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Modelling the effect of El Niño on the persistence of small populations: The Galápagos penguin as a case study

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ABSTRACT

Small populations are vulnerable to long-term declines, even where short-term censuses indicate increasing trends in numbers. Census data for the Galápagos penguin (*Spheniscus mendiculus*) collected between 1970 and 2004 provide evidence that despite year-to-year population increases detected in most of the annual censuses, the strong El Niño events of 1982–83 and 1997–98 were followed by population declines of more than 60% from which the species has yet to recover. Such large declines raise concerns about the future viability of the species because the frequency and severity of El Niño events are predicted to increase. We used the simulation software VORTEX to evaluate the potential effects of El Niño on the risk of extinction of the Galápagos penguin population and its four constituent subpopulations. Weak and strong El Niño events were treated as catastrophes, with varying frequencies, which simulated past, current and future effects on the penguin population. The “Current El Niño” scenario, based on the frequency of El Niño events recorded in the Galápagos between 1965 and 2004, indicated an approximately 30% probability of extinction within the next 100 years for the penguin population. More ominously, the species may be at a greater risk if the frequency of strong El Niño episodes increases only marginally. A probability of extinction greater than 80% was predicted when the current frequency (5%) of strong El Niño events was doubled (to 10%). The probabilities of extinctions were higher for each subpopulation treated individually, ranging from 34% for Isabela and Fernandina, 64% for Bartolomé-Santiago to 78% for the smallest subpopulation on Floreana. Sensitivity analyses identified survival of penguins during El Niño events and sex ratio as influential parameters. The estimates of extinction risk may be conservative as other threats associated with increased human activities on the islands may further compromise species persistence.

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1. Introduction

No bird species is known to have become extinct in the Galápagos Islands in Historical times, and most vertebrate extinctions occurred after the first human contact with the islands in 1535 (Steadman et al., 1991). Smaller population sizes, compared to mainland counterparts, generally make endemic island populations more vulnerable to both stochastic and deterministic factors contributing to extinctions (Frankham, 1998; Reed, 2005). The Galápagos penguin (*Spheniscus mendiculus*) is an endangered species (BirdLife International, 2005), endemic to the upwelling coastal areas of the Galápagos Archipelago (BirdLife International, 2005, 1977) with an estimated mean population size, between 1993 and 2004, of 1500 individuals (Vargas et al., 2005).

Currently, most scientists agree that genetic, demographic and environmental stochasticity and catastrophes can result in extinction of small, isolated populations (Beissinger, 2002; Lande, 1993). For thousands of years, environmental catastrophes such as El Niño events probably had an important effect on the Galápagos ecosystems (Riedinger et al., 2002), exerting strong selection pressures on breeding and survival strategies of island species (Robinson and del Pino, 1985). In fact, the unusual breeding biology of the Galápagos penguin, including its ability to breed rapidly and opportunistically when conditions are favourable, suggests it is well adapted to this unpredictable environment (Boersma, 1977). However, the frequency and severity of El Niño events may be increasing with global climate change (Timmermann et al., 1999) producing significant ecological consequences in marine ecosystems (Chavez et al., 1999; Duffy, 1990; McPhaden, 1999). Global mean air temperature increased by 0.06 °C per decade during the 20th century (Houghton et al., 2001), and by 0.19 °C per decade from 1979 to 1998 (Doran et al., 2002; National Research Council, 2000). The increase is projected to continue (Houghton et al., 2001). Moreover, recent climate simulations indicate that global human activities are accelerating the warming of the oceans (Barnett et al., 2005). Global warming is altering the distribution, abundance and other life-history traits of species and increasing their risk of extinction (Root et al., 2003; Thomas et al., 2004). Although it has been difficult to demonstrate cause and effect between extinctions with recent climate change, preliminary work suggests that climate change can hasten population extinctions (McLaughlin et al., 2002; Root et al., 2006).

While increases in population size are observed over most short census periods, the Galápagos penguin population is, in the longer term, declining (Vargas et al., 2005). The severe impacts of El Niño-induced famine conditions and associated population declines (Boersma, 1998a; Valle and Coulter, 1987; Vargas et al., 2006) may explain this population trend. El Niño events likely affect the species by reducing the availability of schooling fish such as sardines (*Sardinops sagax*) (Mills, 1998), piquitangas (*Lile stolifera*) (Vargas et al., 2006) mullets (*Mugil* sp) (Nicolaides and Murillo, 2001) and anchovies (*Engraulis* sp) (Vargas, 2006) which are suspected to be the primary prey species for the Galápagos penguin (Vargas et al., 2006).

Population viability analysis (PVA) is a conservation management tool which, despite uncertainties in predicted risks

of decline (McCarthy et al., 2003), has increasingly been used by conservation biologists to inform management of threatened species by identifying the factors that make them vulnerable to extinction (Brook et al., 2000). To date, no efforts have been made to model the effect of El Niño events on any bird species of the Galápagos Islands. Here, we present the results of the first modelling exercise of this kind for the Galápagos penguin. We used the PVA simulation program VORTEX, version 9.57 (Lacy, 1993, 2000; Miller and Lacy, 2003) to: (1) build a baseline model of the current effect of El Niño events on the Galápagos penguin populations using frequencies of El Niño events recorded in the Galápagos Archipelago during the last 40 years; (2) conduct sensitivity analyses of the effects of past and future El Niño events by changing the frequencies of El Niño events and their effects on penguin demographic factors; (3) estimate the minimum viable population (MVP) size for the population, and (4) suggest directions for research and management based on the results of modelling.

2. Method

We incorporated the best available data of both the penguin biology and the impact of El Niño episodes into the population viability analysis (PVA) models. We obtained estimates of vital rates from the published literature, unpublished technical reports of annual censuses (1970–2004) and field studies in progress (2003–2004) (Table 1). Where these data were not available, we used information on related species of the *Spheniscus* penguins. Estimates of vital rates and preliminary simulations were carried out in a PVA workshop held in February 2005 with the participation of international experts on the Spheniscidae family (Matamoros et al., 2006).

We considered VORTEX to be an appropriate simulation model to analyze the viability of the Galápagos penguin population because it is a stochastic population model that includes both demographic and environmental stochasticity, and allows incorporation of the effects of catastrophes, such as El Niño events, on reproduction and survival. The models projected population size over 100 years, in increments of one year. For each specification of input parameters, the models were run 1000 times to estimate the probability of extinction, and to provide the mean and standard deviation of population size throughout the simulation period. Extinction was defined as occurring when only birds of one sex remained alive in the population.

2.1. El Niño events and climate scenarios

We treated weak and strong El Niño events as ‘catastrophes’ as modelled by the VORTEX software (version 9.57). We identified two types of El Niño events on the basis of their different impacts on the penguin population recorded between 1970 and 2004. ‘Strong’ El Niño events are known to have affected survival and reproduction, while ‘weak’ El Niño events appeared to have reduced only reproduction (Vargas et al., 2006). We used different frequencies of El Niño events to simulate historical, current and likely future El Niño climate scenarios. We compared these three models to a “best case” scenario without El Niño events. Models used baseline levels

Table 1 – Simulation model parameters used to conduct the population viability analysis under the Current El Niño (CEN) scenario

Parameter/variable	Current El Niño (CEN) model
Number of iterations	1000
Number of years	100
Extinction definition	One sex remains
Number of populations	4
Inbreeding depression	No
Correlation of demographic rates among subpopulations	0.9
Concordance of variation in reproduction and survival	Yes
Breeding system	Long-term monogamy
Number of types of catastrophes	2
Dispersing age range (youngest-oldest)	(1–1)
Dispersing sex(es)	Both
Percent survival of dispersers	80
Age of first offspring for females	3
Age of first offspring for males	3
Maximum age of reproduction	20
Maximum number of progeny per year	2
Sex ratio at birth (% males)	50%
Annual reproductive rates	
% adult females breeding	56.7
Annual variation in % breeding	SD = 13
% females producing 1 progeny	33.5
% females producing 2 progeny	46.4
% females producing 3 progeny	12.4
% females producing 4 progeny	7.7
Mortality rates – same for both sexes	
% mortality between ages 0 and 1	67
Annual variation in % 0–1 mortality:	SD = 10
% mortality between ages 1 and 2	25
Annual variation in % 1–2 mortality:	SD = 5
% mortality between ages 2 and 3	5
Annual variation in % 2–3 mortality:	SD = 3
% mortality after age 3	5
Annual variation in % 3+ mortality:	SD = 3
% males in the breeding pool	100
Catastrophe 1. Strong Niño	
Frequency	5%
Multiplicative impacts on reproduction, survival	0.01, 0.30
Catastrophe 2. Weak Niño	
Frequency	20%
Multiplicative impacts on reproduction, survival	0.20, 1.00
Initially at stable age distribution	Yes
Initial population size	1500
Carrying capacity (K)	4200
SD in K due to environmental variation (EV)	420
Harvest	No
Supplementation	No

of breeding and other vital parameters of the “Current El Niño Scenario” referred as the “baseline model”.

2.1.1. Best case (BC)

A scenario without El Niño events was run using the life history parameters typical of the species. This scenario is unrealistic as it describes the performance (persistence, population growth and population size) in the absence of El Niño events

and other potential catastrophes, but it does provide a basis for testing the effects of El Niño events on population viability.

2.1.2. Historical El Niño (HEN)

The two most extreme El Niño events in the past century occurred in 1982–1983 and 1997–1998 (Chavez et al., 1999; McPhaden, 1999), and it is thought that such severe events are now more common than was previously (before mid-1970s) the case (Trenberth and Hoar, 1996). Therefore, a value of 2% was used as an estimate of the frequency of strong El Niño events that may have occurred over historical times. The frequency of weak El Niño events was set at 20% (see explanation in Current El Niño Scenario).

2.1.3. Current El Niño (CEN)

The parameters specified in this model were based on the period between 1965 and 2004, for which accurate meteorological (1965–2004) and biological (1970–2004) penguin data exist. Analysis of instrumental sea surface temperature (SST) from the Charles Darwin Research Station (CDRS), Isla Santa Cruz, indicates two strong (1982–83 and 1997–98) and seven weak (1965–66, 1968–69, 1972–73, 1976, 1986–87, 1991–92 and 1993) El Niño episodes in the Galápagos Islands during the period 1965–2004 (Vargas et al., 2006). Therefore, the frequency of strong and weak events for the Current El Niño scenario was set at 5% and 20% per 100 years, respectively. The rationale for using a 20% frequency (and not 18% as calculations indicate) was that some of the weak events persisted for more than one year (Snell and Rea, 1999).

Census data of the Galápagos penguin collected by Boersma (in the early 1970s), the CDRS and the Galápagos National Park Service (GNPS), between 1980 and 2004 indicate that the strong El Niño events caused mortalities of 77% and 65% of the population, respectively (Boersma, 1998a; Valle and Coulter, 1987; Vargas et al., 2006). In our PVA model, therefore, survival of adult and juvenile birds (combined), during strong El Niño events, was reduced to 30% of survival estimates in non-El Niño years. In both severe events, Galápagos penguins failed to reproduce: hence, the proportion of mature birds breeding was decreased in the model to 1% of normal rates. Weak El Niño events had no effect on survival and were estimated to reduce reproduction by 20%.

2.1.4. Future El Niño (FEN)

Continued global warming may lead to an increased frequency of El Niño events. Therefore, we considered that frequency values above those of the Current El Niño (CEN) scenario to simulate Future El Niño (FEN) scenarios.

2.2. Vital parameters for population modelling

Below, we describe briefly the population parameters that were used in the VORTEX model of the Galápagos penguin. More details on the sources of information and the calculations used to derive these estimates are provided in the report of the workshop (Matamoros et al., 2006).

2.2.1. Inbreeding depression

Although the species has probably lost part of the genetic diversity through multiple bottlenecks after strong El Niño

events (Akst et al., 2002), based on the finding that other species which had experienced bottlenecks have been able to prosper by purging most of their inbreeding load (Ellegren et al., 1993; Hoelzel et al., 1993), inbreeding depression was not included in our model. Furthermore, current census data indicate that Fernandina and Isabela have sufficient numbers of individuals so that significantly inbreeding is not likely.

2.2.2. Breeding system

We assumed that Galápagos penguins are monogamous, with generally long-lasting pair bonds. Of 50 pairs followed for two breeding seasons, only 11% switched mates (Boersma, 1977).

2.2.3. Age at first breeding

The age of first breeding for Galápagos penguins is not known. We assumed both sexes could breed at three years of age. In other *Spheniscus* species, age at breeding has been reported as: African penguin *S. demersus* 3–6 years, usually 4 years (Crawford et al., 1999; Randall, 1983; Whittington et al., 2000); Humboldt penguin *S. humboldti* 3–4 years (Guerra and Oyarzo, 1992 in Ellis et al., 1998; Zavalaga, personal communication); Magellanic penguin *S. magellanicus* females 4–5 years (12.8% start breeding at 4 years), males 6–7 years (30.7% of males start breeding at 5 years (Williams, 1995)).

2.2.4. Maximum age at breeding

We assumed the maximum age was 20 years. The Humboldt penguin in the wild may not breed beyond about 20 years of age (Zavalaga, unpublished data). In the captive North American population of Humboldt penguins, females generally cease breeding at about age 22, whereas males can breed into their 30s (Brandt, 2004). A male Galápagos penguin aged 11 years bred on Fernandina (Boersma, 1974; Williams, 1995). The model outcome was not sensitive to this parameter because most penguins are projected to die (based on the annual mortality rates) before they reach 20 years. Although about 10% of the penguins could reach this age in the absence of any El Niño events, a much smaller proportion would survive to reach 20 years of age if they have also to survive through several El Niño events, as would typically be the case in the actual population and in each of our models except for the idealistic Best Case scenario.

2.2.5. Sex ratio of offspring at birth

We assumed that 50% of the population at birth was males and 50% was females. For the Humboldt penguin, of about 350 birds killed in fishing nets at Punta San Juan, Peru, the sex ratio was close to 1:1 (Zavalaga and Paredes, 1997). For the Galápagos penguin, results of genetic sexing of 266 adult birds sampled between August 2003 and March 2005 indicated a 68% male-biased sex ratio (Vargas, unpublished data). Therefore, we also tested our model with 60% and 68% males, assuming that this was the sex ratio value at birth.

2.2.6. Maximum clutch size

Galápagos penguins produce two eggs per clutch, but birds tend to nest twice within the same year.

2.2.7. Proportion of females that breed

Between 2003 and 2004, 56.7% of mature females successfully fledged young in a breeding season (Matamoros et al., 2006). The standard deviation of the percentage of females breeding was taken to be 13% using information from the African penguin (Shannon and Crawford, 1999). Although it is possible that females may breed at an earlier age or with greater success when population density is very low during good (La Niña) years that might follow an El Niño event, we did not have data with which to document nor to estimate the magnitude of such a density dependent effect and we did not include it in our models. A different form of density dependent response would occur in our model, in that a greater proportion of the population would be of breeding age for a year or two following the El Niño years in which there was little successful breeding.

2.2.8. Breeding success

Of the 56.7% of penguins that successfully fledged young in a breeding season in 2003 and 2004, 33.5% fledged one chick, 46.4% two chicks, 12.4% three chicks and 7.7% four chicks (Matamoros et al., 2006; Steinfurth et al., unpublished data).

2.2.9. Mortality

In the absence of information on sex-specific mortality rates for the Galápagos penguin or any other *Spheniscus* species, the mortality of males and females was assumed to be the same. This is supported by preliminary findings that suggest that sexes forage in the same areas (Vargas, 2006; Steinfurth et al., unpublished data) and therefore likely to be exposed to similar mortality risks. Mortality of adults (birds >3 years old) was assumed to be 5% per annum based on recent trends in numbers of birds (in adult and immature plumage) counted during censuses conducted between 1993 and 2004 (Matamoros et al., 2006; Vargas, unpublished data presented in PVA workshop). The standard deviation representing annual variation in this parameter was taken as 3%, as used for PVA of African penguins (Shannon and Crawford, 1999). Mortality of sub-adults (birds aged 1–2 years) was taken to be 25% per annum, a value intermediate between that estimated for younger and older birds. Standard deviation was taken to be 5%. Mortality of juveniles (<1 year) was taken to be 67% per annum, which was measured in the early 1970s (Williams, 1995). Standard deviation was taken to be 10%, similar to the value of 11% reported for African penguins (Shannon and Crawford, 1999).

2.2.10. Correlation between reproduction and survival

In most years, the factors (e.g., El Niño or La Niña) that affect survival of Galápagos penguins probably also affect reproduction (Vargas et al., 2006). In adverse conditions such as in El Niño years, birds may not breed. In particularly severe conditions of strong El Niño events, they also die (Boersma, 1998b; Valle and Coulter, 1987; Vargas et al., 2006). Therefore, we ran models in which good years for reproduction were also good years for survival.

2.2.11. Number of populations

Based on geography and penguin distribution, we divided the Galápagos penguin population into four subpopulations: Isa-

bela, Fernandina, Bartolomé-Santiago and Floreana (Table 2). Bartolomé and Santiago were treated as a single subpopulation because of their proximity (less than 0.5 km) and because of the likelihood that birds observed on Santiago nest on Bartolomé (no nests have yet been recorded on Santiago).

2.2.12. Concordance among subpopulations

Although there is a possibility that subpopulations experience partly independent causes of mortality and reproductive success, annual variation in environmental conditions is probably largely concordant across the archipelago. During “normal years”, penguins reproduce only in upwelling areas where sea temperatures are the coldest (Boersma, 1977). During El Niño years penguins cease reproducing and part of the population dies as consequence of the widespread warming, with ocean temperatures above 25 °C, occurring in the archipelago (Wellington et al., 2001). We assumed, therefore, that there is a correlation of 0.9 in rates of reproduction and mortality common to all four subpopulations.

2.2.13. Dispersal and survival of dispersing birds

Dispersal and survival rates were estimated on the basis of limited mark recapture records of tagged birds in the early 1970s and late 1990s, recent field research (2001–2004), and estimates of geographical isolation among subpopulations. Therefore, the rates included here are only plausible estimates. We estimated that most of the dispersal events take place between Isabela and Fernandina, and less frequently, from these islands to Bartolomé-Santiago and to Floreana. In the model, dispersal between the four subpopulations was restricted to birds less than one year old and was estimated as: 15% between Isabela and Fernandina, 1% between Isabela and Bartolomé-Santiago, 0.5% between Isabela and Floreana, 0% between Fernandina and Bartolomé-Santiago, 0% between Fernandina and Floreana, and 0% between Bartolomé-Santiago and Floreana. Survival of dispersing birds was taken to be 80% of the value of those that remained at natal localities.

2.2.14. Carrying capacity

The population carrying capacity was set at 4200 individuals based on estimates of maximum population size in 1971 when the highest number of penguins was counted (Vargas et al., 2005). The carrying capacities for the four subpopula-

tions were taken to be: Isabela = 3000, Fernandina = 1000, Bartolomé-Santiago = 150 and Floreana = 50 individuals with a 10% SD due to environmental variability. These specific carrying capacities are modelled in VORTEX as a “ceiling” type of density dependence: when the population size exceeded carrying capacity, additional mortality was imposed across all age classes to bring the population back down to carrying capacity. If there is also a density dependent reduction in breeding or survival as a population approaches carrying capacity then the populations would take longer to recover from El Niño events than is projected in our models. We used sensitivity testing to explore possible impacts of reduced (50% and 75%) carrying capacity over values estimated for the baseline model.

2.2.15. Initial population size

We used an initial population size of 1500 individuals, which corresponds to the mean population size between 1993 and 2004 and also represents the size of the population in 2004 (Vargas, unpublished data, Table 2). This estimate is based on census data for 1993–2004 and protocols to estimate population size (Vargas et al., 2005). The initial sizes of the 4 subpopulations were estimated at: Isabela = 1020, Fernandina = 405, Bartolomé-Santiago = 60 and Floreana = 15 individuals (Table 2).

2.3. Sensitivity tests

Sensitivity tests explored the consequences of strong and weak El Niño events, occurring at different frequencies and severities, reflecting past and future climate regimes. We used frequencies between 0% and 15% and between 0% and 50% in 100 years for strong and weak El Niño events, respectively. Varying severity of El Niño events was modelled by changing survival rates. We modelled survival rates between 30% and 80% of the rates in non-El Niño years. We also used sensitivity testing to explore the effect of alternative demographic values believed to be important to the persistence of the species and for which some degree of variability and uncertainty were suspected. Since our principal conservation goal is to reduce the probability of extinction as far as possible by counteracting the effects of El Niño, we conducted sensitivity testing of various key parameters that might be amenable to improvement through management actions. We tested models with

Table 2 – Estimates of population size of the Galápagos penguin for different periods based on census data (between 1970 and 2004) and established method for estimating population size

Island (s)	Mean percent of population (1993–2004)	Lower El Niño population size (1983, 1998)	Mean population size (1993–2004)	Upper Population size (1970–1980)
Isabela	68	476	1020	2040
Fernandina	27	189	405	810
Bartolomé-Santiago	4	28	60	120
Floreana	1	7	15	30
Archipelago	100	700	1500	3000

Immediate post El Niño population size is shown for 1983 and 1998 when the population crashed following strong El Niño events. Floreana, Santiago and Bartolomé were incorporated in the regular annual censuses since 1993; therefore, for our calculations of mean percent of island populations, we used data gathered between 1993 and 2004. Estimate of mean population size for the period between 1993 and 2004 excluded the count in 1998 when the population crashed.

a range of values including adult and juvenile survival and percentage of females breeding successfully (Matamoros et al., 2006).

2.4. Minimum viable population (MVP) size and probabilities of extinction

Following Primack (1993) and the World Conservation Union (IUCN, 2004), we defined the MVP as the population of penguins having a $\geq 90\%$ chance of surviving in 100 years. The probability of extinction was defined as the proportion of simulations that became extinct in 100 years. We calculated the probabilities of extinction for the population and subpopulations of the Galápagos penguin.

3. Results

The Current El Niño model estimated that the population has a 30% probability of extinction within 100 years (Fig. 1). The population declined at mean growth rate (r) = -0.03 (0.003 SE; 0.30 SD) and individual island subpopulations also showed negative growth rates. The probabilities of extinctions were much higher for each subpopulation treated individually ranging from 34% for the larger subpopulations of Isabela

and Fernandina, 64% for Bartolomé-Santiago to 78% for the smallest and more isolated population on Floreana (Fig. 2). The two smaller subpopulations lost more than 15% of their genetic diversity in spite of receiving occasional immigrants. The population and subpopulations were viable ($>90\%$ probability of persistence) when survival of penguins through strong El Niño events was greater than 50% and 70%, respectively (Fig. 2). The mean time of extinction for simulated populations that went extinct was 41 years.

Infrequent strong El Niño events affected the long-term population dynamics more than did frequent weak El Niño events (Fig. 3). When the frequency of strong El Niño events was greater than 3%, the simulated population declined and the risk of extinction increased. A 1% increase in frequency of strong El Niño events increased the probability of extinction of the population by approximately 10% (Fig. 3). The risk of extinction increased to more than 80% when the frequency of strong El Niño events was doubled from the current rate (from 5% to 10%, Fig. 3).

With frequencies of 12% or greater for strong El Niño events, the probability of extinction was 100%, whereas substantial increases in the frequency of weak El Niño events had relatively little additional impact on population viability (Fig. 4).

Varying the baseline sex ratio (50%), to 60% and 68% males, increased the probabilities of extinction from 30% to 50% and 73%, respectively (Fig. 5).

Under the Current El Niño scenario there was no minimum viable population size ($<10\%$ chance of extinction), and the size of the total population declined from 1500 to about 700 birds on average in 100 years (Fig. 1). However, under the Historical El Niño conditions (2% risk of strong El Niño and 20% of weak El Niño) the population size that met our MVP definition was 1400 individuals.

Substantial decreases in carrying capacity had a moderate effect on the probabilities of extinction of the population. Reducing the baseline carrying capacity by 50% and 75% increased the probabilities of extinction from 30% to 36% and 47%, respectively.

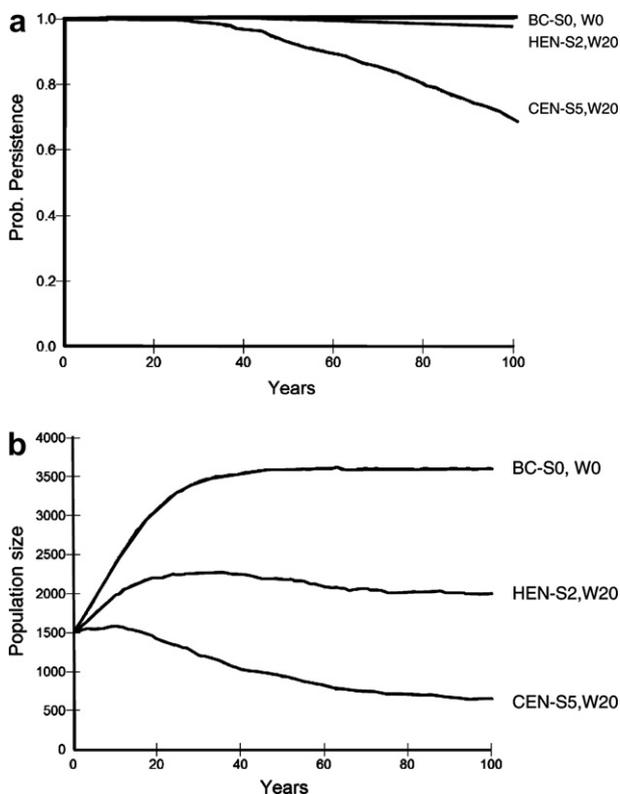


Fig. 1 – Mean persistence probability (a) and mean population size (b) of the Galápagos penguin population under the Best Case (BC-S0-W0, with no El Niño episodes), Historical El Niño (HEN-S2,W20) and Current El Niño (CEN-S5,W20) scenarios. S = Strong El Niño, W = Weak El Niño, Numbers = percent frequencies of El Niño events in 100 years (e.g., S5, W20 = Strong EL Niño with 5% frequency + Weak El Niño with 20% frequency).

4. Discussion

4.1. Differential effects of El Niño events

No two El Niño events are the same. Thus, their effects on the Galápagos penguin and food supplies are expected to vary according to the strength and timing of onset of each episode. In our model, only strong El Niño events were catastrophic to the Galápagos penguin (Fig. 3). Therefore, survival during extreme El Niño events appears to be a critical factor for the persistence of the Galápagos penguin, as it is for other long lived seabird species whose populations can decline even with small increases in mortality (Croxall and Rothery, 1991). Since penguins do not nest, and probably expand their foraging areas, during strong El Niño events (Boersma, 1978; Vargas et al., 2005), it is likely that a lower detectability of birds would account for part of the large declines recorded during the strong 1982–83 and 1997–98 El Niño events (Vargas, unpublished data). Hence the 30% survival rate (based on these two “very strong” El Niño events) used in the Current El Niño

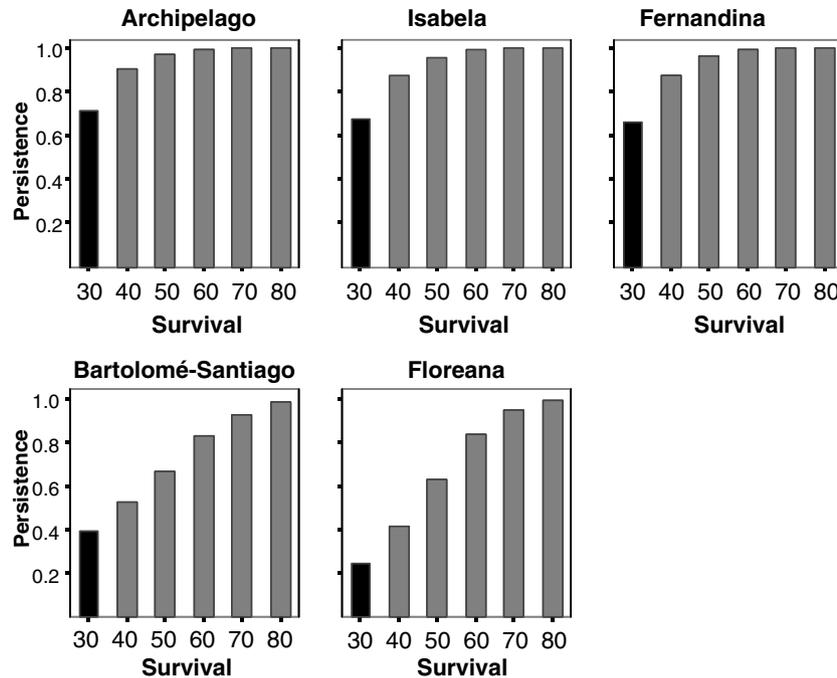


Fig. 2 – Sensitivity testing showing the effect of El Niño on the probability of persistence of the Galápagos penguin population in the Archipelago and subpopulations with varying survival rates. The black bars indicate persistence based on 30% survival derived from actual census data (1970–2004). Higher values of survival, between 40% and 80%, in grey bars simulate other possible survival rates or higher detectability of birds during field surveys. Starting population sizes for Isabela, Fernandina, Bartolomé-Santiago and Floreana were 1500, 1020, 405, 60 and 15 individuals, respectively. The impact of El Niño on the proportion of birds breeding was not changed. Note the relatively stronger effect of El Niño events on the persistence of smaller subpopulations of Bartolomé-Santiago and Floreana which show higher probabilities of extinction.

model could represent a “worst case scenario”. Higher survival rates are also possible in other weaker El Niño events.

In 15 years, between 1982 and 1997, two “very strong El Niño events” (1982–83 and 1997–98) occurred in the Galápagos (Snell and Rea, 1999; Vargas et al., 2006). This is a frequency of 13% in 100 years which is likely to persist under the current global warming scenario. Therefore, with similar or higher frequencies of strong El Niño events in future climate scenarios, the Galápagos penguin populations will be significantly threatened (Fig. 4). On the other hand, simulated increases in the frequency of weak El Niño events had only a moderate impact on the penguin population. This may be because weak El Niño events were simulated to affect only reproduction.

4.2. Differential effects of El Niño scenarios

The Historical El Niño (HEN) model indicated that the Galápagos penguin would have persisted in the face of past frequencies of strong El Niño events of less than 3% in 100 years, which provide adequate time for population recovery in between El Niño declines. Above this threshold, the penguin population is in a long-term decline.

The estimated reduction in numbers, from 1500 to about 700 birds, shown by the Current El Niño model suggests that the Galápagos penguin population is likely to continue to decrease if strong El Niño events continue at the frequency recently observed. In the absence of El Niño events (BC model), the simulated populations of Galápagos penguins (based on demographic rates) were, as expected, safe and

the population grew to carrying capacity at a mean rate of about 4.5% per year and then remained near carrying capacity (Fig. 1). In fact, the standard deviation in annual growth rates in the model was about 9%, which encompasses the 8–12% annual recovery rate observed in population field surveys in years of high marine productivity.

This demonstrates that the estimated rates of reproduction and survival result in a demographically healthy population, with recruitment of fledglings to the population sufficient to offset mortality, thus enabling growth of the population to the carrying capacity of the habitat.

Indeed, the breeding biology suggests that Galápagos penguins are relatively ‘r’ selected compared to other seabirds, responding to the unpredictable environment by moulting before they breed and by breeding whenever conditions are right at any time of the year (Boersma, 1977). Cool La Niña events with abundant food supply have the potential to provide adequate conditions for the penguin population to recover after the crashes of strong El Niño events (Boersma, 1998b; Vargas et al., 2006).

Population projections were sensitive to changes in sex ratio values (Fig. 5). A 68% male biased sex ratio resulted in pessimistic projections of persistence in the “virtual population” (73% probability of extinction). However, caution must be exercised when interpreting the resulting high risk of extinction because the deviation from the expected 1:1 sex ratio in the “wild population” could have been at least partly due to sampling error (Ewen et al., 2004). By sexing birds based on morphology, Boersma (1998a,b) noted that females lost body

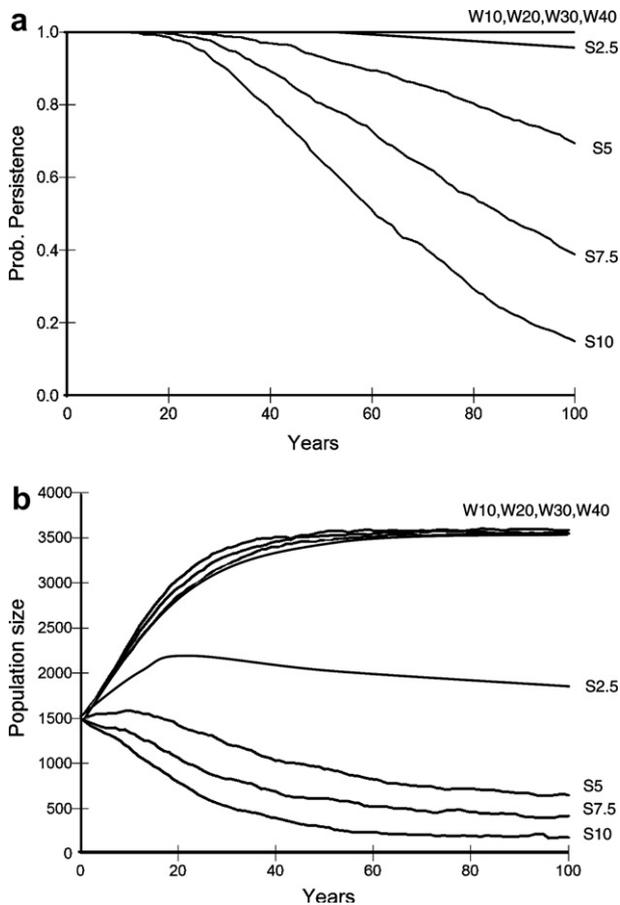


Fig. 3 – Differential impacts of weak (W) and strong (S) El Niño events, treated independently, on the probability of persistence (a) and population size (b) of the Galápagos penguin with frequencies of El Niño events below and above those currently observed (S5 and W20). Increases of weak events have no negative impact on the population, whilst increases or decreases of strong El Niño episodes have significant effects. Numbers indicate frequencies of El Niño episodes in 100 years.

weight at a faster rate than did males during El Niño events (1971–72, 1997–98) and speculated that there was higher mortality of females in these periods of food shortage. At present, we do not know whether the sex ratio at hatching is also biased toward males. At least with Magellanic penguins sex ratio at hatching is equal (Akst and Boersma, unpublished data). It is therefore possible that El Niño could be the cause of the current unbalanced sex ratio in the wild population. This effect would depress breeding for perhaps decades after an initial crash of the population and therefore could slow the recovery of the penguin population.

Under the Current El Niño conditions, our results suggest that none of the four subpopulations are assured of persistence over the next 100 years. The higher values of persistence shown by the nearby and larger subpopulations of Isabela and Fernandina are probably associated with their higher population sizes and more frequent exchange of dispersing birds. However, the persistence of the two isolated subpopulations on Bartolomé-Santiago and Floreana (both in the model and in the wild as evidence from census data be-

tween 1993 and 2004) indicated that dispersal from the source populations of Isabela and Fernandina should be sufficient (see Wang, 2004 and the “one migrant per generation rule”) to rescue them from extinction.

We conclude that only strong (and not the weak) El Niño events are catastrophic as they occur with sufficient frequency and severity to pose substantial risk to the persistence of the Galápagos penguin. Our multiple (HEN, CEN and FEN) scenarios and sensitivity testing allowed us to incorporate past, present and Future El Niño scenarios and parameter uncertainty, respectively, therefore increasing the predictive accuracy of PVA models. However, our models of population dynamics also included assumptions, and comparison of projected to observed trends will be necessary to validate our PVA model for the species.

4.3. Conservation implications and directions for research and management

Under the Current El Niño scenario, our simulations predict a high likelihood that the overall population of Galápagos penguins will continue to decrease in the next 100 years. The major factor driving the decrease, strong El Niño events, cannot be controlled other than by global alteration in the human activities contributing to global warming. Regional action cannot alter frequencies and severities of strong El Niño events. The only mitigating actions which can be achieved are steps to reduce mortality caused by other factors. Mortality brought about by oil spills (even low-level chronic oiling), incidental captures of birds in fisheries, diseases (Travis et al., 2006), and predation by feral animals (e.g., feral cats, Steinfurth and Merlen, unpublished data) should be prevented, especially during and immediately after strong El Niño events. Therefore, we recommend, in the interests of maximizing the survival prospects of the species in advance of global action to reverse climate change, further research to determine levels of mortality of adults (especially of females) and its variation from year to year.

As El Niño events are known to reduce primary productivity and disrupt marine food webs (Barber and Chavez, 1983), improved knowledge of the diet of the Galápagos penguin is desirable. Future PVA models can be further improved with data that are more accurate on age of first breeding, dispersal among islands, estimates of genetic diversity, inbreeding and sex ratio at birth.

A captive breeding program should be considered when there is a 10% probability of extinction within 50 years. This occurs in our model when the population drops to 500 individuals. Before any captive program is started, a plan needs to be developed according to the IUCN Technical Guidelines for the Management of *ex situ* Populations for Conservation (available at <http://www.iucn.org/themes/ssc/pubs/policy/exsituen.htm>) and the guidelines for the management of captive penguins (Diebold et al., 1999).

A key recommendation is to continue the annual censuses. Regular monitoring of population size is necessary to identify when precipitous or accumulated population declines raise the need for additional conservation actions.

We encourage management actions that would improve demographic performance so that the population could

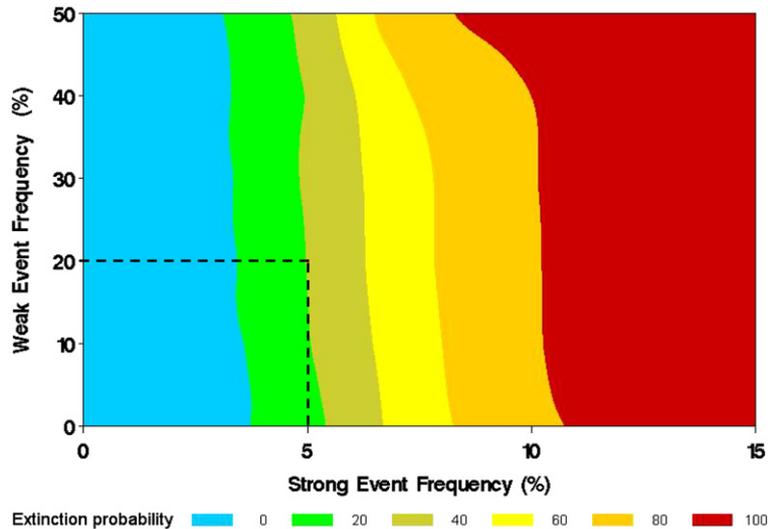


Fig. 4 – Simulated mean extinction probability of the Galápagos penguin in 100 years at varying frequencies of weak and strong El Niño events. The intersection of lines indicates estimated mean extinction probability under the Current El Niño (CEN) scenario with frequencies of 5% for strong and 20% for weak El Niño events. The Best Case El Niño scenario is represented by the lower left hand corner. Frequencies between those of the Best Case and Current El Niño scenarios were considered to simulate Historical El Niño (HEN) scenarios (range = 1–4% of strong El Niño events and 1–19% of weak El Niño events). Values above those of the Current El Niño (CEN) scenario simulate Future El Niño (FEN) scenarios. Contour lines from a minimum of 500 iterations were generated by interpolating a grid of 5% increments with a smoothing algorithm (SPLINE of SAS G3GRID). For 500 iterations, the standard error of estimated extinction probability values is between 2% and 4%.

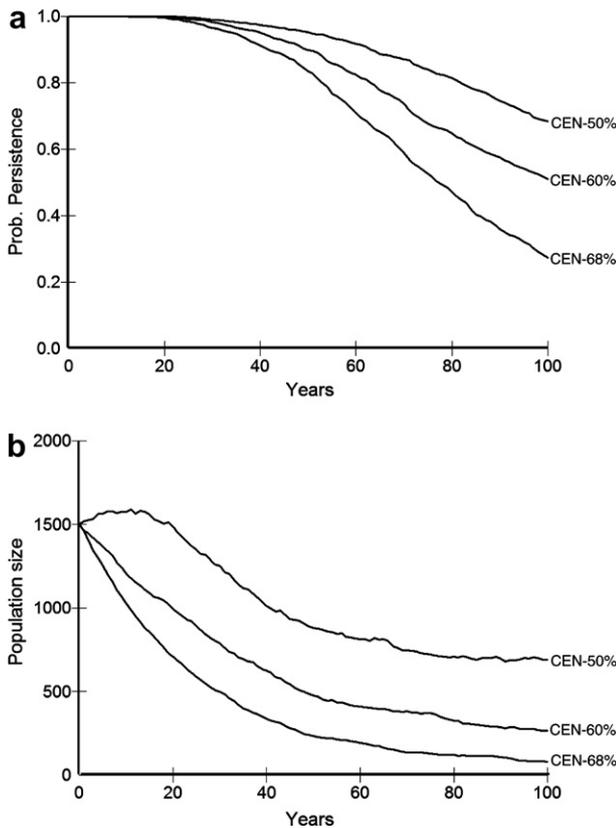


Fig. 5 – Simulated effects of the Current El Niño (CEN) scenario with varying sex ratios on the probability of persistence (a) and population size (b). The proportion of males in the population was set at 50% (base model), 60% and 68%.

recover more quickly after strong El Niño events. To reduce the risk of extinction to near 0% within 100 years under the Current El Niño scenario, our modelling indicated that the following targets, ranked in order of priority, need to be achieved:

1. Hold annual adult mortality at no more than 5%.
2. Increase the proportion of mature females that successfully breed each year from 57% to 67%.
3. Increase annual juvenile (fledging to 1 y) survival from 33% to 50%.
4. Decrease annual mortality in the sub-adult class (1–2 years age) from 25% to 20%.

Restrictions on fishing and other human activities in sensitive areas, control of introduced predators and enhancement of breeding sites might help achieve these targets.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2007.02.005.

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