**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

Climate change, anthropogenic threats, population modelling, survival, species management, penguins

# 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

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

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

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

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

(Boessenkool et al. 2009b).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

the causation of population developments.

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

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

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

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

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

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

the long-term viability of the mainland YEP population.

## 2. Methods

### 2.1 Species information

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

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

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

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

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

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

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

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

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

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

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

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

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

statistics of demographic and environmental parameters.

### 2.2 Study sites

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

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

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

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

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

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

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

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

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

Mattern 2012).

## 118     2.3 Population monitoring & Yellow-eyed penguin database (YEPDB)

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

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

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

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

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

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

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

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

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

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

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

patchy and were deemed too unreliable for analysis.

## 131     2.4 Data

### 132     2.4.1 Demographic data

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

***2.4.2 Environmental data***

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

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

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

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

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

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

susceptible to environmental perturbations due the increased energy requirements for feather

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

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

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

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

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

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

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

shifted backwards in time by one and two years.

## 2.5 Population model

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

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

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

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

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

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

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

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

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

Selection (GVS, Tevacchia et al. 2016)

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

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

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

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

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

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

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

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

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

environmental factors.

Detailed descriptions of all modelling procedures are provided as Electronic Supplementary

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:

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

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

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

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

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

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

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

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

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

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

since 1996.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

female YEPs overlapped (Fig 5).

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

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

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

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

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

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

**3.4 Future projections**

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

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

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

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

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

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

locally extinct by 2043.

# 4. Discussion

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

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

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

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

unclear due to a lack of data.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

and possibly explains the overall deteriorating reproductive success.

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

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

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

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

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

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

1990s (Fig 4).

## 311    4.1 Sea surface temperature effects

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

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

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

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

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

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

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

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

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

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

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

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

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

al. 2011; Mattern et al. 2013).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

likely compromised under stratified, warm-water conditions.

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

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

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

## 4.2 SST and relevance of die-off events

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

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

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

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

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

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

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

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

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

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

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

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

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

km upstream from Boulder Beach.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

important roles for population dynamics.

## 4.3 Other climate factors

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

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

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

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

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

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

al. 2015).

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

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

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

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

survival chances of inexperienced fledglings.

## 4.4 Non-climate factors

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

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

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

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

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

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

the remaining variation in survival rates.

### 4.4.1 Fisheries interactions

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

and, hence, population trends.

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

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

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

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

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

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

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

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

***4.4.2 Disease outbreaks***

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

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

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

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

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

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

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

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

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

***4.4.3 Predators***

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

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

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

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

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

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

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

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

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

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

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

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

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

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

*4.4.4 Human disturbance*

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

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

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

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

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

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

## 461    4.5 Conservation implications

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

and regional factors can mitigate the increasing pressure that climate change will impose on populations of some vulnerable species.

The virtual absence of quantifiable data to examine the effects of non-climatic factors makes it difficult to provide fact-based management recommendations and puts a potentially overbearing emphasis on climate change. However, these principally anthropogenic factors likely also explain significant portions of the variation in survival rates, so that the focus should be on improving our understanding and management of these impacts to enhance this species' resilience to climate change.

## 5. Acknowledgements

We would like to extend our gratitude to the many field workers and students involved in penguin monitoring that contributed data to the YEPDB.

## 6. References

Alterio, N., Moller, H., Ratz, H., 1998. Movements and habitat use of feral house cats Felis catus, stoats Mustela erminea and ferrets Mustela furo, in grassland surrounding yellow-eyed penguin Megadyptes antipodes breeding areas in spring. Biological Conservation 83, 187-194.

Beentjes, M., Bull, B., Hurst, R., Bagley, N., 2002. Demersal fish assemblages along the continental shelf and upper slope of the east coast of the South Island, New Zealand. New Zealand Journal of Marine and Freshwater Research 36, 197-223.

Beentjes, M., Renwick, J., 2001. The relationship between red cod, *Pseudophycis bachus*, recruitment and environmental variables in New Zealand. Environmental Biology of Fishes 61, 315-328.

Benton, T.G., Grant, A., 1999. Elasticity analysis as an important tool in evolutionary and population ecology. Trends in Ecology & Evolution 14, 467-471.

BirdLife International, 2012. Medayptes antipodes, In The IUCN Red List of Threatened Species
2012. p. e.T22697800A40186242.

Boessenkool, S., Austin, J.J., Worthy, T.H., Scofield, P., Cooper, A., Seddon, P.J., Waters, J.M., 2009a.
Relict or colonizer? Extinction and range expansion of penguins in southern New Zealand.

Boessenkool, S., Star, B., Waters, J.M., Seddon, P.J., 2009b. Multilocus assignment analyses reveal
multiple units and rare migration events in the recently expanded yellow-eyed penguin
(Megadyptes antipodes). Molecular ecology 18, 2390-2400.

Browne, T., Lalas, C., Mattern, T., Van Heezik, Y., 2011. Chick starvation in yellow-eyed penguins:
Evidence for poor diet quality and selective provisioning of chicks from conventional diet
analysis and stable isotopes. Austral Ecology 36, 99-108.

Cannell, B.L., Campbell, K., Fitzgerald, L., Lewis, J.A., Baran, I.J., Stephens, N.S., 2016.
Anthropogenic trauma is the most prevalent cause of mortality in Little Penguins,
*Eudyptula minor*, in Perth, Western Australia. Emu 116, 52-61.

Croxall, J., 1982. Energy costs of incubation and moult in petrels and penguins. The Journal of
Animal Ecology, 177-194.

Dann, P., 1991. Distribution, Population Trends and Factors Influencing the Population Size of
Little Penguins <I>Eudyptula minor</I> on Phillip Island, Victoria. Emu 91, 263-272.

Dann, P., 2013. Little Penguin (*Eudyptula minor*), In Penguins: Natural History and Conservation.
eds P. Garcia Borboroglu, P.D. Boersma, pp. 304-319. University of Washington Press,
Seattle & London.

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

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

Darby, J., Seddon, P., 1990. Breedig biology of Yellow-eyed Penguins (*Megadyptes antipodes*), In
Penguin Biology. eds L. Davis, J. Darby, pp. 45-62. Academic Press, San Diego.

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

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

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

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

Functional Ecology 21, 561-567.

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

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

Penguin. PloS one 8, e79487.

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

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

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

progress report. Department of Conservation, Wellington.

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

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

Wellington, New Zealand.

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

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

289-296.

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

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

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

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

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

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

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

Garcia Borboroglu, P., Boersma, P., 2013. Penguins: Natural History and Conservation. University

of Washington Press.

Gill, J., Darby, J., 1993. Deaths in yellow-eyed penguins (Megadyptes antipodes) on the Otago

Peninsula during the summer of 1990. New Zealand Veterinary Journal 41, 39-42.

Graczyk, T.K., Cranfield, M.R., Brossy, J.J., Cockrem, J., Jouventin, P., Seddon, P., 1995. Detection of

avian malaria infections in wild and captive penguins. JOURNAL-HELMINTHOLOGICAL

SOCIETY WASHINGTON 62, 135-142.

Grémillet, D., Boulinier, T., 2009. Spatial ecology and conservation of seabirds facing global

climate change: a review. Marine Ecology Progress Series 391, 121-137.

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.

Guan, B., Nigam, S., 2008. Pacific Sea Surface Temperatures in the Twentieth Century: An

Evolution-Centric Analysis of Variability and Trend. Journal of Climate 21, 2790-2809.

Hawke, D., 1989. Hydrology and near-surface nutrient distribution along the South Otago

continental shelf, New Zealand, in summer and winter 1986. New Zealand Journal of

Marine and Freshwater Research 23, 411-420.

Houston, D.M., 2005. Diphtheritic stomatitis in yellow-eyed penguins, In Oamaru Penguin

Symposium 2005. ed. A. Hocken, p. 267. New Zealand Journal of Zoology, Oamaru, New

Zealand.

Jones, D.O.B., Yool, A., Wei, C.-L., Henson, S.A., Ruhl, H.A., Watson, R.A., Gehlen, M., 2014. Global

reductions in seafloor biomass in response to climate change. Global Change Biology 20,

1861-1872.

King, S., Harper, G., Wright, J., McInnes, J., van der Lubbe, J., Dobbins, M., Murray, S., 2012. Site-

specific reproductive failure and decline of a population of the Endangered yellow-eyed

penguin: a case for foraging habitat quality. Marine Ecology Progress Series 467, 233.

Lalas, C., Ratz, H., McEwan, K., McConkey, S.D., 2007. Predation by New Zealand sea lions

(Phocarctos hookeri) as a threat to the viability of yellow-eyed penguins (Megadyptes

antipodes) at Otago Peninsula, New Zealand. Biological Conservation 135, 235-246.

Limmer, B., Becker, P.H., 2009. Improvement in chick provisioning with parental experience in a

seabird. Animal Behaviour 77, 1095-1101.

Mattern, T., Ellenberg, U., Houston, D.M., Davis, L.S., 2007. Consistent foraging routes and benthic

foraging behaviour in yellow-eyed penguins. Marine Ecology Progress Series 343, 295-

306.

Mattern, T., Ellenberg, U., Houston, D.M., Lamare, M., Davis, L.S., van Heezik, Y., Seddon, P.J., 2013.

Straight line foraging in yellow-eyed penguins: new insights into cascading fisheries

effects and orientation capabilities of marine predators. PloS one 8, e84381.

McClung, M.R., Seddon, P.J., Massaro, M., Setiawan, A., 2004. Nature-based tourism impacts on

yellow-eyed penguins Megadyptes antipodes: does unregulated visitor access affect

fledging weight and juvenile survival? Biological Conservation 119, 279-285.

Moore, P., 1999. Foraging range of the Yellow-eyed Penguin Megadyptes antipodes. Marine

Ornithology 27, 49-58.

Moore, P., Wakelin, M., 1997. Diet of the yellow-eyed penguin Megadyptes antipodes, South

Island, New Zealand, 1991-1993. Marine Ornithology 25, 17-29.

Moore, P.J., 2001. Historical records of yellow-eyed penguin (Megadyptes antipodes) in southern

New Zealand. Notornis 48, 145-156.

Nisbet, I.C., Dann, P., 2009. Reproductive performance of little penguins Eudyptula minor in
relation to year, age, pair-bond duration, breeding date and individual quality. Journal of
Avian Biology 40, 296-308.

Oliver, E., Wotherspoon, S., Chamberlain, M., Holbrook, N., 2014. Projected Tasman Sea Extremes
in Sea Surface Temperature through the Twenty-First Century. Journal of Climate 27,
1980-1998.

Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape
and biogeographical scale levels in research and conservation. Biological Conservation
117, 285-297.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annual
Review of Ecology, Evolution, and Systematics, 637-669.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across
natural systems. Nature 421, 37-42.

Peacock, L., Paulin, M., Darby, J.T., 2000. Investigations into the climate influence on population
dynamics of yellow-eyed penguins Megadyptes antipodes. New Zealand Journal of Zoology
27, 317-325.

Perriman, L., Houston, D., Steen, H., Johannesen, E., 2000. Climate fluctuation effects on breeding
of blue penguins (*Eudyptula minor*). New Zealand Journal of Zoology 27, 261-267.

Ratz, H., Murphy, B., 1999. Effects of habitat and introduced mammalian predators on the
breeding success of Yellow-eyed Penguins Megadyptes antipodes, South Island, New
Zealand. Pacific Conservation Biology 5, 16-27.

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

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

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

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

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

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

Conservation, Wellington, New Zealand, 22p.

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

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

110. University of Washington Press, Seattle & London.

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

Penguins: Natural History and Conservation, 97-100.

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

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

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

limits.

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

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

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

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

Change. Cambridge University Press.

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

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

Zealand Veterinary Journal 55, 158-160.

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

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

Progress Series 360, 211-217.

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

Tavecchia, G., Tenan, S., Pradel, R., Igual, J.M., Genovart, M., Oro, D., 2016. Climate-driven vital
rates do not always mean climate-drievn population. Global Change Biology, doi:
10.1111/gcb.13330

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus,
B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S.,
Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L., Williams,
S.E., 2004. Extinction risk from climate change. Nature 427, 145-148.

Thuiller, W., Lavorel, S., Araújo, M., 2005. Niche properties and geographical extent as predictors
of species sensitivity to climate change. Global Ecology and Biogeography 14, 347-357.

Trathan, P.N., García-Borboroglu, P., Boersma, D., Bost, C.A., Crawford, R.J., Crossin, G.T.,
Cuthbert, R.J., Dann, P., Davis, L.S., De La Puente, S., 2015. Pollution, habitat loss, fishing,
and climate change as critical threats to penguins. Conservation Biology 29, 31-41.

van Heezik, Y., 1990. Seasonal, geographical, and age-related variations in the diet of the yellow-
eyed penguin (Megadyptes antipodes). New Zealand Journal of Zoology 17, 201-212.

van Heezik, Y., Davis, L., 1990. Effects of food variability on growth rates, fledging sizes and
reproductive success in the Yellow-eyed Penguin *Megadyptes antipodes.* Ibis 132, 354-365.

Whittington, P.A., Randall, R.M., Crawford, R.J.M., Wolfaardt, A.C., Klages, N.T.W., Randall, B.M.,
Bartlett, P.A., Chesselet, Y.J., Jones, R., 2005. Patterns of immigration to and emigration
from breeding colonies by African penguins. African Journal of Marine Science 27, 205-
213.

Wilson, K.-J., 2004. Flight of the Huia: Ecology and conservation of New Zealand's frogs, reptiles,
birds and mammals. Canterbury University Press Christchurch.

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

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

**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.

**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.

**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').

700 **Figure 6.** Probability density functions for deterministic annual population growth rates derived

701 from survival rates that were rescaled for periods of cooler (1982-1996) and warmer

702 (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. $\Phi$ indicates estimated
706　survival rates, $\sigma^2$ stands for the temporal variance of the stage-specific survival. Refer to ESM1
707　for details.

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

# 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 $\sigma_k^2$:

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

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

where $\varepsilon_{k,t}$ denotes the temporal residuals for $\mu_k$. 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 $\mu_k$ using the link function $\mu_k = \log(\bar{\phi}_k/(1-\bar{\phi}_k))$. We supplied uniform prior distributions for $\sigma_k$ 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 $\phi_{k,t}$:

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

where $\beta_k$ denotes the stage-specific effect size fitted to the time-specific covariate $x_t$. Except for covariates reflecting SST anomaly we standardized $((x_t - \bar{x}_t) / \text{sd}(x_t))$ 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 $\beta_k$ after varying the standard deviation of the normal prior supplied for $\beta_k$ (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 $\hat{R}$ (Gelman and Rubin 1992) using the output of three MCMC chains and assumed convergence if $\hat{R}$ was near to 1. For all estimated parameters $\hat{R}$ 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:

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

where $\sigma_k^2$ 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 $\sigma_k^2$ (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 $\beta_k$ 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 $\lambda$ ($\lambda < 1$: 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 $\lambda$ 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:

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

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). $\mu_k$ and $\varepsilon_{k,t}$ reflect the stage-specific mean survival and random effects (see ESM1 eq. E1.1 and eq. E1.2). $\gamma_j$ 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 $\gamma_j$ 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:

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

where $\kappa_j$ and $S_j$ are user-defined tuning parameters and $\Sigma_j$ 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, 10⁶); (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 $\beta_k$. 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 | | | | |
|---|---|---|---|---|---|
| | 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 | 0.00 |
| 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 $\beta_k$: 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 $\beta_k$: 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.

| | Model configuration | | | | |
|---|---|---|---|---|---|
| $M_i$ | A | B | C | D | $p(M_i|y)$ |
| 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 $\beta_k$: 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 $\beta_k$: $N(0, 10^6)$. 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.

| | Model configuration | | | | |
|------|---|---|---|---|-----------|
| $M_i$ | 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 $\beta_k$: 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.

| $M_i$ | Model configuration | | | | |
|---|---|---|---|---|---|
| | **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.