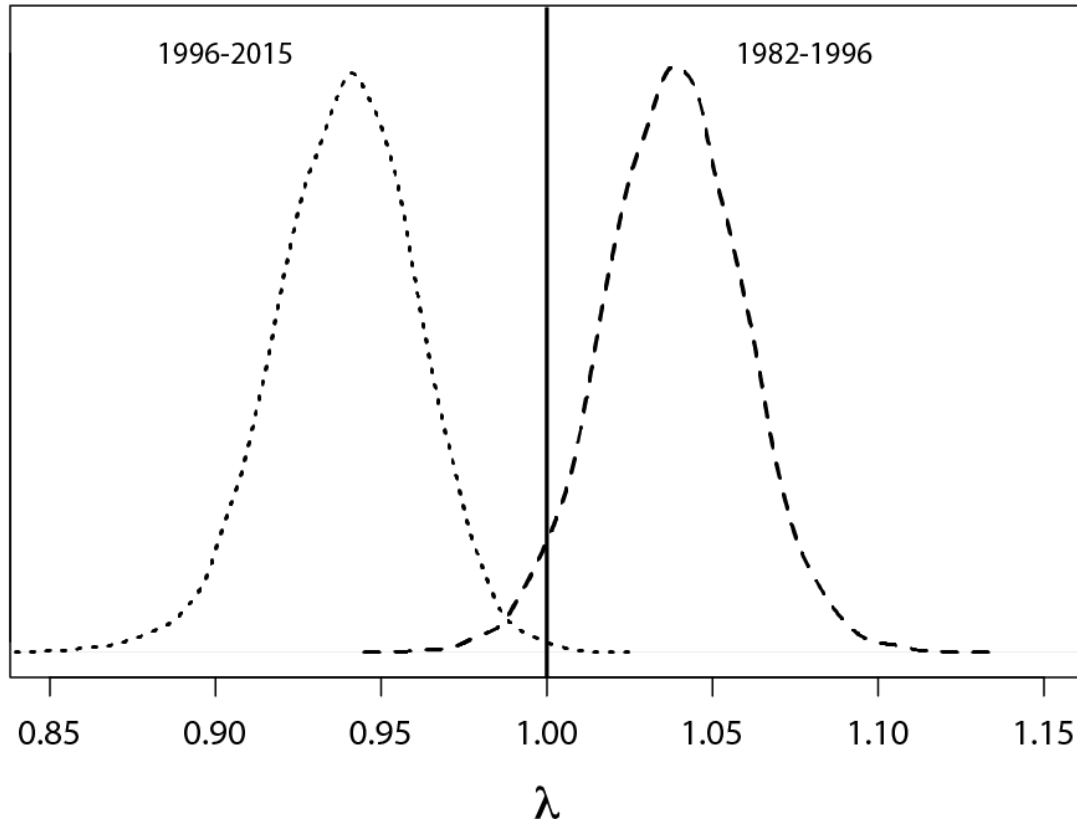
Figure 6. Probability density functions for deterministic annual population growth rates derived from survival rates that were rescaled for periods of cooler (1982-1996) and warmer (1996-2014) than average sea surface temperatures.

703   **Table 1.** Description of basic environmental parameters used for the development of a YEP

704   population model.

Parameter	shorthand	Station
Total Rainfall (mm)	total_rainfall	Southern Reservoir (National Climate database, CliFlo ID 5400)
Wet Days - Number Of Days With 1mm Or More Of Rain (days)	wet_days	Southern Reservoir (5400)
Maximum 1-Day Rainfall - 9am To 9am Local Time	max_1day_rain	Dunedin, Musselburgh (5402)
Mean Air Temperature	mean_air_temp	Dunedin, Musselburgh (5402)
Mean Daily Minimum Air Temperature	daily_min_temp	Dunedin, Musselburgh (5402)
Days Of Wind Gusts >=33 Knots	days_wind_gusts_33	Dunedin, Musselburgh (5402)
Sea Surface Temperature anomaly	sst_anomaly	Portobello Marine Lab, University of Otago

705 **Table 2.** Parameter estimates from the Bayesian mark-recapture model. Φ indicates estimated

706 survival rates, σ^2 stands for the temporal variance of the stage-specific survival. Refer to ESM1

707 for details.

		Credible interval	
Parameters	**Median**	**2.5%**	**95.5%**
$\bar{\Phi}_{chicks}$	0.124	0.077	0.189
σ^2_{chicks}	1.877	1.001	3.847
σ^2_{chicks} (on probability scale)	0.021	0.009	0.065
$\bar{\Phi}_{adults}$	0.872	0.832	0.904
σ^2_{adults}	0.732	0.414	1.398
σ^2_{adults} (on probability scale)	0.009	0.005	0.021

708   **Table 3a.** Estimated effect size for fledgling survival ($\beta_{fledlings}$); PVE: percentage of variance in

709   fledgling survival explained by each covariate. Note, that negative values resulted from models

710   that estimated slightly higher (or less precise) variance in fledgling survival, as it would result

711   for the model without covariate. Except for covariate 2, 3, 4 and 15 all variables were

712   standardized before fitted to the MR model.

ID	Covariate	Median	Credible interval 2.5%	95.5%	PVE
1	days_wind_gusts_33_annual	0.850	0.377	1.329	33.2
2	sst_anomaly_austral	-1.967	-3.148	-0.964	33.2
3	sst_anomaly_minus_1yr	-1.516	-2.649	-0.392	24.8
4	sst_anomaly_mar_june	-0.970	-1.845	-0.111	17.4
5	days_wind_gusts_33_mar_may	0.696	0.198	1.241	16.5
6	daily_min_temp_annual	-0.644	-1.190	-0.143	15.4
7	mean_air_temp_annual	-0.590	-1.167	-0.102	12.4
8	daily_min_temp_mar_may	-0.303	-0.829	0.204	0.7
9	mean_air_temp_mar_may	-0.304	-0.850	0.190	0.2
10	total_rainfall_may_may	-0.254	-0.823	0.296	-2.3
11	max_1day_rain_mar_may	-0.250	-0.835	0.318	-3.3
12	total_rainfall_annual	-0.260	-0.841	0.316	-3.5
13	max_1day_rain_annual	-0.167	-0.738	0.394	-5.2
14	wet_days_mar_may	-0.141	-0.702	0.431	-5.6
15	sst_anomaly_minus_2yr	-0.217	-1.451	1.045	-5.6
16	wet_days_annual	0.073	-0.461	0.623	-6.7

713 **Table 3b.** Estimated effect size for adult survival (β_{adults}); PVE: percentage of variance in adult

714 survival explained by each covariate. Note, that negative values resulted from models that

715 estimated slightly higher (or less precise) variance in adult survival, as it would result for the

716 model without covariate. Except for covariate 1, 4, 5 and 14 all variables were standardized

717 before fitted to the MR model.

ID	Covariate	Median	Credible interval		PVE
			2.5%	95.5%	
1	sst_anomaly_austral	-1.267	-1.925	-0.631	36.8
2	mean_air_temp_annual	-0.529	-0.817	-0.251	34.4
3	daily_min_temp_annual	-0.516	-0.796	-0.227	34.4
4	sst_anomaly_mar_june	-0.808	-1.329	-0.310	26.2
5	sst_anomaly_minus_1yr	-1.056	-1.719	-0.406	25.7
6	days_wind_gusts_33_annual	0.377	0.075	0.690	16.5
7	days_wind_gusts_33_mar_may	0.350	0.052	0.666	12.8
8	daily_min_temp_mar_may	-0.214	-0.537	0.088	2.0
9	total_rainfall_may_may	-0.146	-0.461	0.193	1.0
10	mean_air_temp_mar_may	-0.181	-0.513	0.140	-0.3
11	wet_days_mar_may	-0.113	-0.434	0.207	-1.0
12	max_1day_rain_mar_may	-0.098	-0.416	0.234	-2.0
13	max_1day_rain_annual	0.112	-0.206	0.435	-2.2
14	sst_anomaly_minus_2yr	-0.055	-0.867	0.720	-3.1
15	wet_days_annual	0.064	-0.275	0.393	-3.8
16	total_rainfall_annual	0.057	-0.268	0.391	-4.0

718 **Table 4.** Results of the Gibbs Variable Selection. 0 and 1 indicate whether each covariate is not

719 included or included in the model, respectively. The MR considers covariates

720 'sst_anomaly_austral' for fledgling (A) and adult survival (C), 'days_wind_gusts_33_annual' (B)

721 and 'mean_air_temp_annual' (D). For a detailed description of the GVS refer to ESM4.

	Model configuration				
	Fledgling survival		Adult survival		
M_i	A	B	C	D	$p(M_i\|y)$
1	1	0	1	0	0.42
2	0	1	1	0	0.13
3	1	1	1	0	0.12
4	1	0	0	1	0.09
5	0	1	0	1	0.06
6	0	0	0	0	0.04
7	1	0	0	0	0.03
8	0	1	0	0	0.03
9	1	1	0	0	0.02
10	0	0	1	0	0.01
11	0	0	0	1	0.01
12	1	1	0	1	0.01
13	0	0	1	1	0
14	1	0	1	1	0
15	0	1	1	1	0
16	1	1	1	1	0

722

Electronic Supplementary Material 1.

Estimation of demographic parameters

Using banding records of Yellow-eyed penguins, we developed a Bayesian mark-recapture (MR) model that was structured into 2 stages: (1) fledglings (age: 0 years) and (2) adults (1+ years). The MR model could not be sex-specific, because information on the gender was reported for only 58% of the individuals in the banding table. The only way to identify individuals were bands which are applied to chicks shortly prior to fledging. This means that our MR model did not consider chicks that died before they could be banded. Overall a total number of 2,967 individuals recorded over a 34-year period were used for analysis.

For the analysis we converted the data into two m-arrays for (1) individuals that were banded as fledglings and recaptured as adults, and (2) individuals that were banded as adults and recaptured as adults (ESM2). Both m-arrays are 2-dimensional matrices providing the number of recaptured individuals in any year (columns) following any release year (rows) (Burnham 1987). These m-arrays were analysed using the multinomial distribution, and parameters stage-specific survival $\phi_{k,t}$, with k = fledglings or adults in year t, and adult recapture (Kéry and Schaub 2012; Lebreton et al. 1992). We fixed the adult recapture probability to one, because the analysed data do not contain reliable recovery records, unless an individual had died or not returned to the breeding colony.

We allowed survival to be time-variant by modelling $\phi_{k,t}$ on logit scale, which we assume to vary following a normal distribution with mean zero and stage-specific variance σ_k^2:

$$\text{logit}(\phi_{k,t}) = \mu_k + \varepsilon_{k,t} \qquad [E1.1]$$

$$\varepsilon_{k,t} \sim \text{Normal}(0, \sigma_k^2) \qquad [E1.2]$$

where $\varepsilon_{k,t}$ denotes the temporal residuals for μ_k. We supplied a uniform prior distribution on the interval [0, 1] for the mean survival on probability scale ($\bar{\phi}_k$), which was linked to μ_k using the link function $\mu_k = \log(\bar{\phi}_k/(1-\bar{\phi}_k))$. We supplied uniform prior distributions for σ_k on the three

alternative intervals for [0, 2], [0, 5], and [0, 10], and found no prior sensitivity for estimated $\sigma_k{}^2$ (ESM3).

Moreover, we extended the model described in eq. E1.1 to examine the effect of environmental covariates on $\phi_{k,t}$:

$$\text{logit}(\phi_{k,t}) = \mu_k + \beta_k * x_t + \varepsilon_{k,t} \qquad [E1.3]$$

where β_k denotes the stage-specific effect size fitted to the time-specific covariate x_t. Except for covariates reflecting SST anomaly we standardized $((x_t - \bar{x}_t) / sd(x_t))$ all covariates before model fitting. To ensure that the data provide sufficient information to estimate each parameter, we assessed correlation matrices for each model parameterization (ESM4) (Gimenez et al. 2008), which was generally low (range [-0.14, 0.14]), although moderate cross correlation existed between the posterior estimates for mean survival and the effect size (range [-0.38, -0.21]) when we fitted models to covariates reflecting sst anomaly (ESM4). However, we found no sensitivity of estimates for β_k after varying the standard deviation of the normal prior supplied for β_k (N(0, 0.001) and N(0, 0.01)) (ESM4). Additional prior configurations were imposed during the model selection procedure (see below).

For all models (eq. E1.1 and eq. E1.3) we found no indication for a lack-of-fit, based on Bayesian p-values (Gelman 2013; Gelman et al. 1996) that ranged between 0.28 and 0.48.

The model was analysed using JAGS (Plummer 2003). The burn-in was 2,000 iterations followed by 25,000 iterations, and posterior samples were drawn using a thinning interval of 3. We computed the potential scale reduction factor $\widehat{R}$ (Gelman and Rubin 1992) using the output of three MCMC chains and assumed convergence if $\widehat{R}$ was near to 1. For all estimated parameters $\widehat{R}$ was smaller than or equal to 1.01.

Model selection

First, we fitted the model described in eq. 3 to each covariate separately and computed the percentage of temporal variance explained by each covariate (Grosbois et al. 2008) as:

$$((\sigma_k{}^2 - \sigma_{k,x}{}^2) / \sigma_k{}^2) * 100 \qquad [E1.4]$$

where σ_k^2 and $\sigma_{k,x}^2$ are the temporal variance of the stage-specific survival from eq. E1.1 and eq. E1.3, respectively. We considered covariates as influential predictors if they explained at least 20% of σ_k^2 (Grosbois et al. 2008). For each stage, the two strongest predictors were implemented into the MR model (i.e. eq. E1.3 plus an additional β_k for the second covariate in each stage). We assessed the posterior model probability for each combination of these four covariates using Gibbs Variable Selection (GVS) (Ntzoufras 2002; Tenan et al. 2014; Hooten and Hobbs 2015). Importantly, we repeated the analysis with various prior distributions and found that our results were not affected by the choice of priors required for GVS (ESM5).

Population model

To model YEP population dynamics we developed a female-only model assuming a birth-pulse population (Tang and Chen 2002). Due to the lack of consistent data on gender in the database, we followed Richdale (1952) and assumed the sex ratio in YEP to be equal at hatching. As pointed out above, the MR model being based on banding information could not incorporate chick survival/fecundity. For the population model we accounted for this by determining the proportion of female chicks that hatched and remained within the population until fledging. We denoted this as

$$\bar{\gamma}_{chicks} = \bar{\rho} * \bar{\omega} * 0.5 \qquad [E1.5]$$

where $\bar{\rho}$ is the average proportion of breeding adults derived from the data of all banded adults (i.e. breeders vs. non-breeders with an age of 1+ years). $\bar{\omega}$ denotes the average proportion of chicks per nest, which was obtained from annual nest monitoring at Boulder Beach. To ensure that only female individuals enter the model, we multiplied $\bar{\omega}$ by 0.5 (i.e. based on a 1:1 sex ratio).

After leaving the nest in March, fledglings only have to survive 7 months (on average 212.971 days) until they can be recaptured again at the beginning of the following nesting season in November. Because of this we rescaled the fledgling survival from our MR model to reflect survival over 12-month time interval:

$$\Phi_{fledgling\ t} = \phi_{fledglings,t}{}^{(1/(365/212.917))} \qquad [E1.6]$$

Using this information we can now describe $\gamma_{adult,t}$, the proportion of adult YEPs within the population in year t as:

$$\gamma_{adult,t} = \phi_{adults,t} + \phi_{fledgling,t} * \bar{\gamma}_{chicks} \qquad [E1.7]$$

where $\phi_{adult,t}$ and $\phi_{fledgling,t}$ are the only time-varying components, which were derived from posterior distributions for $\phi_{fledglings,t}$ and $\phi_{adults,t}$ from the model in eq. E1.3 using the covariates that were preserved during the model selection exercise.

For the study years 1982 to 2014 we projected $n_{adult,t+1}$, the number of adult YEPs in the year $t+1$ as:

$$n_{adult,t+1} = n_{adult,t} * \gamma_{adult,t} \qquad [E1.8]$$

where the initial adult population size at t=1 was calculated as:

$$n_{adult,1} = n_{nest,1} / \bar{\rho} \qquad [E1.9]$$

where $n_{nest,1}$ is the observed number of nests in the first year (i.e. 1982) and $\bar{\rho}$ is the proportion of breeders in the same year.

The average population size is determined by the survival parameters, the average proportion of breeders, and the proportion of fledglings per nest (i.e. a proxy for fecundity); the latter two contained in the variable $\bar{\gamma}_{chicks}$. The temporal fluctuation of $n_{adult,t+1}$ only depends on the annual survival rates. Therefore, we visually assessed whether the use of the estimated temporal variance in survival is sufficient to predict the observed change in the adult population size, which was calculated through eq. 9 using the year-specific number of nest between 1982 and 2014.

Effect of covariates on the population growth rate

The linear function described in eq. E1.7 reflects the proportional change of adult individuals between years and thus the population growth rates from year t to $t+1$. Thus, replacing temporal

varying components $\phi_{fledgling,t}$ and $\phi_{adults,t}$ in eq. E1.7 with average survival rates can be used to approximate the deterministic population growth rate λ ($\lambda < 1$: population decline, $\lambda = 1$: stable population, $\lambda > 1$: population growth) between 1982 and 2014:

$$\lambda = \bar{\phi}_{adults} + \bar{\phi}_{fledgling} * \bar{\gamma}_{chicks} \qquad [E1.10]$$

with $\bar{\phi}_{adults}$ and $\bar{\phi}_{fledgling}$ derived from the model described in eq. E1.3. Moreover, we calculated λ after rescaling each $\bar{\phi}_k$ using the average sea surface temperature (SST) anomaly (the predictor variable preserved during the model selection exercise; see 'Results') (1) between the years 1982 and 1996; (2) between the years 1996 and 2014. This cut-off was based on visual examination of the SST anomaly, which implies that the SST increased above average after 1996.

Future projections

To assess the future developments of the penguin population we ran a series of stochastic projections based on our population model. Firstly we simulated future SST anomaly developments until 2060 which included the predicted SST rise for the Otago region of 2.0°C between 1990 and 2090 which translates to a mean 0.02°C increase per year (Ministry for the Environment 2008). For each future year up until 2065, we firstly randomly selected 12 monthly averages (i.e. Jan-Dec) from the SST data recorded between 1982 and 2015 data to calculate an annual mean. We then cumulatively added 0.02°C to each simulated annual mean (i.e. 2015-2060) and calculated the corresponding SST anomaly as difference of the average annual SST anomaly. We ran 1,000 iterations of this simulation and used the mean of all simulations as the projected SST anomaly, which served to predict future survival rates using eq. 1 and 2 and parameters estimated from the MR data. Each forward prediction of survival rates was repeated 500 times for all posterior samples to allow for uncertainty owing to temporal stochasticity. These predicted survival rates were then used to forward project the adult population size from 2015 onwards. After 2012 it was difficult to determine whether an individual's absence was due to absence from breeding or actual mortality. To ensure that the future projections are not affected through underestimated survival rates between 2012 and 2014, we re-fitted the MR

model to data sets limited to the years 1982-2011, 1982-2012 and 1982-2013; and started each projection in 2012, 2013 and 2014, respectively.

References

Burnham, K.P., 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society.

Gelman, A., 2013. Two simple examples for understanding posterior p-values whose distributions are far from unform. Electronic Journal of Statistics 7, 2595-2602.

Gelman, A., Meng, X.-L., Stern, H., 1996. Posterior predictive assessment of model fitness via realized discrepancies. Statistica sinica, 733-760.

Gimenez, O., Morgan, B., Brooks, S., 2008. Weak identifiability in models for mark-recapture-recovery data, In Modeling demographic processes in marked populations. eds D.L. Thomson, E.G. Cooch, M.J. Conroy, pp. 1055-1067. Springer Science & Business Media.

Grosbois, V., Gimenez, O., Gaillard, J.M., Pradel, R., Barbraud, C., Clobert, J., Møller, A., Weimerskirch, H., 2008. Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews 83, 357-399.

Kéry, M., Schaub, M., 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press.

Lebreton, J., Bunham, K., Clobert J, Anderson, D., 1992. Modeling survival and testing biological hypotheses using marked animals - A unified approach with case-studies. Ecological Monographs 62, 67-118.

Ministry for the Environment, 2008. Climate Change Effects and Impacts Assessment: A Guidance Manual for Local Government in New Zealand. 2nd Edition., eds B. Mullan, D. Wratt, S. Dean, M. Hollis, S. Allan, T. Williams, G. Kenny, p. xviii + 149 p. Ministry for the Environment,, Wellington.

Plummer, M., 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling, In Proceedings of the 3rd international workshop on distributed statistical computing. p. 125. Technische Universit at Wien Wien, Austria.

Tang, S., Chen, L., 2002. Density-dependent birth rate, birth pulses and their population dynamic consequences. Journal of Mathematical Biology 44, 185-199.

m-array adults

	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	never recaptured
1982	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1983	0	53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1984	0	0	90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32
1985	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33
1986	0	0	0	0	95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
1987	0	0	0	0	0	94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
1988	0	0	0	0	0	0	115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
1989	0	0	0	0	0	0	0	125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30
1990	0	0	0	0	0	0	0	0	139	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
1991	0	0	0	0	0	0	0	0	0	153	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
1992	0	0	0	0	0	0	0	0	0	0	162	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
1993	0	0	0	0	0	0	0	0	0	0	0	202	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
1994	0	0	0	0	0	0	0	0	0	0	0	0	242	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15
1995	0	0	0	0	0	0	0	0	0	0	0	0	0	270	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22
1996	0	0	0	0	0	0	0	0	0	0	0	0	0	0	258	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	66
1997	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	254	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44
1998	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	245	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35
1999	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	225	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35
2000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	208	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27
2001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	171	0	0	0	0	0	0	0	0	0	0	0	0	0	68
2002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	158	0	0	0	0	0	0	0	0	0	0	0	0	26
2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	153	0	0	0	0	0	0	0	0	0	0	0	19
2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	169	0	0	0	0	0	0	0	0	0	0	17
2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	173	0	0	0	0	0	0	0	0	0	22
2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	163	0	0	0	0	0	0	0	0	31
2007	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	146	0	0	0	0	0	0	0	21
2008	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	125	0	0	0	0	0	0	32
2009	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	112	0	0	0	0	0	15
2010	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	136	0	0	0	0	17
2011	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	137	0	0	0	10
2012	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	120	0	0	45
2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	76	0	62
2014	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37	39

m-array fledglings

	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	never recaptured
1982	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1983	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16
1984	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	182
1985	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	158
1986	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30
1987	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60
1988	0	0	0	0	0	0	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	92
1989	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	65
1990	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27
1991	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	65
1992	0	0	0	0	0	0	0	0	0	0	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	51
1993	0	0	0	0	0	0	0	0	0	0	0	47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44
1994	0	0	0	0	0	0	0	0	0	0	0	0	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	55
1995	0	0	0	0	0	0	0	0	0	0	0	0	0	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	88
1996	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	126
1997	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	97
1998	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	66
1999	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25
2000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	70
2001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	81
2002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	39
2003	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	0	0	0	0	0	0	0	0	0	0	0	46
2004	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	25
2005	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	70
2006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	49
2007	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	85
2008	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	45
2009	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	73
2010	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	65
2011	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	71
2012	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	87
2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38
2014	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
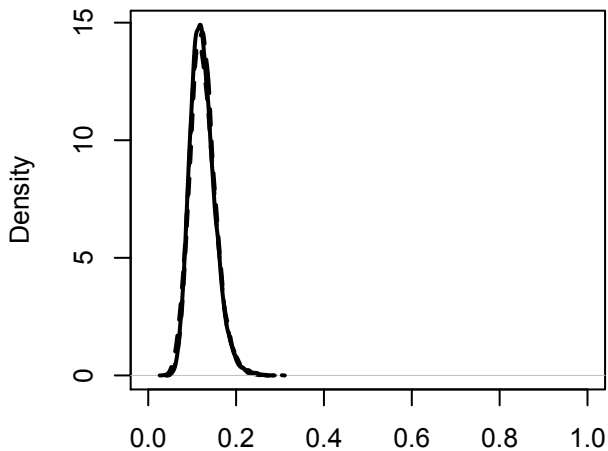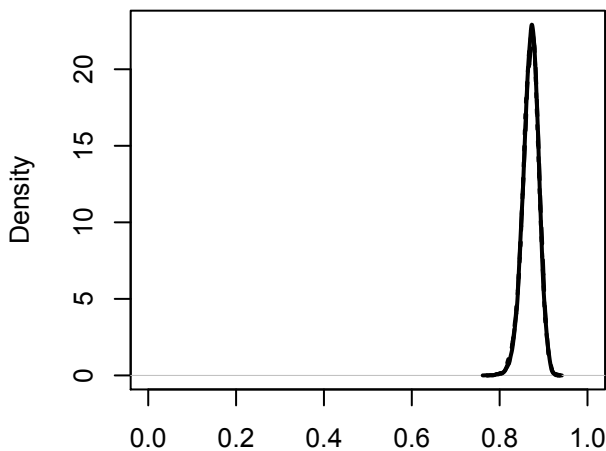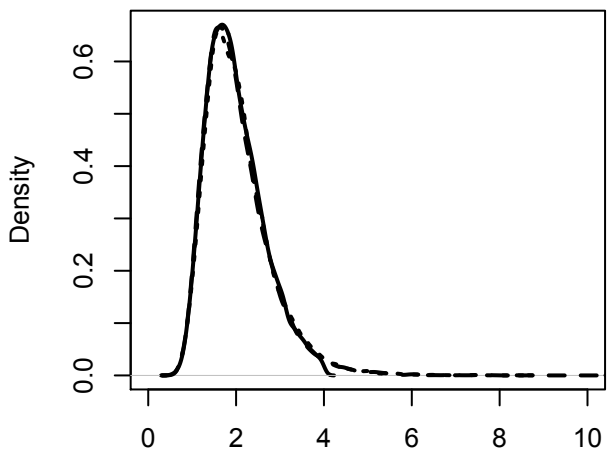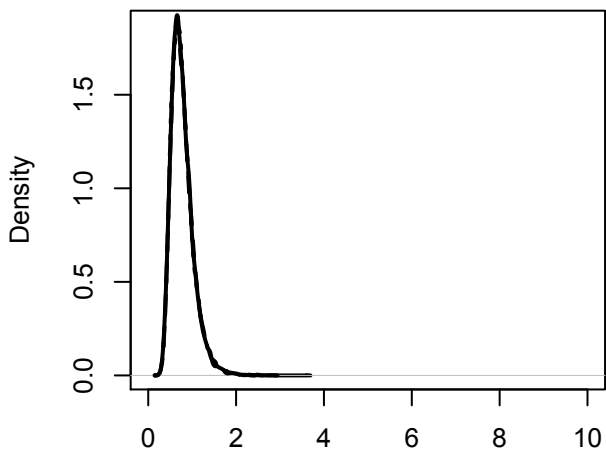
crosscorr.cjs.yep.daily_min_temp_annual

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	-0.02	-0.12	0.02	-0.05	-0.02
beta.j		1	-0.02	0.07	0	-0.13
mean.phiad			1	-0.05	0.08	0
mean.phijuv				1	0	-0.08
sigma2.a					1	-0.01
sigma2.j						1

crosscorr.cjs.yep.daily_min_temp_mar_may

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	0	-0.07	-0.01	-0.06	-0.02
beta.j		1	0	0.08	0	-0.02
mean.phiad			1	0	0.08	0.01
mean.phijuv				1	0	-0.03
sigma2.a					1	0
sigma2.j						1

crosscorr.cjs.yep.days_wind_gusts_33_annual

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	0	0.08	0.02	0.07	0.01
beta.j		1	0	-0.1	-0.01	0.12
mean.phiad			1	0	0.05	0
mean.phijuv				1	-0.01	-0.08
sigma2.a					1	0
sigma2.j						1

crosscorr.cjs.yep.days_wind_gusts_33_mar_may

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	-0.02	0.06	0.01	0.09	0
beta.j		1	-0.01	-0.07	0	0.14
mean.phiad			1	0.04	0.05	-0.02
mean.phijuv				1	0	-0.05
sigma2.a					1	0
sigma2.j						1

crosscorr.cjs.yep.max_1day_rain_annual

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	-0.01	0.02	0	0.03	0
beta.j		1	0.01	-0.01	0	-0.03
mean.phiad			1	-0.01	0.02	0.01
mean.phijuv				1	0.01	-0.01
sigma2.a					1	0
sigma2.j						1

crosscorr.cjs.yep.max_1day_rain_mar_may

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	0.01	0.04	-0.02	0.03	0.01
beta.j		1	0.02	0.1	0.01	-0.04
mean.phiad			1	0.01	0.03	0.01
mean.phijuv				1	-0.01	-0.07
sigma2.a					1	0
sigma2.j						1

crosscorr.cjs.yep.mean_air_temp_annual

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	0	-0.08	-0.02	-0.09	0
beta.j		1	0.02	0.08	-0.01	-0.14
mean.phiad			1	-0.03	0.06	0
mean.phijuv				1	-0.01	-0.06
sigma2.a					1	0.01
sigma2.j						1

crosscorr.cjs.yep.mean_air_temp_mar_may

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	0.05	-0.07	0	-0.04	0
beta.j		1	-0.02	0.09	-0.01	-0.06
mean.phiad			1	0.01	0.06	0
mean.phijuv				1	0	-0.07
sigma2.a					1	0.01
sigma2.j						1

crosscorr.cjs.yep.sst_anomaly_austral

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	-0.01	-0.38	0.01	-0.06	0.01
beta.j		1	0.01	-0.25	0	-0.2
mean.phiad			1	-0.03	0.06	-0.02
mean.phijuv				1	-0.01	0.03
sigma2.a					1	0
sigma2.j						1

crosscorr.cjs.yep.sst_anomaly_mar_june

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	-0.03	-0.36	0.02	-0.07	-0.01
beta.j		1	0.01	-0.21	0	-0.04
mean.phiad			1	-0.02	0.09	0.01
mean.phijuv				1	-0.01	-0.03
sigma2.a					1	-0.01
sigma2.j						1

crosscorr.cjs.yep.sst_anomaly_minus_1yr

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	0	-0.35	-0.01	-0.06	-0.01
beta.j		1	-0.02	-0.21	-0.02	0
mean.phiad			1	0	0.08	-0.01
mean.phijuv				1	0.01	-0.04
sigma2.a					1	0
sigma2.j						1

crosscorr.cjs.yep.sst_anomaly_minus_2yrs

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	0.01	-0.21	-0.01	0.01	0.01
beta.j		1	0	-0.22	-0.02	0.01
mean.phiad			1	-0.04	0.05	0
mean.phijuv				1	0	0.02
sigma2.a					1	0
sigma2.j						1

crosscorr.cjs.yep.total_rainfall_annual

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	-0.01	0	0.01	0.03	0.01
beta.j		1	0.01	0.02	0	-0.06
mean.phiad			1	-0.03	0.04	-0.01
mean.phijuv				1	0	-0.02
sigma2.a					1	0
sigma2.j						1

crosscorr.cjs.yep.total_rainfall_mar_may

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	0	0.01	0.02	0.06	-0.01
beta.j		1	0.01	0.09	0.01	-0.05
mean.phiad			1	0	0.02	0
mean.phijuv				1	-0.01	-0.05
sigma2.a					1	0
sigma2.j						1

crosscorr.cjs.yep.wet_days_annual

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	0	0.01	-0.02	0.01	-0.02
beta.j		1	0.03	-0.04	0.02	0.06
mean.phiad			1	0.01	0.06	0
mean.phijuv				1	0.02	-0.02
sigma2.a					1	-0.01
sigma2.j						1

crosscorr.cjs.yep.wet_days_mar_may

	beta.a	beta.j	mean.phiad	mean.phijuv	sigma2.a	sigma2.j
beta.a	1	-0.01	-0.01	0.02	0	-0.01
beta.j		1	0.01	0.04	0	-0.01
mean.phiad			1	0	0.07	0
mean.phijuv				1	0	0
sigma2.a					1	0.01
sigma2.j						1
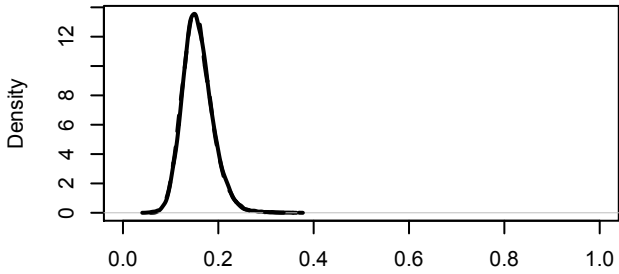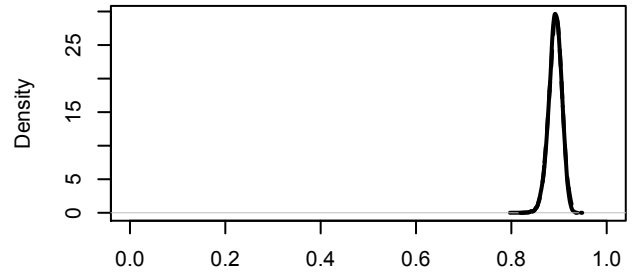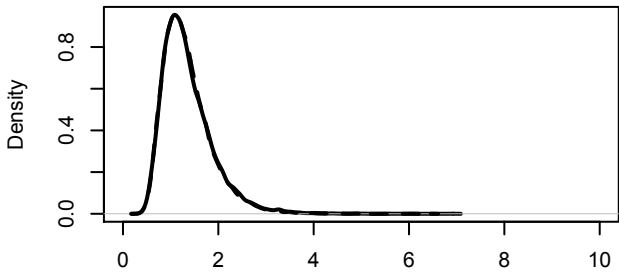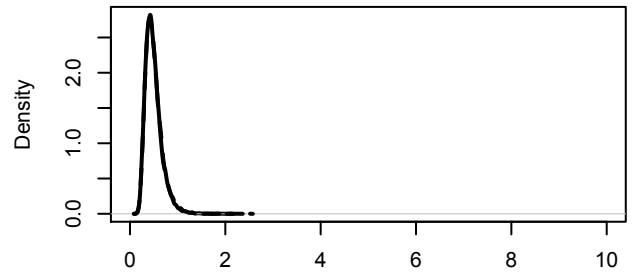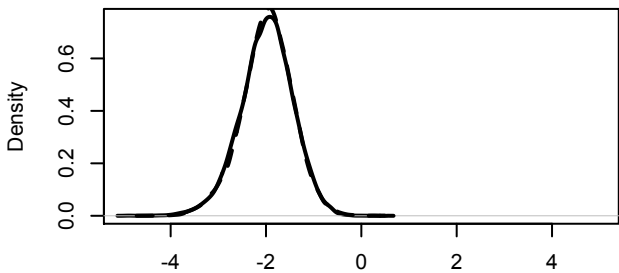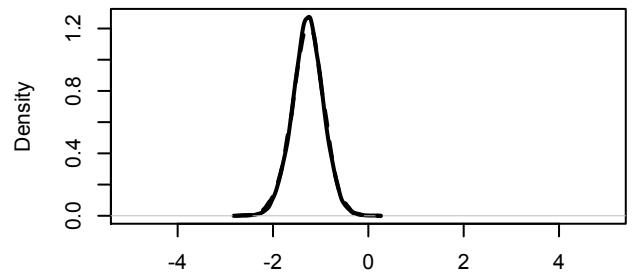
Electronic Supplementary Material 5.

Estimation of the posterior model probability using Gibbs Variable Selection (GVS)

The MR model was simultaneously fitted to the covariates 'sst_anomaly_austral' and 'days_wind_gusts_33_annual' for chick survival (Table 2 in main text) and covariates 'sst_anomaly_austral' and 'mean_air_temp_annual' for adult survival . We assessed the posterior model probability ($p(M_i|y)$) for each combination of these four covariates using Gibbs variable selection (GVS) (Ntzoufras 2002; Tenan et al. 2014; Hooten and Hobbs 2015). For this purpose we modeled survival in stage k at time t as:

$$logit(\eta_{k,t}) = \mu_k + \sum_{j=0}^{w} \gamma_j X_{j,t}\beta_{k,j} + \varepsilon_{k,t} \qquad \text{[E5.1]}$$

where $X_{j,t}$ and $\beta_{k,j}$ denote the design matrix of covariate j in year t and the slope parameter j for stage k, respectively (w is the maximum number of covariates considered). μ_k and $\varepsilon_{k,t}$ reflect the stage-specific mean survival and random effects (see ESM1 eq. E1.1 and eq. E1.2). γ_j denotes the auxiliary indicator variable and is a binary response variable that indicates whether covariate $\beta_{k,j}$ is present ($\gamma_j = 1$) or absent ($\gamma_j = 0$) in the model. We assumed that the chance that $\gamma_j = 1$ follows a Bernoulli trial with probability 0.5. To ensure good mixing for indicator γ_j and effect variable $\beta_{k,j}$ we assumed that both variables depend on each other (Ntzoufras 2002; Tenan et al. 2014) by modeling the prior for $\beta_{k,j} |(\gamma_j = 1)$ and a pseudoprior for $\beta_{k,j} |(\gamma_j = 0)$ using a mixture prior:

$$p(\beta_{k,j}|\gamma_j) = (1 - \gamma_j)Normal(\kappa_j, S_j) + \gamma_j Normal(0, \Sigma_j) \qquad \text{[E5.2]}$$

where κ_j and S_j are user-defined tuning parameters and Σ_j denotes the fixed prior variance for $\beta_{k,j}$. The posterior model probability $p(M_i|y)$ for each model M_i ($i = 16$ possible models for each combination of the considered covariates) is given by:

$p(M_i|y) =$ Number of occurrences of M = i / Total number of iterations

We followed Tenan *et al.* (2014) and checked whether $p(M_i|y)$ is sensitive to the mixture prior by repeating the analysis with different priors for $Normal(\kappa_j, S_j)$:(1) $Normal(\overline{\beta_{k,j}},\ SD(\beta_{k,j}))$, which is a normal prior for $\beta_{k,j}$ with mean and standard deviation taken from the posterior distribution of each $\beta_{k,j}$ of separate model runs; (2) $N(0, 10)$; (3) $N(0, 100)$; (4) $N(0, 1000)$; (5) $N(0, 10^6)$; (6) $N(0.2, 100)$ (Tenan *et al.* 2014).

The burn-in was 1,400,000 iterations followed by 1,500,000 iterations and posterior samples were drawn using a thinning interval 3. We computed the potential scale reducing factor (Gelman and Rubin 1992) using the output of three MCMC chains and assumed convergence if was near to 1. For all estimated parameters was smaller than or equal to 1.01. Overall there exist no sensitivity of the estimated posterior model probability to the set of prior distributions used (Table E5.1-Table E5.6). Prior set (5) did not fully converge, but produced similar results to all other prior configurations (Table E5.5).

Table E5.1 Posterior model probability $p(M_i|y)$ using actual posterior distributions estimated for each β_k. Column A: The MR model considers the covariate sst_anomaly_austral for chick survival; Column B: The MR model considers the covariate days_wind_gusts_33_annual for chick survival; Column C: The MR model considers the covariate sst_anomaly_austral for adult survival; Column D: The MR model considers the covariate mean_air_temp_annual for adult survival.

M_i	Model configuration				$p(M_i\|y)$
	A	B	C	D	
1	1	0	1	0	0.42
2	0	1	1	0	0.13
3	1	1	1	0	0.12
4	1	0	0	1	0.09
5	0	1	0	1	0.06
6	0	0	0	0	0.04
7	1	0	0	0	0.03
8	0	1	0	0	0.03
9	1	1	0	0	0.02
10	0	0	1	0	0.01
11	0	0	0	1	0.01
12	1	1	0	1	0.01
13	0	0	1	1	0.00
14	1	0	1	1	0.00
15	0	1	1	1	0.00
16	1	1	1	1	0.00

Table E5.2 Posterior model probability $p(M_i|y)$ using a normally distributed prior for β_k: N(0, 10). See Column A: The MR model considers the covariate sst_anomaly_austral for chick survival; Column B: The MR model considers the covariate days_wind_gusts_33_annual for chick survival; Column C: The MR model considers the covariate sst_anomaly_austral for adult survival; Column D: The MR model considers the covariate mean_air_temp_annual for adult survival.

	Model configuration				
M_i	A	B	C	D	$p(M_i|y)$
1	1	0	1	0	0.35
2	1	0	0	1	0.17
3	0	1	1	0	0.15
4	1	1	1	0	0.07
5	0	1	0	1	0.05
6	0	0	0	0	0.04
7	1	0	0	0	0.04
8	0	1	0	0	0.03
9	1	1	0	0	0.03
10	0	0	1	0	0.02
11	0	0	0	1	0.01
12	1	1	0	1	0.01
13	0	0	1	1	0.00
14	1	0	1	1	0.00
15	0	1	1	1	0.00
16	1	1	1	1	0.00

Table E5.3 Posterior model probability $p(M_i|y)$ using a normally distributed prior for β_k: $N(0, 100)$. Column A: The MR model considers the covariate sst_anomaly_austral for chick survival; Column B: The MR model considers the covariate days_wind_gusts_33_annual for chick survival; Column C: The MR model considers the covariate sst_anomaly_austral for adult survival; Column D: The MR model considers the covariate mean_air_temp_annual for adult survival.

M_i	Model configuration				$p(M_i|y)$
	A	B	C	D	
1	1	0	1	0	0.43
2	1	0	0	1	0.19
3	0	1	1	0	0.11
4	1	1	1	0	0.06
5	0	1	0	1	0.05
6	0	0	0	0	0.05
7	1	0	0	0	0.04
8	0	1	0	0	0.02
9	1	1	0	0	0.02
10	0	0	1	0	0.01
11	0	0	0	1	0.01
12	1	1	0	1	0.00
13	0	0	1	1	0.00
14	1	0	1	1	0.00
15	0	1	1	1	0.00
16	1	1	1	1	0.00

Table E5.4 Posterior model probability $p(M_i|y)$ using a normally distributed prior for β_k: N(0, 1000). Column A: The MR model considers the covariate sst_anomaly_austral for chick survival; Column B: The MR model considers the covariate days_wind_gusts_33_annual for chick survival; Column C: The MR model considers the covariate sst_anomaly_austral for adult survival; Column D: The MR model considers the covariate mean_air_temp_annual for adult survival.

	Model configuration				
M_i	A	B	C	D	$p(M_i|y)$
1	1	0	1	0	0.42
2	1	0	0	0	0.14
3	0	1	1	0	0.13
4	1	1	1	0	0.09
5	1	0	0	1	0.05
6	0	0	0	0	0.04
7	0	1	0	0	0.04
8	1	1	0	0	0.03
9	0	0	1	0	0.02
10	0	0	0	1	0.01
11	0	1	0	1	0.01
12	1	1	0	1	0.01
13	0	0	1	1	0.01
14	1	0	1	1	0.00
15	0	1	1	1	0.00
16	1	1	1	1	0.00

Table E5.5 Posterior model probability $p(M_i|y)$ using a normally distributed prior for β_k: $N(0, 10^6)$. See Column A: The MR model considers the covariate sst_anomaly_austral for chick survival; Column B: The MR model considers the covariate days_wind_gusts_33_annual for chick survival; Column C: The MR model considers the covariate sst_anomaly_austral for adult survival; Column D: The MR model considers the covariate mean_air_temp_annual for adult survival.

M_i	Model configuration				
	A	**B**	**C**	**D**	$p(M_i|y)$
1	1	0	1	0	0.43
2	1	0	0	1	0.13
3	0	1	1	0	0.12
4	1	1	1	0	0.08
5	0	0	0	0	0.06
6	1	0	0	0	0.05
7	0	1	0	0	0.04
8	1	1	0	0	0.03
9	0	0	1	0	0.02
10	0	0	0	1	0.01
11	0	1	0	1	0.01
12	1	1	0	1	0.01
13	0	0	1	1	0.01
14	1	0	1	1	0.00
15	0	1	1	1	0.00
16	1	1	1	1	0.00

Table E5.6 Posterior model probability $p(M_i|y)$ using a normally distributed prior for β_k: $N(0.2, 100)$. Column A: The MR model considers the covariate sst_anomaly_austral for chick survival; Column B: The MR model considers the covariate days_wind_gusts_33_annual for chick survival; Column C: The MR model considers the covariate sst_anomaly_austral for adult survival; Column D: The MR model considers the covariate mean_air_temp_annual for adult survival.

	Model configuration				
M_i	A	B	C	D	$p(M_i|y)$
1	1	0	1	0	0.47
2	1	0	0	0	0.16
3	0	1	1	0	0.11
4	1	1	1	0	0.10
5	1	0	0	1	0.04
6	0	0	0	0	0.03
7	0	1	0	0	0.03
8	1	1	0	0	0.02
9	0	0	1	0	0.02
10	0	0	0	1	0.01
11	0	1	0	1	0.01
12	1	1	0	1	0.00
13	0	0	1	1	0.00
14	1	0	1	1	0.00
15	0	1	1	1	0.00
16	1	1	1	1	0.00

References

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. Statistical science, 7(4), 457-472.

Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. Ecological Monographs, 85(1), 3-28.

Ntzoufras, I. (2002). Gibbs variable selection using BUGS. Journal of Statistical Software, 7(7), 1-19.

Tenan, S., O'Hara, R. B., Hendriks, I., & Tavecchia, G. (2014). Bayesian model selection: the steepest mountain to climb. Ecological Modelling, 283, 62-69.