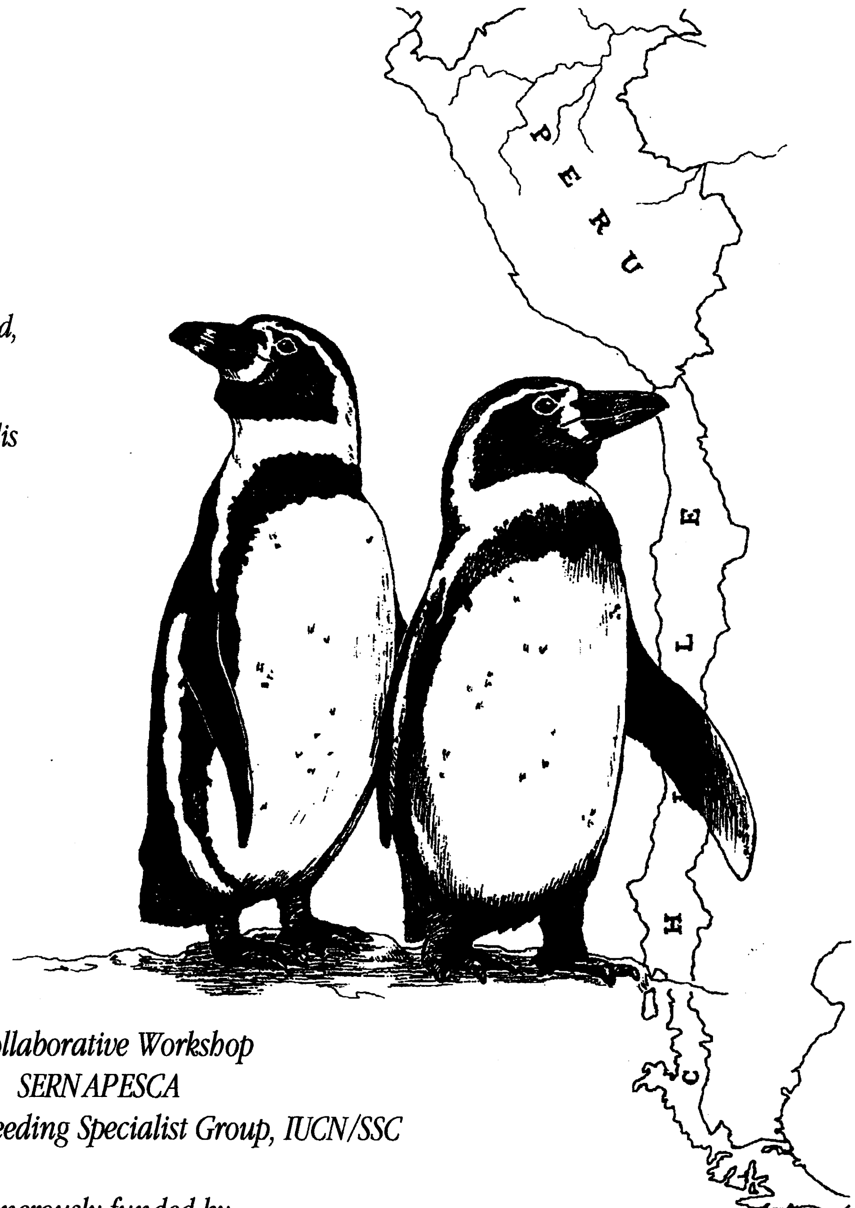
Population & Habitat Viability Assessment for the Humboldt Penguin (<u>Spheniscus humboldti</u>)

Olmüe, Chile
28 September - 1 October 1998

FINAL REPORT



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A Collaborative Workshop
SERNAPESCA
Conservation Breeding Specialist Group, IUCN/SSC

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February 2000

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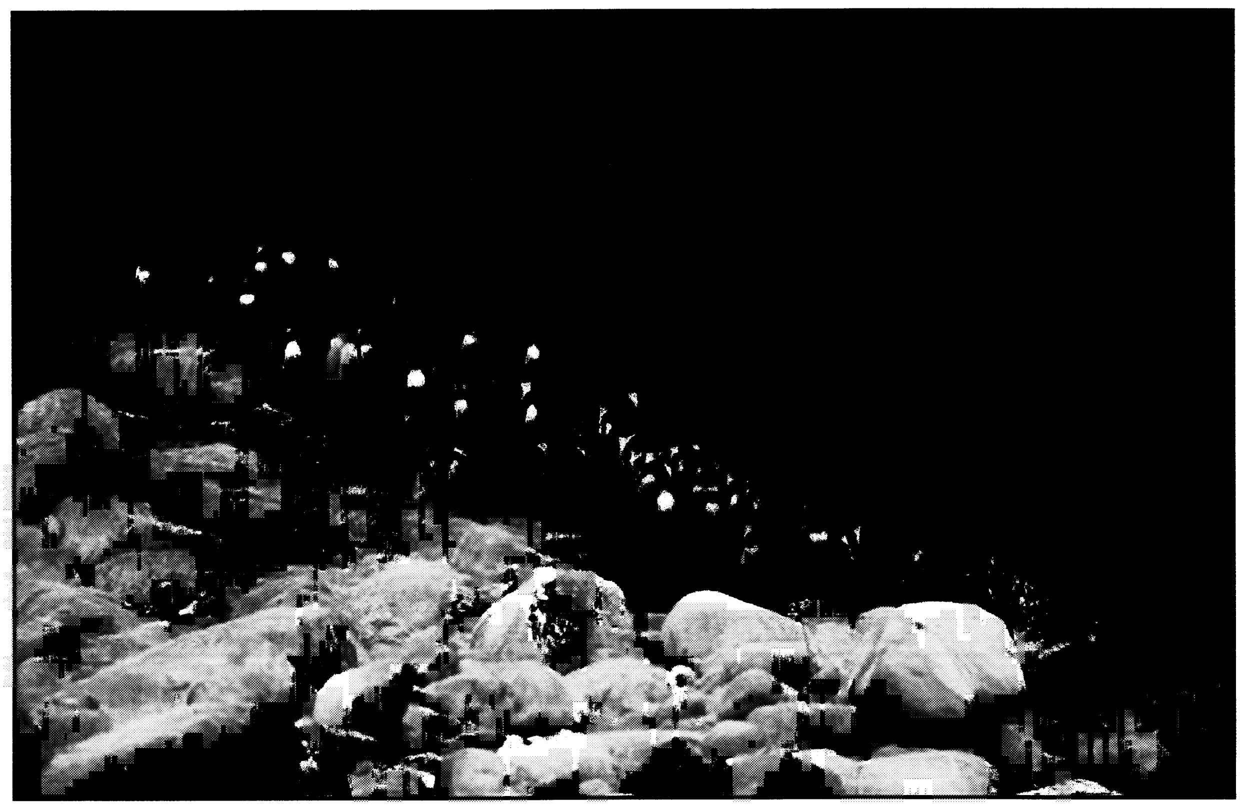

Section 1

INTRODUCTION AND SUMMARY

Population and Habitat Viability Assessment for the Humboldt Penguin (*Spheniscus humboldti*): Introduction and Summary

Introduction

The Humboldt Penguin is endemic to the Humboldt Current region and is restricted to the coasts and islands of Chile and Peru. The species' reproductive range includes Foca Island (5° 12'S) in Peru through the Pinihuil Islands in Chile (42 ° S) (Araya et al. in press). According to the Penguin Conservation and Management Plan (Ellis et al. 1997), the Humboldt Penguin is considered to be Vulnerable (Appendix I, Section 3). In Chile, the Humboldt Penguin also is considered to be Vulnerable (CONAF 1988; Rottman and Lopez 1992; Araya and Bernal 1995). In Peru, this species is listed as being in danger of extinction (Pulido 1991).

Humboldt Penguin populations have been declining over the last three decades. The decline may be caused by many factors, including lack of reproductive success, high chick mortality rates, entanglement in fishing nets or high mortality during El Niño years. At present, the population in Chile has been estimated to be approximately 7500 individuals; in Peru, the most recent census, which took place in 1996, estimated 5500 individuals.

Murphy (1936) suggested that the Humboldt Penguin was numerous in the Humboldt Current area. There are mid-19th century estimates of more than a million birds. By the time Murphy published his account, the population decline already was evident. He reported that 100 or more islands in Peru were "periodically allowed to become merely ankle-deep in new guano before they are swept clean. The breeding penguins must resort, therefore, to precarious nesting sites." Murphy (1936) emphasized that the Humboldt Penguin population had already suffered a noticeable decrease.

At present, the Humboldt Penguin is threatened by many factors. Among the main causes for concern are: climate change, including heavy rainfall, which in many regions results in nest destruction and the loss of eggs or chicks; decreased abundance of prey populations due to fishing activities; entanglement in fishing nets; hunting of penguins for human consumption and use as bait; human interference; loss of habitat because of guano exploitation and ocean disturbances. Secondary threats include: loss of eggs and chicks through predation by mice and introduced animals, and contamination from increasing human activities associated with urban development and inadequate planning.

As part of the Species Survival Commission (SSC) of IUCN – The World Conservation Union, the Conservation Breeding Specialist Group (CBSG) contributes to the development of holistic and viable conservation strategies as well as the implementation of action plans for species recovery and survival. The CBSG works intensively with wildlife agencies, governmental organizations as well as other specialist groups from around the world in developing scientifically based processes toward this end. Working both at a regional and international level, CBSG has developed a number of tools that facilitate an integrated approach to species conservation and management. One of these tools is called Population and Habitat Viability Assessment (PHVA).

To address the concerns outlined above, as well as the growing concern for the future of the Humboldt Penguin, the Servicio Nacional de Pesca del Ministerio de Economia, Fomento y Reconstrucciốn (SERNAPESCA) contacted the CBSG to conduct a PHVA workshop on the species. This workshop was a high priority recommendation for the Humboldt Penguin in the CAMP workshop report on penguins (Ellis *et al.* 1997).

The PHVA Process

The ability to conserve threatened species is based, in part, on assembling and reviewing the best available knowledge concerning the species in question. At the beginning of each PHVA workshop, the participants come to agreement on the goals of the meeting which include preventing the extinction of the species and maintaining a viable population. The PHVA process involves a thorough examination of the ecology, population demographics and trends, the current conservation status, threats and means of conservation.

One of the primary results of a PHVA process is the compilation of unpublished information. We estimate that approximately 80% of the information regarding particular species is held in the minds of the experts and possibly will never be published. Combined with published data, this information provides a basis from which to build computer simulations of the risk of extinction for each population. These models allow analysis of stochastic and deterministic effects, as well as the interactions between genetic, demographic, environmental and catastrophic factors on population dynamics and extinction risk.

The development of information to be included in the model requires that both the data and the assumptions being used are explicitly explained. The process of assembling this information leads to construction of a basic consensus model for the species/populations under consideration. The model simulates species biology, as presently known, and allows continuing discussions of management alternatives and adaptive management for the species or population as additional information is obtained. The model also allows the establishment of management programs, which, as scientific exercises resting on continuous evaluation of newly obtained information, provide a framework for management practices as well as the flexibility to adjust them as necessary.

In a PHVA workshop, all participants are equal and recognition is given to the fact that all contributions are needed for the process to be a success. The information offered by park rangers, landowners, researchers and managers is given importance. The value in a PHVA process also resides in communication. Occasionally, different people have been working on the same species for years but they have never had the opportunity to discuss important issues face to face. During a PHVA workshop, the participants work in small groups to discuss all the topics that have been identified as crucial for the conservation of the species. These topics might include: prevention of mortality, habitat conservation, management of the prey species, captive breeding, etc.

The Humboldt Penguin PHVA

The purpose of the Humboldt Penguin PHVA workshop was to contribute to the development of a conservation strategy for the species. From 28 September 28 to 1 October 1998, 31 participants from four countries gathered in Olmüe, Chile to review and develop conservation strategies for the Humboldt Penguin. The list of participants can be found in Appendix II, Section 3.

The workshop began with presentations on the current situation and status of the Humboldt Penguin. Following these presentations, participants worked in a plenary session to identify the main problems related to the species' conservation. Each participant wrote down the problem(s) that they considered most urgent on a single sheet of paper. Each sheet then was placed on an adhesive panel, with each given the same value. Later on, a small group of people organized them by basic topics (Appendix III, Section 3). Based on this categorization, five working groups were established:

- Habitat Conservation and Management
- Fisheries Interactions
- Research and Monitoring
- Legislation and Education
- VORTEX Modeling

Each group presented several reports on their topic (Section 2) in plenary session. Each expanded the identified main problems and proposed actions to solve them.

In several of the plenary discussions, there were conflicting points of view, primarily between researchers and those managing fisheries. Plenary discussions allowed each group to see and understand the other's perspective. Both groups agreed that the Humboldt Penguin's situation is a cause for concern and that the problems are complex. The main problems and needs for each group were:

The Humboldt Penguin is Listed
As "Vulnerable" on the IUCN Red List

Problem:
The biologists want to protect the penguins and assure their long-term survival.

Needs:
1. The biologists need help to obtain their data.
2. The biologists need to have their data considered credible and not disregarded so that the penguin can survive.
3. The biologists do not want to paint a scenario so positive that it leads to the extinction or decline of the penguins.

Problem:
SERNAPESCA needs to protect the penguins without the destruction of the fisheries.

Needs:
1. SERNAPESCA needs reliable data (for example what are the actual numbers?) to make decisions and convince their constituencies of needed changes. .
2. SERNAPESCA does not want to paint a scenario so negative that it leads to the collapse of the fisheries.

It is necessary to consider and respect the different perspectives of both these groups in order to confront the challenges presented by Humboldt Penguin conservation.

SUMMARY OF WORKING GROUP RECOMMENDATIONS

The following section discusses only the main ideas developed by each of the working groups. Each group's detailed recommendations are presented in Section 2.

1. Conservation and Habitat Management

a) With respect to the unavailability of adequate nests, the working group recommended the creation of artificial colonies in places located away from tidal influence. In addition, actions should be taken towards the protection of native vegetation in those localities, as well as replanting in areas where the vegetation has been destroyed.

b) Regarding the impact of predators, the group recommended elimination of introduced animals; at the same time, native predators should be captured and set free in areas far away from the colonies.

c) Recommendations regarding human disturbance primarily were directed to guano companies, mainly in Peru. The group agreed that these companies should perform their guano extraction activities with minimal impact on the bird colonies. In addition, measures should be taken to reduce the negative impact from colonies of fishermen, tourists, and researchers (e.g., fencing protected areas, placement of warning posters that deny access to colony areas). In this context, it is recommended that places where the main penguin colonies are located in Peru and Chile be declared as reserves or marine parks according to the legislation of each country.

2. Fisheries Interactions

a) To address the effects of extractive fishing activities on penguin populations, the group recommended that authorities, fishermen and industries be involved so as to carry out palliative measures to ensure that negative impacts are decreased, especially entanglement in nets. Among the recommended measures are: the design of artifacts that scare the bids away from nets and encouraging the modification of artesanal fishing, fishing customs and the timing of fishing activities.

b) With respect to competition for marine resources, the group recommended involving the authorities, informing them about the ecological implications of high extraction of one or more marine resources, in this particular case, of the prey resources used by penguins and other protected species.

c) When the group examined human consumption, including the use of penguins as pets, it recommended that educational programs and mass media be used to inform the public of the impacts of these practices on penguin populations. The group also suggested involving fishermen in ecotourism programs, which could help increase the species' intrinsic value, thus avoiding their capture.

d) Because there is a lack of reliable information about the interactions between different fisheries and Humboldt Penguin populations, research focusing on this topic is essential, including penguin foraging patterns, transit routes, behavior near/in front of nets, and effects on the Humboldt Penguin on declines in anchovy populations, among others.

3. Research and Monitoring

a) To surmount the challenge presented by different conceptual interpretations of data emerging from population studies, one recommendation was to standardize the terminology to be used. This will permit comparison of the penguins' situation with respect to other resources (e.g., fish populations) with which penguin populations interact. The group recommended a standardized methodology for censusing and monitoring, which is presented in the Group Report.

b) Some of the causes for penguin mortality have been identified, but it has not been possible to quantify them. Among those that deserve attention are entanglement, the El Niño phenomenon, illegal hunting of chicks and adults and egg recollection.

c) Participants discussed their experiences related to the species' reproductive ecology, specifically the determination of reproductive success and the factors that affect it, such as food availability, nest quality, and chick mortality.

d) To identify the most relevant aspects of the interaction between penguins and the fishing industry or other human activities, it is necessary to undertake studies aimed at determining the species' energetic requirements during key periods of its natural history. In this context, other research items identified included migration patterns, dispersion, genetic structure, re-population and pollution, both environmental and of the individuals themselves.

4. Legislation and Education

a) Regarding the need for stronger governmental commitment to protect Humboldt Penguin colonies, the group recommended that authorities create special protection areas wherein fishing is prohibited, such as parks or marine reserves, in those areas that harbor the principal colonies. Likewise, it is essential to generate the political will necessary to implement international agreements regarding the protection of endangered species, as well as providing the data and resources needed to undertake required actions. It was suggested that, if necessary, a special agency be created, where all nature conservancy activities would be concentrated.

b) With the goal that the general public, especially artesanal fishing communities living close to penguin colonies, become conscious of the need to protect this Vulnerable species. The group recommended targeted formal and informal education; actions to achieve this goal are outlined in the working group report. NGOs can play an important role in the process as well, through communication with governments and the funding of educational and public awareness programs.

5. VORTEX Models

VORTEX models showed that current rates of reproductive success and survival in Chilean populations of Humboldt Penguin would cause their slow decrease, even without severe El Niño phenomena and human extraction. An increase in the percentage of penguin pairs with successful annual reproduction, or a reduction of mortality, are needed to promote positive growth in the population. Based on the best reproductive rates observed (in Punta San Juan, Peru), Chilean penguin populations could be expected to grow in the absence of additional threats.

If severe El Niño events cause penguin mortality rates of 50%, or even 25%, then the long-term growth of the populations in Peru will be slow (but still positive). The decrease of the Chilean population will be faster (2.3-4.4 % annually, in the absence of extraction by humans) and the species would be projected to decrease in abundance, becoming vulnerable to extinction. An improvement in reproductive success is essential to allow population recovery between El Niño years.

Intentional or deliberate human-induced penguin mortality (extraction) above 1% annually was not generally sustainable in simulated populations. Thus, under present mortality rates, suggested by the workshop as being the most probable, human impact would cause (or accelerate) population decrease, and possibly extinction. If the average annual extraction rate is 5% or higher, the species' rate of decline, even in years without El Niño is projected to be 2% annually.

It is believed that movement rates between Humboldt Penguin colonies probably are very low. With low dispersion rates between populations, a modest benefit was obtained in some simulations, as penguins from growing populations (in Peru) could periodically supplement those populations in decline (in Chile). However, with dispersion rates above 1% annually, the potential population growth could decrease due to loss of individuals and its attendant effects on overall species abundance. Thus, high dispersion rates among reproductive colonies do not effectively protect local populations from decline.

It is uncertain if currently available reproductive trends and feeding habitats can sustain Humboldt Penguin populations. However, even if there were abundant and unoccupied habitats, low reproductive success and high mortality rates would prevent the species' expansion into vacant habitat. Similarly, present Humboldt Penguin numbers are not precisely known because the number of individuals that survived the El Niño Phenomenon in 1997-98 has not yet been established. The simulation model shows that the species is in danger of decline and possibly extinction, even if estimated present numbers (as well as carrying capacity) are doubled. The main threats faced by this species are not the result of random events that can cause instability and extinction in small populations. Instead, and in the long term, current reproductive rates are not sufficient to maintain population growth under continued high rates of fledgling mortality, adult mortality due to enmeshment, and overall mortality during severe El Niño years.

In conclusion, the predictions based on our best estimates of fertility and mortality in Humboldt Penguin populations indicated a continuous decline of the species, with high probability of extinction for individual colonies, and even entire populations in some cases. To reverse this tendency, the following management strategies are recommendable:

1. Limit extraction of adult penguins (accidental capture in fishing nets) to less than 1%.

2. Increase the reproductive success of Chilean colonies and increase first-year survival rates.

3. Our ability to understand the threats facing Humboldt penguins, and thus design effective management plans for them, is limited by the uncertainty regarding reproduction and mortality rates, the impacts of El Niño, current population size and the possible variability in demographic rates among reproductive colonies. Whereas management action is currently focused on improving reproduction and survival, additional field studies need to be carried out in such a way that future management decisions are based on refined population-dynamics models.

Success of the PHVA Process

The success of this process relies on a final product in which all participants "win" and are in agreement with, despite different ideas or interests. It is important that any solutions recommended be applied at a local level and that those responsible for management in each territory be responsible for the field application of conservation measures.

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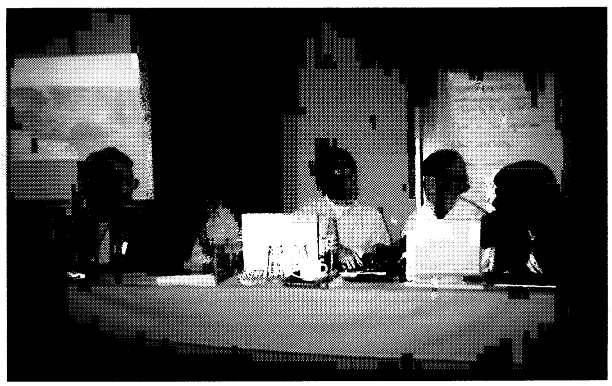

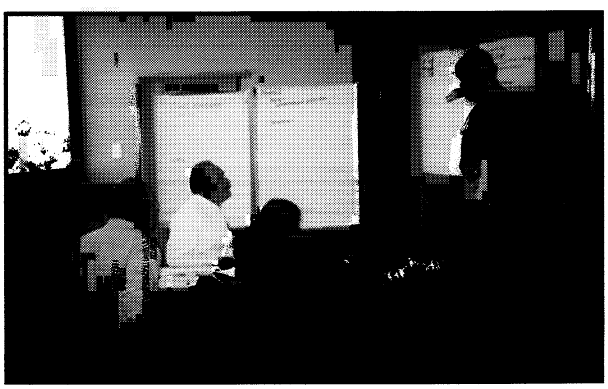

Section 2

WORKING GROUP REPORTS

Habitat Conservation and Management Working Group Report

Participants: Braulio Araya, Cynthia Cheney, Ed Diebold, Gloria Espinoza, Rosana Paredes, Kazuoki Ueda

The group began by identifying conservation and management problems in relation to Humboldt Penguin habitats. The following problems were identified:

1. Problems with Habitat Management
a) Lack of good nests
b) Human Disturbance
c) Guano Extraction
d) Storms and tidal surges
e) Terrestrial and aerial predators
f) Pelicans and seals

2. Main Problems
a) Human Interference
b) Climate
c) Nests
d) Predators

3. Availability of covered nests
a) Guano extraction
b) Climatic events: rain and tidal surges

1. Guano extraction

There is evidence that reproductive success is better in covered nests because of protection from rain, predators, fights between penguins and other disturbances (competition for the same nest areas between pelicans and penguins).

2. Climatic events

Rains: In Peru, rains are a threat only when El Niño phenomena are intense. In Chile, rains are the main cause of complete reproductive loss. In both Peru and Chile, tidal surges cause the destruction of nests within the tidal zone.

3. Predators
Aerial:
Seagulls and caracaras
Vultures occasionally kill solitary chicks in surface nests.

Terrestrial:
Introduced: Rats and cats
Native: Foxes, seagulls, and owls

Humboldt penguin predators in Peru and Chile are:

Peru

Foxes in Punta San Juan cause mortality of eggs and chicks.

Seagulls occasionally prey on eggs and chicks, especially in uncovered nests.

Chile

Rats on Isla Pajaros are numerous and a danger to eggs and chicks.

Same as in Peru.

Cats regularly are seen on Algarrobo, where they use the walkway to the island to gain access to penguin colonies.

Dogs can cause considerable mortality when they come to islands on board fishing boats.

4. Human Disturbance

a) Guano extraction disturbs birds in the colonies
b) Fishermen capture birds; cut the vegetation for use as fuel and disturb the birds during extraction of shellfish on the coast.
c) Tourist activities disturb the colonies.
d) Airplanes, helicopters, jet-skis, etc. disturb the colonies.
e) Scientists create the opportunity for seagulls to capture eggs and chicks from nests uncovered during penguin manipulation. Introduction of domestic animals: goats and sheep have been introduced to some islands (such as Puñihuil).

Note: In Chile, reserves include only land and not the sea surrounding islands, so fishermen can operate very close to shore.

SOLUTIONS TO THE MAIN PROBLEMS FACING HABITAT CONSERVATION AND MANAGEMENT.

1. Lack of good covered nests in the colonies.
Various studies have shown that penguins using covered nests have better reproductive success in comparison to those using uncovered nests. In Peru, guano extraction has decreased the substrate used by penguins during the excavation of covered nests. This forces penguins to use surface nests, in which they are less successful reproductively. Additionally, remnant native vegetation in some places has progressively disappeared, with concomitant habitat impoverishment.

Proposed solutions:

a) Use of artificial nests
In Peru, artificial nests have been used successfully by Humboldt penguins. In Punta San Juan, penguin reproductive success in artificial nests was better than that in surface nests and similar to that of covered ones (Paredes y Zavalaga, unpublished data).

Peru: the group recommends placing nests in areas where there is not enough guano for extraction to provide penguins with covered nests. Likewise, PROABONO authorities are recommended not to extract guano in the penguin reproductive areas.

Chile: artificial nests should be placed on those islands and locations where rain destroys penguin nests. Use of information on nests utilized in Punta San Juan, Peru, is recommended for their adequate construction. The design of artificial nests, however, must be modified to ensure drainage.

b) Create artificial colonies in areas far away from the tidal zone, in order to provide penguins currently nesting on the beach with better sites in locations not affected by tides.

c) Increase the native vegetation used by penguins for nesting. In places where fishermen have cut the vegetation for firewood, original plant species should be replanted, and attempts should be made to increase the previous ground cover available to penguins.

2. Predators
Most penguin colonies in Peru and Chile are located on islands and guano points, which means that access to them by terrestrial predators could cause considerable mortality.

Proposed solutions:

a) Eliminate terrestrial predators using non-lethal traps (dogs and cats), as well as lethal ones. Likewise, we recommend capturing native predators such as the fox

(Pseudalopex culpaeus) in Peru, to be liberated in other areas far from penguin colonies.

b) Construct and improve maintenance of walls (Punta San Juan, Peru) and access doors and hedges (Algarrobo, Chile) thus preventing the entrance of terrestrial predators. Additionally, install signs that prohibit entry into the areas with pets such as dogs or cats.

c) Increase the number of covered nests by using artificially constructed ones and-or enhancing and conserving vegetation that protects penguins against aerial predators such as the Peruvian gull *(Larus belcheri),* the Dominican gull *(Larus dominicanus),* and caracaras *(Polyborus plancus).* Vultures *(Cathartes aura)* also occasionally capture chicks from unattended nests.

3. Human disturbance

Humboldt Penguins are very shy when compared to congeners, and for that reason need to be protected against any type of disturbance. Proximity to, or presence of, human activity causes stress and could affect successful penguin reproduction.

Proposed solutions:

a) Coordinate with the authorities (PROABONOS-Peru) for an improved guano collecting method that has minimum impact on penguin colonies.
   - Extraction should take place when a majority of the penguins are not in the reserve.
   - Frequency of extraction should be reduced.
   - Workers should be kept out of the colonies during non-working hours.
   - Observers (researchers or volunteers) from non-governmental organizations or universities can be asked to witness guano extraction so as to supervise that the activities are undertaken in accordance to the recommendations.
   - Investigate the potential of private non-governmental organizations for developing new agreements with PROABONOS towards managing other guano reserves that have important populations of penguins and other marine birds and mammals.

b) Build or renovate walls and hedges around the reserves and-or protected areas in order to avoid disturbance by humans (tourists) to the penguin colonies. Additionally, so as to avoid access by fishermen and reduce the negative effect that their presence and activity (shellfish extraction) causes, the group recommends creating or reinforcing vigilance systems in protected areas. We also recommend putting up signs that prohibit access to the colonies.

c) Motivate changes in fishing habits and schedules; identify times of exclusion for artesanal fishing in migration routes.

d) With regards to researchers and their studies, discourage the use of unprotected nests so as to avoid predator capture of eggs and chicks. Also discourage, as much as possible, the manipulation of covered nests in proximity to nests with no coverage or protection.

e) In accordance with Chilean legislation (Ley de Pesca), the group suggests the designation as Marine Parks of all waters, sea-floors, and beaches surrounding those islands and islets currently harboring the main Humboldt Penguin colonies in Chile, including Isla Chanaral, Islote Cachagua, Isla Pan de Azucar, ex-Isla Pajaro Niño and Isla Pajaros no. 1.

   In Peru, we recommend the declaration of Marine Reserves in places where the main Humboldt penguin colonies are found, including guano reserves such as Punta San Juan and also unprotected islands such as Hornillos and Pachacamac. This way, fishermen and other people would be prevented from entering penguin colonies.

Fisheries Interaction Working Group Report

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GENERAL DESCRIPTION OF FISHERIES

Two kinds of fishing are utilized in Peru and Chile: industrial and artesanal. There is little information on the former, and its effects on the Humboldt Penguin are unknown. Interactions potentially exist nonetheless, since the penguin's diet consists principally of anchovy *(Engraulis ringens)* and sardine *(Clupea bentincki)*, two primary species utilized by this fishery.

On the other hand clear interactions with artesanal fishing have been documented in both countries. The interactions are attributable primarily to the use of gill nets for fishing corvina *(Cilus gilberti)* or cojinova *(Seriorella violacea).* In Chile, nets are made of monofilament with a net opening of 20 cm, 35 fathoms long and 8 fathoms high. On average, each boat uses four to five nets. In Peru, the nets are made of braided nylon thread with a mesh-size of 13 cm; they are 60-100 m long and 130-175 meshes high; each boat takes six nets. The nets are laid out on the surface -- in Chile up to two miles from the coast (sometimes perpendicular to it) and in Peru up to five miles from the coast in open sea. In Chile, fishing begins at dawn and ends at dusk. In Peru, fishing begins between 15:00 and 17:00 hrs, and the nets are taken in between 0600 and 1100 hrs the next day. Particularly in Chile, nets are in place during the entire time that penguins feed at sea, thus increasing the probability of penguins becoming entangled (see figure 8.2 in Wilson and Wilson 1990:187). In general, individuals that become entangled in the nets have anchovy and sardines in their stomachs, the species that corvina and cojinova feed on. The latter, in turn, are the species targeted by the fisheries.

Mortality attributable to fishing:

Chile:

<u>Northern Zone</u>. Since 1986, personnel from the Corporación Nacional Forestal (CONAF) have periodically visited the island Pan de Azucar (26° 9' S), the surrounding waters of which are used for artesanal corvina fishing with gill nets and medium sized boats (12 m long; 4-6 crew members). Fishing zones are concentrated from 30 to 50 km off the island, particularly towards the west. Recently, new industrial fishing zones have opened up in front of the island; these are based mainly on purse-seine nets.

Medium-size boats also participate. There is no information on the probable effects of these fisheries. In earlier times, it was common practice to hunt penguins as bait for congrio *(Genypterus chilensis).*

Central Zone. Information from three villages dedicated to corvina fishing off the coast of Valparaiso (32° S) suggests an average of 120 entangled penguins per year in a zone of only 14 kilometers (Simeone et al. 1998). Periodic monitoring of six villages between Algarrobo (33° 2' S) and Rapel (33° 56' S) registered 73 dead penguins between 1997 and 1998 in a 90 km-long coastal zone (J.L. Brito, pers. obs.). The animals wash up on shore along with fishing gear, remains of discarded fish, and occasionally other marine birds such as guanay (*Phalacrocorax bougainvilli),* lile *(Phalacrocorax gaimardi)* and piquero *(Sula variegata).*

In central Chile, there are other villages that utilize artesanal fishing. Some observers believe that possibly 200 to 300 entangled individuals die each year[1], both adults and juveniles. Almost 80% of deaths occur in the winter months of July and August, coinciding with the period when penguins are most dispersed at sea (Simeone et al. 1998). The intensity of entanglements varies somewhat between years, but seems to occur constantly. There apparently is no correlation between fishing and the frequency of accidental entanglements. **([1] Not all members of the group agree with these figures, and disagree as to the scientific data that support this projection.)**

Southern Zone. On the islands of Puñihuil (41° 55' S), the capture of penguins for bait in fishing for crustaceans has been reported (Simeone and Schlatter 1998). This apparently does not happen anymore because of the protection afforded by CONAF as well as a change in the fishery, which now is principally dedicated to extraction of the loco (Mollusca: *Concholepas concholepas*). Fishing with gill nets also is practiced in the zone, but the number of incidental penguin captures is unknown (Janos Hennicke, pers. comm.). It is important to note that Chilean fishing legislation includes the Decreto Supremo del Ministerio de Economia 225 of 1995, forbidding the capture of different species of reptiles, birds and marine mammals, among them the Humboldt Penguin. The official authority tasked with enforcement of fishing legislation in Chile is the Servicio Nacional de Pesca (SERNAPESCA), which also serves as Chile's scientific and administrative authority for CITES, which lists the Humboldt Penguin in its appendices.

Peru:

The data are limited to the zone of Punta San Juan (15° S), where 80% of the Humboldt Penguin population in Peru is found. Between December 1991 and December 1997, 970 penguins were captured: 731 of them were entangled between August 1992 and November 1993, 61 from May to June in 1996, and 75 in June and July of 1997. During the remainder of the study period, the level of capture was very low, with less than 10 captured animals per month. Of the animals captured from 1992 to 1993, 20 were banded (95 of the total banded that year). Eighty-two percent of the total of entangled penguins fell into surface gill nets, the rest in other types of nets, and fewer than 2% were captured by harpoon or hand lines. There is a significant correlation between the number of entangled penguins and the number of surface nets used in a given amount of time. Additionally, a greater number of penguins were captured in the most frequently used fishing zones.

Eighty-five percent of the penguins were captured north of Punta San Juan, principally between Punta San Juan and San Fernando. The level of capture in other parts of the coast is unknown. There exists no marked seasonality in captures, which are unpredictable and sporadic, generally coinciding with changes in the vertical distribution of cojinova. When the latter is found close to the surface, fishermen elevate their nets and more penguins are caught in them. The only time of year when no penguins are caught is between December and January, when most are on land and molting.

In Peru, fishermen eat penguins and penguins are directly persecuted for human consumption. On one occasion, a single boat was reported to have captured 150 penguins in the main cave of San Fernando for a baptism party. In the caves of La Chira (300 km south of San Juan) fishermen have relayed stories of using ropes to extract penguins from the caves.

Fishermen also capture penguins for pets. Generally, these animals do not survive for long because they are kept with other domesticated birds, which in turn transmit their diseases to the penguins. The levels of capture for this purpose are unknown.

Indirect effects of fishing activities

The actual impact of industrial fishing activities on Humboldt Penguin populations is unknown. In Peru, it is known that the decrease in anchovy biomass, resulting from industrial fishing and the El Niño phenomenon, has made it impossible for some bird populations, e.g., guanay, piquero and pelican (*Pelecanus thagus)* to recover. They have not been able to recuperate numerically after El Niño events (Tovar y Cabrera 1985). Faced with scarcity of this important prey species, marine birds change from a specialized diet that includes anchovy to a broader one that includes sardines, pejerreyes, agujillas and squid. The change in diet probably implies an increase in the costs of feeding. In the north of Chile, the availability of anchovy and Humboldt Penguin feeding efforts are highly correlated (Culik and Luna-Jorquera 1997).

RESEARCH PRIORITIES

- Evaluate the nature and impact of industrial fishing on Humboldt Penguin populations and other marine birds.
- Replicate studies on the interaction with fishing activities in the rest of the species' distribution range from which there is no information, in order to obtain estimates of total captures and its relation with birth/recruiting rates.

- Study penguin foraging patterns, their transit routes, and their relationship to fishing areas, in order to identify zones with the greatest potential of conflict.
- Determine the factors that affect the vertical distribution of artesanal fishery target-species, and predict the patterns of net usage and thus their impact on Humboldt Penguin populations.
- Examine the consequences of the anchovy decline on the composition
- of penguin diet and energy budget.
- Determine the rates of penguin capture for direct consumption and use
- as pets in Peru.

PROBLEMS AND SOLUTIONS

1. **Artesanal fishing**

   Proposed solutions:

   a) **Involve fishermen and public authorities in the problem by means of workshops.**
   Organize workshops with interested parties (fishermen and authorities independently) for discussing the problem and seeking solutions jointly, in such a manner as to minimize the incidental capture of penguins and with a reduced effect on the income of fishermen.

   b) **Design depth-control mechanisms for nets and/or for driving away other species from the nets.**
   As penguins generally become entangled within the first five meters of depth, it would be desirable to design a mechanism for regulating the depth of nets. Alternatively, a mechanism could be designed that drives away penguins and other species that could become entangled (birds and marine mammals).

   c) **Modify fishing schedules and habits of fishermen to create areas where fishing is prohibited.**
   To seek ways for the fishermen to modify certain habits and schedules, so that they accomplish their activities in times and areas where it is less probable for penguins to become entangled.

2. **Industrial Fishing**

   Proposed solutions:

   a) **Involve entrepreneurs, fishermen and public authorities in the problem by means of workshops and surveys.**
   As with the problem of artesanal fishing, we propose organizing workshops with interested parties, to discuss the problem and seek solutions jointly.

   b) **Design mechanisms aimed at preventing animal entrapment in during industrial fishing operations.**
   Adapt or try out known exclusion devices to allow the escape of trapped birds.

3. **Competition for Marine Resources**

Proposed solutions:

a) **Involve authorities in the problem by means of workshops and advisories.** Organize workshops with public authorities to explain the potential effects of ecosystem changes arising from industrial fishing activities, as well as the benefits of considering other species in the design of fishing policies.

b) **Seek alternative management strategies for industrial fishing.** This would permit recuperation of the anchovy by re-directing fishing effort towards other species, such as jurel and caballa, during anchovy egg laying time, reducing both fishing pressure and predation of larvae at the same time.

4. **Human consumption and penguin pet usage**

Proposed solutions:

a) **Education and awareness programs aimed at users.** The programs would show the impact on penguin populations of direct consumption and pet keeping, as well as point out how avoiding such practices will contribute to the species' conservation.

b) **Introduction of negative myths (e.g., penguins as the cause of impotence?).** This could cause an aversion to the consumption of penguins among users.

c) **To create structures that re-value the use of live penguins.** To involve fishermen in eco-tourism projects based on penguin colonies could cause a re-valuation of the species, thus diminishing its capture and/or use.

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Research and Monitoring Working Group Report

Participants: Gabriella Battistini, Janos Hennicke, Guillermo Luna, Patty McGill, Roberta Wallace

In order for Humboldt Penguin conservation efforts to be effective over the species' distribution range in Peru and Chile, it is important to obtain quality information for use in the development of models and the monitoring of populations, as well as in the formulation of recommendations for management and conservation action. Among the critical information needs are: documentation of reproduction rates in the main Humboldt penguin colonies; the effects of El Niño Southern Oscillation phenomena on the survival of adults; numbers of penguins entangled and drowned in fishing nets; the requirements for and use of prey species; and, the causes for nest abandonment, as well as loss of eggs and chicks. Even though long-term studies are of great value in this variable environment, key data should be obtained for use in short-term recommendations. It should also be noted that the Humboldt Penguin is a Vulnerable species, very sensitive to human disturbance. For that reason, research programs should be designed so as to cause as little disturbance as possible.

1. Standardizing terminology and methodology
In order to identify the problems confronting penguins, it is necessary to first standardize the methods by which population levels and trends are determined. This allows comparison of data from independent groups of penguins.

The two most important points are:
a) Ag*e class denominations:*
- Chicks-- When penguins are still dependent of parents for food.
- Juveniles-- From the time penguins leave the nest (with real feathers) until their first adult molt.
- Adults

b) Det*ermination of reproductive success:*
- % of reproductive females: means the proportion of females in the population that reproduce in a given mating season.
- Reproductive success: fledglings per active nest during a given breeding season.

2. Censusing and monitoring
The next step would be to determine the number of penguins that presently exist on the coasts of Peru and Chile, and thus have a baseline datum for efforts aimed at the

species' conservation. Within this framework, two estimates useful for determining future trends can be identified.

a) *Global estimate*
Current plans call for total abundance counts throughout the Humboldt Penguin's distribution range. The first count will be held during the first day of molting (when the first penguin arrivals are recorded), typically during the first week of January. The other three counts will take place at intervals of 21 days. The counts will take place during the hour of greatest penguin concentration on the beaches, according to the different locations. If this information is unknown, counts will take place during the early hours of the morning.

Juveniles that are not molting will be counted but not included in the total; juveniles recognizable as such but that are starting to molt will be taken as adults.

b) *Estimate of the reproductive population*
Entails counts of active nests during the reproductive season. In accessible colonies, the total number of individuals will be counted during mating and/or nest building; later counts will focus on the number of active nests. In inaccessible areas (sites that can not be accessed more than once), only active nests will be counted. For extremely inaccessible sites, approximations or samples of active nests will be used to estimate the total.

3. Mortality rates and causes
Several causes of penguin mortality have been identified in Peru and Chile, but it has proved impossible to quantify them. Below we list the three most important causes, and propose ways of quantification.

a) *Entanglement*
Counts will take place using interviews with fishermen (known not to be exact) as well as direct counts of entangled animals in ports or beaches (investigate with experts what methodology is best). It is important to determine if there are age, gender or location patterns to penguin enmeshment.

b) *El Niño*
El Niño phenomena are known to produce drastic changes in the availability of penguin prey, but the effect on adult mortality it is not yet clear. These data could be gathered using total population counts before and after the events.

c) *Illegal hunting of eggs, chicks and adults*
Two points must be considered / analyzed. The first is the quantification of illegal extraction of penguins and eggs, thus determining their degree of importance. This can be achieved by accumulating casual observations in ports and beaches (areas where the behavior is most probable).

The second point concerns education and public awareness of the present situation of Humboldt Penguins, as well as providing incentives for the public to report cases of extraction to authorities.

4. Reproductive Ecology

a) Determination of Reproductive Success
   Production: fledglings per nest
   Potential: reproductive females by population

b) Factors that affect Reproductive Success
   i. Food Availability:
   - Acoustic cruise (in Peru IMARPE and in Chile IFOP or Subsecretaria de Pesca -- SERNAPESCA), fishery evaluation reports.
   - Information on unloading in ports and by species through interviews.
   - Penguin capture per unit effort, determined by field research, including interactions between predator and prey.

   ii. Nest quality
   - Differences between natural and artificial nests (habitat management group).

   iii. Chick mortality
   - Determine and quantify the causes of mortality by necropsy and research.
   - Possible causes:
     - Inanition
     - Predation
     - Rain
     - Negative impacts of research

5. Bioenergy and foraging ecology

Studies aimed at understanding energetic requirements during key aspects of natural history are necessary for identifying the most important aspects of the interaction between birds (penguins), fisheries, and other human activities.

a) Identification of prey items.
b) Energy and nutritional content of prey items.

ADDITIONAL RESEARCH

Movement patterns
- Daily
- Seasonal
- Unpredictable events

Dispersion (Genetic and demographic components)
- Emigration.
- Immigration.
- Transmission of diseases introduced by migrants.

Genetic structure

- Individual colonies.
- Entire populations.
- Other related topics such as hybridization.

Artificial population enhancement

- Reintroduction
- Cryopreservation
- Rescue of chicks when abandoned during El Niño events
- Artificial incubation, hand-rearing and release to support populations
- with poor reproductive success
- Rehabilitation
- Investigation by veterinarians

Contamination of penguins and environmental pollution

- Petroleum
- Heavy metals
- Chemicals (pesticides)
- Sampling for the presence and incidence of contaminants (in eggs, feathers, shells, blood, etc.)
- Pollution incident monitoring and determination of impact.

Legislation and Education Working Group Report

Participants: A. Sanhueza, H. Takahashi, H. Hori

PROBLEMS AND ISSUES:

1. Education, information and public relations.
2. Public awareness.
3. Conservation education, including formal and informal education.
1. Education for the fishermen who live near areas of the habitat of the Humboldt penguin.
2. How to help non-governmental organizations with penguins.
6. How to exchange research results with broader communities.

LEGISLATION
Problems/issues:

1. There is a lack of interest from governmental authorities for more protection of the endangered species.
2. There is a need for enforcing laws protecting Humboldt penguins and their habitat.
3. There is a need for legal action for the protection of the colony of Humboldt penguins and their habitat with participation of authorities and researchers: marine reserves.
4. Fishing gear needs to be prohibited in/near Humboldt penguin habitat areas.
5. We need to increase the availability of information and communication with governmental authorities.

Issue 1. There is a lack of interest from governmental authorities for more protection of the endangered species. The priority of the authorities is the conservation of economical resources, because they may not clearly understand the relation between the economically important species (e.g., anchovy) and other species (e.g., Humboldt penguins) in the marine ecosystem.

Proposed solutions:

1. Discuss with authorities the interaction among the species in ecosystem and that it is impossible to preserve economical resources without conservation of the entire ecosystem.

2. Augment the interaction between NGOs and government authorities so as to define and agree upon concrete actions in benefit of Humboldt Penguin protection.

3. Recommend government compliance with treaties and conventions related to the protection of endangered species, as well as the allotment of the necessary resources to relevant institutions.

Issue 2. There is a need for enforcing laws protecting Humboldt penguins and their habitat.

Proposed solutions:
1. Coordinated actions among government institutions so as to achieve conservation objectives for Humboldt Penguin populations.

2. If necessary, a specialized agency should be created to coordinate all the functions related to the conservation of nature.

Issue 3. There is a need for legal action for the protection of the colony of Humboldt penguins and their habitat with participation of authorities and researchers: marine reserves.

Proposed solution:
1. There is a specific law on the subject in Chile, but it is necessary to take concrete political decisions in the short term. In Peru, the colonies are in protected areas.

EDUCATION

Issue 1.
There is a need for education of artesanal fishing communities that live close to Humboldt Penguin populations.

Proposed solutions:
1. Develop and disseminate materials emphasizing the need for preservation of Humboldt Penguins by posters, pamphlets and films.

2. Develop radio programs to be broadcast during peak listening periods.

3. Give educational conferences to artesanal fishing communities. Contact fishermen's organizations (e.g. the Sindicatos and federations in Chile)

4. Formal education (schools) and informal education (to the general public).
   Formal education:
   a) Promote to local and national educational authorities the need to incorporate the protection of endangered species into the curriculum.
   b) Develop formal environmental education tools and programs to educate children (basic education; elementary school, junior high school, high school).

c) Environmental Education should be specially emphasized for children in school and should not only focus on particular endangered species (e.g., Humboldt penguin, guanaco), but also carry out education to help save the species from the extinction in each local area.

Informal education:

a) Develop special programs for television emphasizing the situation facing the Humboldt Penguin.
b) Promote educational activities in zoos, aquaria, and museums around the world.
c) Create wildlife observation posts aimed at ecotourism that does not disturb reproductive colonies, with strict control by guides and/or caretakers. Concomitantly, governments should train guards or guides in the care of wildlife.

Issue 2.

How can NGOs contribute to the protection of Humboldt Penguins? Governmental organizations mainly are interested in the preservation of economic resources (e.g. fisheries or agriculture). Therefore, we need to help NGOs by providing information on the situation facing the Humboldt penguin (e.g., CODEF in Chile, APECO, WCS in Peru).

Proposed solutions:

1. There are nature reserves (e.g., marine reserves or marine parks, forest reserves) by law, and they are not sufficiently functional at present because of political problems and financial difficulties. Therefore, we need to encourage voluntary activities by general public in the nature reserves.

2. Increase communication between/among NGOs and governmental institutions.

3. Obtain financial help for the development of radio and TV programs.

Modeling and Population Viability Analysis Working Group Report

Participants: Rosana Paredes, Carlos Zavalaga, Dee Boersma, David Garland, Andrew Teare, Robert Lacy

INTRODUCTION

A model is any simplified representation of a real system. We use models in all aspects of our lives, in order to: (1) extract the important trends from complex processes, (2) permit comparison among systems, (3) facilitate analysis of causes of processes acting on the system, and (4) make predictions about the future. A complete description of a natural system, if it were possible, would often decrease our understanding relative to that provided by a good model, because there is "noise" in the system that is extraneous to the processes we wish to understand. For example, the typical representation of the growth of a wildlife population by an annual percent growth rate is a simplified mathematical model of the much more complex changes in population size. Representing population growth as an annual percent change assumes constant exponential growth, ignoring the irregular fluctuations as individuals are born or immigrate, and die or emigrate. For many purposes, such a simplified model of population growth is very useful, because it captures the essential information we might need regarding the average change in population size, and it allows us to make predictions about the future size of the population. A detailed description of the exact changes in numbers of individuals, while a true description of the population, would often be of much less value because the essential pattern would be obscured, and it would be difficult or impossible to make predictions about the future population size.

In considerations of the vulnerability of a population to extinction, as is so often required for conservation planning and management, the simple model of population growth as a constant annual rate of change is inadequate for our needs. The fluctuations in population size that are omitted from the standard ecological models of population change can cause population extinction, and therefore are often the primary focus of concern. In order to understand and predict the vulnerability of a wildlife population to extinction, we need to use a model that incorporates the processes that cause fluctuations in the population, as well as those that control the long-term trends in population size (Shaffer 1981). Many processes can cause fluctuations in population size: variation in the environment (such as weather, food supplies, and predation), genetic changes in the population (such as genetic drift, inbreeding, and response to natural selection), catastrophic effects (such as disease epidemics, floods, and droughts), decimation of the population or its habitats by humans, the chance results of the probabilistic events in the lives of individuals (sex determination, location of mates, breeding success, survival), and interactions among these factors (Gilpin and Soulé 1986).

Models of population dynamics which incorporate causes of fluctuations in population size in order to predict probabilities of extinction, and to help identify the processes which contribute to a population's vulnerability, are used in "Population Viability Analysis" (PVA) (Lacy 1993/4). For the purpose of predicting vulnerability to extinction, any and all population processes that impact population dynamics can be important. Much analysis of conservation issues is conducted by largely intuitive assessments by biologists with experience with the system. Assessments by experts can be quite valuable, and are often contrasted with "models" used to evaluate population vulnerability to extinction. Such a contrast is not valid, however, as *any* synthesis of facts and understanding of processes constitutes a model, even if it is a mental model within the mind of the expert and perhaps only vaguely specified to others (or even to the expert himself or herself).

A number of properties of the problem of assessing vulnerability of a population to extinction make it difficult to rely on mental or intuitive models. Numerous processes impact population dynamics, and many of the factors interact in complex ways. For example, increased fragmentation of habitat can make it more difficult to locate mates, can lead to greater mortality as individuals disperse greater distances across unsuitable habitat, and can lead to increased inbreeding which in turn can further reduce ability to attract mates and to survive. In addition, many of the processes impacting population dynamics are intrinsically probabilistic, with a random component. Sex determination, disease, predation, mate acquisition -- indeed, almost all events in the life of an individual -- are stochastic events, occurring with certain probabilities rather than with absolute certainty at any given time. The consequences of factors influencing population dynamics are often delayed for years or even generations. With a long-lived species, a population might persist for 20 to 40 years beyond the emergence of factors that ultimately cause extinction. Humans can synthesize mentally only a few factors at a time, most people have difficulty assessing probabilities intuitively, and it is difficult to consider delayed effects. Moreover, the data needed for models of population dynamics are often very uncertain. Optimal decision-making when data are uncertain is difficult, as it involves correct assessment of probabilities that the true values fall within certain ranges, adding yet another probabilistic or chance component to the evaluation of the situation.

The difficulty of incorporating multiple, interacting, probabilistic processes into a model that can utilize uncertain data has prevented (to date) development of analytical models (mathematical equations developed from theory) which encompass more than a small subset of the processes known to affect wildlife population dynamics. It is possible that the mental models of some biologists are sufficiently complex to predict accurately population vulnerabilities to extinction under a range of conditions, but it is not possible to assess objectively the precision of such intuitive assessments, and it is difficult to transfer that knowledge to others who need also to evaluate the situation. Computer simulation models have increasingly been used to assist in PVA. Although rarely as elegant as models framed in analytical equations, computer simulation models can be well suited for the complex task of evaluating risks of extinction. Simulation models can include as many factors that influence population dynamics as the modeler and the user of the model want to assess. Interactions between processes can be modeled, if the nature of those interactions can be specified. Probabilistic events can be easily simulated by computer programs, providing output that gives both the mean expected result and the range or distribution of possible outcomes. In theory, simulation programs can be used to build models of population dynamics that include all the knowledge of the system which is available to experts. In practice, the models will be simpler, because some factors are judged unlikely to be important, and because the persons who developed the model did not have access to the full array of expert knowledge.

Although computer simulation models can be complex and confusing, they are precisely defined and all the assumptions and algorithms can be examined. Therefore, the models are objective, testable, and open to challenge and improvement. PVA models allow use of all available data on the biology of the taxon, facilitate testing of the effects of unknown or uncertain data, and expedite the comparison of the likely results of various possible management options.

PVA models also have weaknesses and limitations. A model of the population dynamics does not define the goals for conservation planning. Goals, in terms of population growth, probability of persistence, number of extant populations, genetic diversity, or other measures of population performance must be defined by the management authorities before the results of population modeling can be used. Because the models incorporate many factors, the number of possibilities to test can seem endless, and it can be difficult to determine which of the factors that were analyzed are most important to the population dynamics. PVA models are necessarily incomplete. We can model only those factors which we understand and for which we can specify the parameters. Therefore, it is important to realize that the models probably underestimate the threats facing the population. Finally, the models are used to predict the long-term effects of the processes presently acting on the population. Many aspects of the situation could change radically within the time span that is modeled. Therefore, it is important to reassess the data and model results periodically, with changes made to the conservation programs as needed.

VORTEX Population Viability Analysis Model

For the analyses presented here, the VORTEX computer software (Lacy 1993a) for population viability analysis was used. VORTEX models demographic stochasticity (the randomness of reproduction and deaths among individuals in a population), environmental variation in the annual birth and death rates, the impacts of sporadic catastrophes, and the effects of inbreeding in small populations. VORTEX also allows analysis of the effects of losses or gains in habitat, harvest or supplementation of populations, and movement of individuals among local populations.

Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional morality is imposed across all age classes to bring the population back down to the carrying capacity. The carrying capacity can be specified to change linearly over time, to model losses or gains in the amount or quality of habitat. Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size.

VORTEX models loss of genetic variation in populations, by simulating the transmission of alleles from parents to offspring at a hypothetical genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. During the simulation, VORTEX monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or “expect heterozygosity”) relative to the starting levels. VORTEX also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

VORTEX is an individual-based model. That is, VORTEX creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. VORTEX keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of the events occur. (See figure below.) Events occur according to the specified age and sex-specific probabilities. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

VORTEX requires a lot of population-specific data. For example, the user must specify the amount of annual variation in each demographic rate caused by fluctuations in the environment. In addition, the frequency of each type of catastrophe (drought, flood, epidemic disease) and the effects of the catastrophes on survival and reproduction must be specified. Rates of migration (dispersal) between each pair of local populations must be specified. Because VORTEX requires specification of many biological parameters, it is not necessarily a good model for the examination of population dynamics that would result from some generalized life history. It is most usefully applied to the analysis of a specific population in a specific environment.

Further information on VORTEX is available in Lacy (1993a) and Lacy et al. (1995).

Dealing with uncertainty

It is important to recognize that uncertainty regarding the biological parameters of a population and its consequent fate occurs at several levels and for independent reasons. Uncertainty can occur because the parameters have never been measured on the population. Uncertainty can occur because limited field data have yielded estimates with potentially large sampling error. Uncertainty can occur because independent studies have generated discordant estimates. Uncertainty can occur because environmental conditions or population status have been changing over time, and field surveys were conducted during periods which may not be representative of long-term averages. Uncertainty can occur because the environment will change in the future, so that measurements made in the past may not accurately predict future conditions.

Sensitivity testing is necessary to determine the extent to which uncertainty in input parameters results in uncertainty regarding the future fate of the pronghorn population. If alternative plausible parameter values result in divergent predictions for the population, then it is important to try to resolve the uncertainty with better data. Sensitivity of population dynamics to certain parameters also indicates that those parameters describe factors which could be critical determinants of population viability. Such factors are therefore good candidates for efficient management actions designed to ensure the persistence of the population.

The above kinds of uncertainty should be distinguished from several more sources of uncertainty about the future of the population. Even if long-term average demographic rates are known with precision, variation over time caused by fluctuating environmental conditions will cause uncertainty in the fate of the population at any given time in the future. Such environmental variation should be incorporated into the model used to assess population dynamics, and will generate a range of possible outcomes (perhaps represented as a mean and standard deviation) from the model. In addition, most biological processes are inherently stochastic, having a random component. The stochastic or probabilistic nature of survival, sex determination, transmission of genes, acquisition of mates, reproduction, and other processes preclude exact determination of the future state of a population. Such demographic stochasticity should also be incorporated into a population model, because such variability both increases our uncertainty about the future and can also change the expected or mean outcome relative to that which would result if there were no such variation. Finally, there is "uncertainty" which represents the alternative actions or interventions which might be pursued as a management strategy. The likely effectiveness of such management options can be explored by testing alternative scenarios in the model of population dynamics, in much the same way that sensitivity testing is used to explore the effects of uncertain biological parameters.

Often, the uncertainty regarding a number of aspects of the population biology, current status, and threats to persistence is too large to allow scientifically accurate and reliable projections of population dynamics. Therefore, the predictions made from PVA models should be considered to be projections about what would most likely happen to the population *if* various hypotheses about the status of the populations and the threats are true. Conservation and management decisions must be made based on the most plausible hypotheses about the population status, before sufficient data could be collected to test those hypotheses scientifically. An important advantage of PVA models is that they forced systematic consideration and specification of the assumptions and hypotheses that must be made in the absence of adequate data. This facilitates careful reassessment and improvement in the analyses, as better data become available.

Questions to be Explored

Below are some of the conservation and management questions which can be explored by Population Viability Analysis modeling. Analyses conducted at the workshop address some of these questions; other questions could be explored if it is deemed useful.

Using the best current information on the biology of the taxon and its habitat, are the populations of Humboldt penguins in Chile and Peru projected to persist if conditions remain as they are now? Beyond just the persistence of the population, what is the most likely average population size, range of population sizes across years, and rate of loss of genetic variation? If the population is at risk of extinction, is the extinction expected to result primarily from negative average population growth (mean deaths exceeding mean births), from large fluctuations in numbers, from effects of accumulated inbreeding, or from a combination of these factors?

Given that there is considerable uncertainty about several aspects of the species biology and the its habitat, is the population likely to persist across the plausible ranges of parameters that might characterize the population? In particular, how sensitive are the population dynamics to varying estimates of reproductive success, juvenile survival, adult survival, effects of El Niño years, initial population size, carrying capacity of the habitat, and dispersal among populations? Are there critical values for any of these parameters which demarcate a transition from a population that would be considered viable to one that is not?

Which factors have the greatest influence on the projected population performance? If important factors are identified, management actions might be designed to improve these factors or ameliorate the negative effects. How much change would be required in aspects of the population in order to ensure population survival?

INPUT PARAMETERS FOR POPULATION MODELING

Values for parameters which characterize the current status of the populations of Humboldt penguins and threats to their persistence were provided by workshop participants. Some parameters could be estimated from field studies on the species.

Others could be estimated from field studies on other *Spheniscus* species (especially, Magellanic penguins) and were believed to be similar between the species. Data from captive populations of Humboldt penguins provided information about a few species characteristics. For other aspects of the population biology, no data exist at this time from which to calculate important parameters, but biologists at the workshop made estimates based on their understanding of the general characteristics of the species and its ecology.

Populations analyzed – We simulated the population dynamics in 7 of the large populations (3 in Peru and 4 in Chile). Although several other populations of similar size exist, the results obtained for the 7 populations would represent also the expected viability of other populations of similar size. In addition, there are many very small populations of penguins in both Chile and Peru. However, these small populations do not contribute substantially to the total number of Humboldt penguins, and they would be much less stable than are the larger populations. The populations we analyzed are, in order from the north to south:

in Peru	Estimated size in 1998
Isla Pachacamac	100
Punta San Juan	1 500
Isla Hornillos	200
in Chile	
Isla Pan de Azucar	2 750
Isla Chañaral	4 200
Islote Cachagua	2 300
Algarrobo	1 600

Total size of populations modeled: 12 650

Inbreeding depression – It is not known whether inbreeding (mating between relatives) would cause a reduction in survival and reproductive success in Humboldt penguins. For African penguins in American zoos, inbred chicks are more likely to die. However, the sizes of the wild populations of Humboldt penguins are such that it is unlikely that inbreeding would occur more than very rarely. Also, it is possible that Humboldt penguins would avoid breeding with close relatives (as is the case for some other bird species). Therefore, we assumed that inbreeding would be so rare that it is not necessary to include the deleterious effects of any inbreeding in the population viability analysis models.

Age of first breeding – Humboldt penguins have been observed to breed as early as two years of age in captivity and in the wild. Most birds probably do not breed until they are three or more years old. For the modeling, we assumed that both male and female penguins begin breeding at three years of age.

Sex ratio at birth – Humboldt penguin carcasses recovered at Punta San Juan are approximately half males. In captivity, the sex ratio of fledglings is also about 50:50. Therefore, we assumed that the sex ratio of fledglings in the wild populations would be 50:50.

Maximum age -- VORTEX assumes that animals keep breeding (with normal fecundity) until they die. Based on data on Humboldt penguins in captivity, we set the maximum age at 30 years.

Fecundity – In the field, reproductive success is most easily tallied at the time of fledging. Therefore, in the model, we consider penguins to be "born" at the time of fledging. Penguins have two peak breeding seasons, and we combined the reproductive output of these two seasons into a single annual reproductive event for the model. For the populations in Peru, reproductive rates were estimated from data collected by researchers at Punta San Juan. Researchers in Peru estimated that in an average year, about 25% of females fledge no chicks, about 17% fledge one offspring, about 41% fledge two offspring, about 9% fledge three offspring, and 8% fledge four offspring.

For populations in Chile, reproductive rates were estimated from field data at Isla Chañaral (Vilina 1993). In that population, the percents of females fledging 0, 1, and 2 offspring was estimated at 62%, 23%, and 15% in the first season. The numbers of penguins which fledge young in the second season is only about half as many as fledge young in the first season. Thus, about 81%, 11.5%, and 7.5% would fledge 0, 1, and 2 young in the second season. If the two breeding seasons are independent, the success rate across both breeding seasons of a year would be about 50%, 26%, 19.5%, 3.5%, and 1% fledging 0, 1, 2, 3, and 4 young. Non-independence of which birds breed in the two seasons (as is likely) would not change the population projections from the model, as it is not important which females produce the young.

The estimates of reproductive success are based on only a few studies at a few locations in a few years. It is possible that average rates of reproductive success are higher or lower than described above. For example, the fast increase observed in a few populations could indicate higher breeding rates. On the other hand, the population at Algarrobo has had very low breeding success in recent years. We therefore examined scenarios in which higher reproductive rates were assumed to occur in the Chilean populations. These analyses are described in the section "Additional Simulations" below. If reproductive success is lower than estimated in the modeling, the Chilean populations would rapidly die out, and there is no need to examine further models to understand the impact of this possibility.

Density dependence in breeding – Humboldt penguins are presently at numbers much below historic levels. Therefore, it is not likely that breeding areas are over-crowded. We assumed that reproduction would be density independent.

Survival – Based on the field study at Punta San Juan in Peru, we estimated mortality annual rates to be 80%, 7%, 6%, and 5% for the first year, second, year, third year, and subsequent years of age. No comparable data exist from the Chilean populations, so we assumed the mortality rates to be the same across all populations. In the "Additional Simulations" we examined the effect of slightly lower (75%) first year mortality.

Environmental variation in birth and death rates – There are not data from a sufficient number of years to allow calculation of the fluctuations in birth and death rates over time. However, it is known that fledging success and survival of young birds varies considerably from year to year. For preliminary modeling, we assumed that the percent of females breeding would vary across years with a standard deviation of 25%. First year mortality was estimated to vary with a SD = 10% (around the mean of 80%), and mortality in subsequent age classes was assumed to vary with a SD of one-half the mean mortality rates. In the "Additional Simulations", we tested also the effect of increased environmental variation in first year mortality.

VORTEX can also model catastrophe years as a distinct phenomenon from and in addition to the more typical environmental variation in demographic rates. The only catastrophe included in the modeling was the impact of El Niño Southern Oscillation (ENSO) (see below).

Rates of "harvest," due to entanglement in fishing nets or other direct or indirect killing of penguins by humans – At Punta San Juan in Peru, in one year ('92-'93) 105 penguins (about 7% of the total) were killed by humans. Years with such high rates of killing may occur only about once every 5 years, but lesser numbers of penguins are killed in other years. In Chile, an average of about 100 penguins are found dead, with indications that they died due to entanglement in fishing nets, each year. Thus, observed rates of killing by humans in both countries has been about 1% or more each year. It is expected that many more penguins die in fishing nets, but are not counted because carcasses are not found by biologists or reported to biologists. Participants at the workshop all thought that the true rate of killing by humans exceeds the 1% observed. The actual rate was hypothesized to be 2 times, 4 times, or even 10 times the observed rate. In order to test the impact on the viability of penguin populations of different possible rates of incidental or intentional harvest by humans, we examined scenarios in which the annual rates of harvest were set to 1%, 3% or 5% of the initial population size. We did not test higher rates of harvest, because it was clear from the modeling that populations of Humboldt penguins could not survive if harvest were 5% per year. The lowest rate (1%) is likely lower than the current situation, but results from those scenarios indicate whether the populations would be viable if rates of killing could be kept to that low number in the future.

Catastrophes – The primary climatic event which can have catastrophic effects on the Humboldt penguins is "El Niño Southern Oscillation". Although ENSO events have recently occurred about once every four or five years, the events vary in severity. When an ENSO is not severe, the effects on the penguins have not been large. However, extreme ENSO events, such as the ones that occurred in 1992 and 1997/1998 can be catastrophes for the penguins. Data from the population at Punta San Juan, Peru, and at Algorrobo, Chile, show that almost no penguins were fledged during these ENSO events. Many fewer adults established nests and bred, and rains flooded those nests which were produced. The number of adult birds returning to Punta San Juan during the most recent breeding season was only 40% of the number from the previous year. It is not known whether this indicates that more than half of the adult penguins died, perhaps due to starvation, or whether the adults survived but did not return to the breeding sites during the ENSO.

In the population model, we assumed that severe ENSO events would occur on average once every 12 years (a 8.33% probability of occurrence each year). When these severe ENSO events occur, it was assumed that reproduction was reduced, with only 10% of the normal numbers of females breeding. We initially tested three levels of effects on adult survival: no effect, 25% mortality, or 50% mortality. Tests with 12.5% mortality were included in the "Additional Simulations." We assumed that less severe ENSO events cause no unusual rates of reproduction or survival.

Carrying capacity – Most of the present populations of Humboldt penguins are much smaller than they were early in this century. It is assumed that the populations would increase in numbers if reproduction and survival improved. For the population modeling, we assumed that the carrying capacity of each population was either twice or four times the present numbers of penguins.

Rates of dispersal between major breeding populations – None of the 1 000 Humboldt penguins banded at Punta San Juan have been found breeding later at another colony, but penguins are known to travel over long distances during foraging trips. In a study of Magellanic penguins, about 1 in 7 000 penguins was observed to move from the colony where they were banded to other nearby colonies. Therefore, it is likely that Humboldt penguins very rarely move among breeding colonies. We assumed that only females would disperse between populations, and that birds from 1 to 7 years of age might disperse. We initially tested scenarios in which females penguins had either no dispersal among populations, a 0.5% probability of dispersing each year to a different population, or a 1% annual probability of dispersing to a different population.

It is possible that Humboldt penguins do disperse at much greater rates during some years. For example, the disappearance of many penguins from Punta San Juan during the recent ENSO may be due to dispersal of penguins to other sites rather than death. Also, the high fluctuations in numbers at sites in northern Chile could reflect immigration and emigration rather than (or in addition to) births and deaths. Therefore, we also tested annual dispersal rates of 5% and 10%.

In each model, we assumed that a dispersing penguin would be equally likely to move to each other population. Although movement to closer colonies might be more likely than longer distance dispersal, we do not presently have any data from which we could assess the distances over which penguins might disperse. It is also not likely that simulations with other patterns of dispersal (but the same overall rates) would have given notably different results.

Details of the model -- (number of years simulated, number of simulations, definition of extinction) – The populations were modeled for 100 years, with population performance reported at 10 year intervals. Although management actions may be concerned with shorter time frames, it can be useful to project population dynamics for the longer time period. The impacts of population processes may not be apparent until many years after the onset of the effect, especially in long-lived species. Also, when the probability of extinction predicted for 50 years is low (say, 1% or 2%), it is important to determine whether the population is becoming unstable (so that the probability of extinction at 100 years is much higher) or, alternatively, whether the population was at risk when small, but is relatively safe from extinction if it survives early years of unstable growth (so that the probability of extinction at 100 years remains low). Thus, projecting population dynamics for long periods of time is important not because we expect the predictions for 100 years to be accurate, but rather because the long-term projections can make it easier to identify whether the population was stable or unstable in the earlier years of the simulation.

Each scenario was simulated 100 times. Although this provides only moderately precise estimates of mean population trajectories, uncertainty in many aspects of the current population status would limit the value of more precise model results. Also, the general trend in each scenario was clear even with this limited number of iterations.

MODEL RESULTS

There is uncertainty about the mean reproductive rates and mortality rates of the Humboldt penguins, and the effects of El Niño years on these rates. Also, field data suggest that reproductive success may be much lower in Chilean populations than in the major population in Peru, at Punta San Juan. Table 1 shows the population growth rate (exponential rate of increase, r) calculated from the various demographic rates tested in the models. These deterministic growth rates would be expected as the long--term averages, if there is no inbreeding, no temporary shortages of mates or other demographic stochasticity, no limitations of habitat (carrying capacity), no harvest, no dispersal, and constant rates of reproduction and survival.

These calculations show that the reproductive rates estimated for the Chilean populations are not sufficient to offset the estimated mortality, even if there is no impact of ENSO (r = -0.002, or a 0.2% annual decline, without effects of ENSO). The rate of decline is much larger (approximately 2.3% or 4.4% per year) if 25% or 50% of the adult birds die as a result of severe ENSO events.

For the Peruvian populations, with higher estimated breeding rates, the populations of Humboldt penguins are predicted to grow at rates from 1.4% to 5.7% per year, depending on the impacts of ENSO events.

Table 1. Mean deterministic growth rates calculated from various mean birth and death rates used in the modeling. Values of parameters which were not varied among simulations are given in the text. Numbers in bold are the rates used for the primary modeling of the populations in Chile (with 50% breeding) and Peru (with 75% breeding).

Demographic rates varied			Deterministic Population Growth (r)
% breeding annually	1st year mortality	ENSO survival	
50%	80%	50%	-0.044
		75%	-0.023
		87.5%	-0.012
		100%	-0.002
	75%	75%	-0.005
		87.5%	0.005
		100%	0.016
60%	80%	75%	-0.008
		87.5%	0.002
		100%	0.013
	75%	75%	0.010
		87.5%	0.021
		100%	0.031
75%	80%	50%	0.014
		75%	0.036
		87.5%	0.046
		100%	0.057
	75%	75%	0.058
		87.5%	0.069
		100%	0.079

The deterministic growth rate calculations show that the Humboldt penguins, at least in Chile, may be at risk of continuing decline, even if random factors do not further threaten the populations, and no penguins are harvested, intentionally or unintentionally, by humans. The simulation models were used to explore further the viability of the populations, under various scenarios of altered demographic rates, random factors, and human impacts. Tables 2-8 show the results from a number of these model scenarios.

Legends for tables with modeling results
Each table gives the results from 100 iterations of the seven major populations of Humboldt penguins, projected for 100 years into the future, for a number of scenarios with different parameters. Input values varied in each table are the percent suvival during ENSO years, and the number of adult penguins killed each year by entanglement in fishing nets or other forms of harvest by humans. Simulation results presented in each table are:

r (SD): The mean population growth rate across years (with inter-annual variation in growth rate given as a standard deviation). A negative r indicates that the simulated populations, on average, declined in size. A positive r indicates average population growth. A large SD indicates that the rate of population growth or decline was highly variable across years. About 68% of the years, the annual rate of growth would be expected to be within 1 SD of the mean r.

PE: The probability of metapopulation extinction, determined by the percent of iterations in which the species was extinct by 100 years.

TE: The mean time to extinction of those simulations which did go extinct. "Extinction" was defined in the model as the lack of either sex.

N: The mean number of penguins remaining in the7 populations after 100 years for those simulations in which the species did not go extinct.

Table 2 shows the model results for the scenarios in which we applied the estimated rates of reproduction and mortality, assumed no dispersal among populations, and tested the various possible effects of ENSO events and rates of harvest by humans. In each scenario in Table 2, the species continued to decline. Moreover, the species was projected to be at risk of complete extinction within 100 years unless there is no effect of ENSO events, and annual harvest by humans is kept at just 1%. With 50% mortality during severe ENSO events, and 5% harvest by humans (rates considered most plausible by some workshop participants) the species is projected by be extinct in about 26 years.

Table 2. Predictions for initial N = 12 650, K = 25 300, no dispersal

Input parameters		Simulation results			
ENSO survival	Harvest	r (SD)	PE	TE	N
50%	1%	-0.090 (.286)	0.74	57	835
75%		-0.003 (.126)	0.02	60	2678
100%		0.012 (.054)	0.00		4552
50%	3%	-0.175 (.405)	0.97	39	129
75%		-0.058 (.219)	0.53	57	1570
100%		0.014 (.084)	0.00		3324
50%	5%	-0.286 (.570)	1.00	26	0
75%		-0.153 (.335)	0.94	40	861
100%		-0.019 (.140)	0.15	51	1795

Figures 1-3 show the probabilities of the species persisting over the next 100 years for these cases of 1%, 3%, and 5% annual harvest by humans.

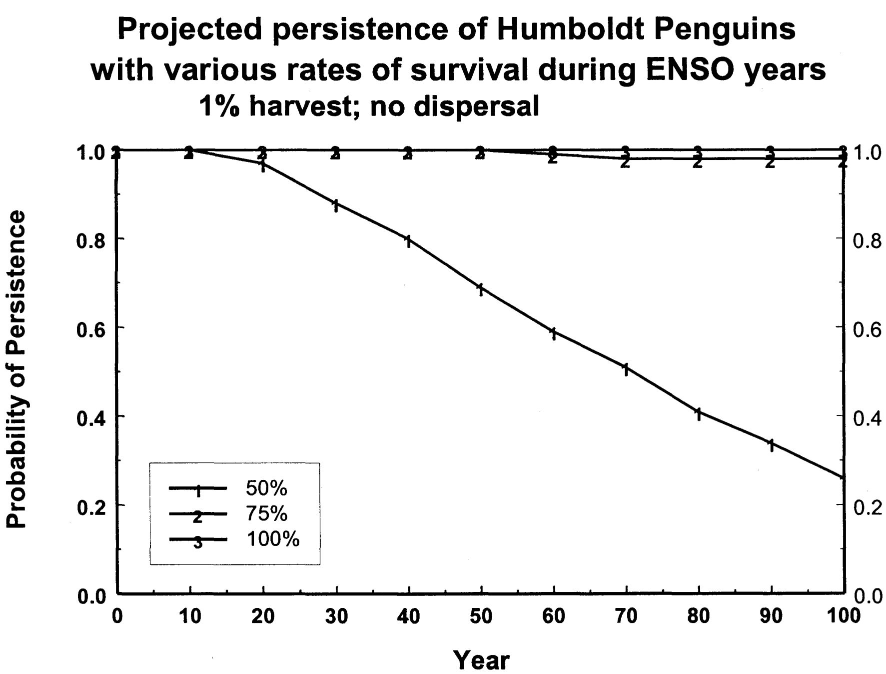

Figure 1. Probability of persistence of Humboldt penguins with 1% harvest, no dispersal between populations, and 50% (line 1), 75% (line 2), or 100% (line 3) survival during El Niño years.

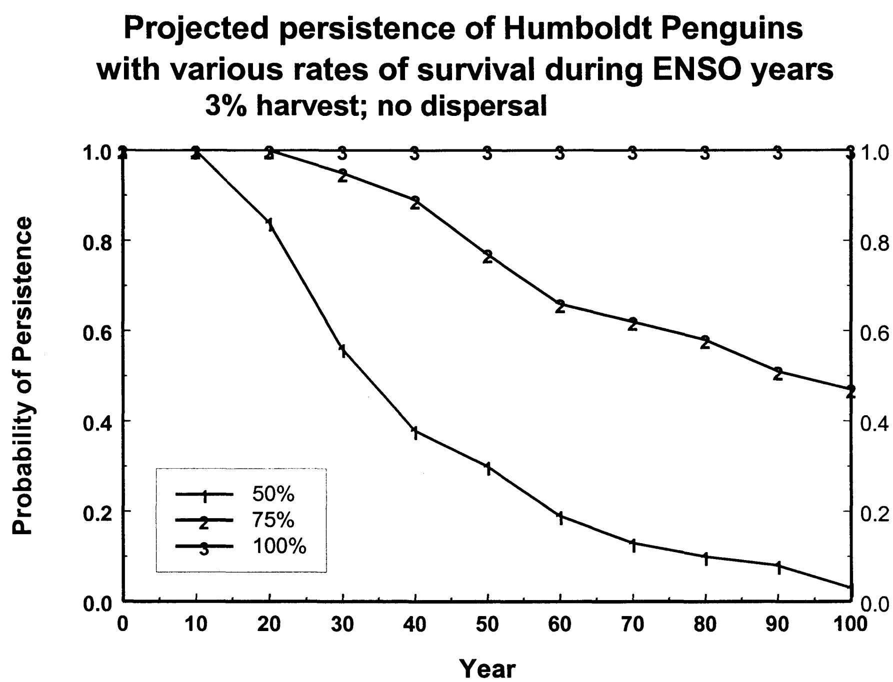

Figure 2. Probability of persistence of Humboldt penguins with 3% harvest, no dispersal between populations, and 50% (line 1), 75% (line 2), or 100% (line 3) survival during El Niño years.

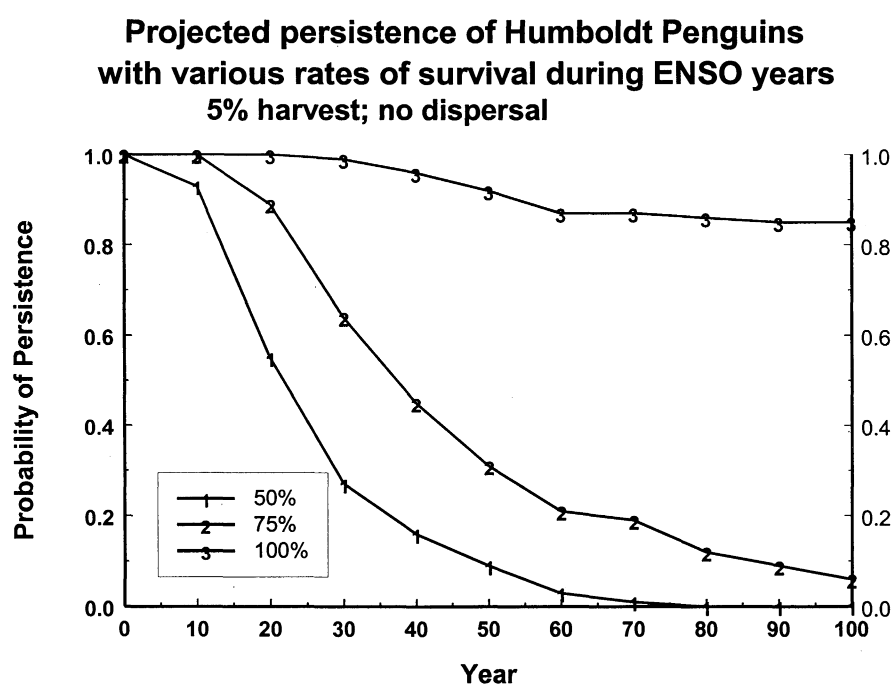

Figure 3. Probability of persistence of Humboldt penguins with 5% harvest, no dispersal between populations, and 50% (line 1), 75% (line 2), or 100% (line 3) survival during El Niño years.

Tables 3-6 show the same set of scenarios, but with increasing rates of dispersal among the populations. Low rates of dispersal (1% or less) had relatively little impact on the viability of populations, typically causing somewhat smaller population sizes, but also leading to slightly greater probability that the species would persist. However, at high rates of dispersal population decline was much faster and complete extinction was much more likely. In the model, the declining populations in Chile act as "ecological sinks" which deplete the species of numbers more rapidly as dispersal among populations is increased.

Table 3. Predictions for initial N = 12 650, K = 25 300, 0.5% annual dispersal

Input parameters		Simulation results			
ENSO survival	Harvest	r (SD)	PE	TE	N
50%	1%	-0.088 (.379)	0.72	60	981
75%		-0.004 (.124)	0.01	79	2598
100%		0.011 (.054)	0.00		4485
50%	3%	-0.164 (.392)	0.95	39	1971
75%		-0.041 (.182)	0.34	59	1561
100%		0.011 (.081)	0.00		3303
50%	5%	-0.251 (.490)	1.00	29	0
75%		-0.125 (.290)	0.88	47	904
100%		-0.016 (.122)	0.04	45	1485

Table 4. Predictions for initial N = 12 650, K = 25 300, 1% annual dispersal

Input parameters		Simulation results			
ENSO survival	Harvest	r (SD)	PE	TE	N
50%	1%	-0.075 (.260)	0.61	63	798
75%		-0.010 (.127)	0.01	41	2175
100%		0.010 (.054)	0.00		4235
50%	3%	-0.161 (.356)	0.97	42	151
75%		-0.053 (.177)	0.42	65	1002
100%		0.008 (.081)	0.00		3160
50%	5%	-0.278 (.493)	1.00	26	0
75%		-0.134 (.279)	0.89	43	435
100%		-0.017 (.116)	0.07	78	1466

Table 5. Predictions for initial N = 12 650, K = 25 300, 5% annual dispersal

Input parameters		Simulation results			
ENSO survival	Harvest	r (SD)	PE	TE	N
50%	1%	-0.100 (.253)	0.84	62	439
75%		-0.041 (.127)	0.15	87	532
100%		-0.004 (.050)	0.00		2963
50%	3%	-0.181 (.336)	0.99	37	39
75%		-0.099 (.182)	0.90	61	141
100%		-0.041 (.090)	0.30	93	487
50%	5%	-0.233 (.385)	1.00	28	0
75%		-0.171 (.256)	1.00	39	0
100%		-0.093 (.143)	0.99	63	148

Table 6. Predictions for initial N = 12 650, K = 25 300, 10% annual dispersal

Input parameters		Simulation results			
ENSO survival	Harvest	r (SD)	PE	TE	N
50%	1%	-0.133 (.261)	0.99	52	21
75%		-0.078 (.133)	0.85	75	90
100%		-0.031 (.058)	0.03	93	522
50%	3%	-0.209 (.343)	1.00	31	0
75%		-0.142 (.215)	1.00	44	0
100%		-0.089 (.112)	1.00	61	0
50%	5%	-0.285 (.416)	1.00	22	0
75%		-0.210 (.279)	1.00	30	0
100%		-0.147 (.201)	1.00	40	0

Figures 4 and 5 show the effects of four levels of dispersal on population persistence for the case of low (1%) harvest and either 50% (Figure 4) or 75% (Figure 5) survival during severe ENSO events.

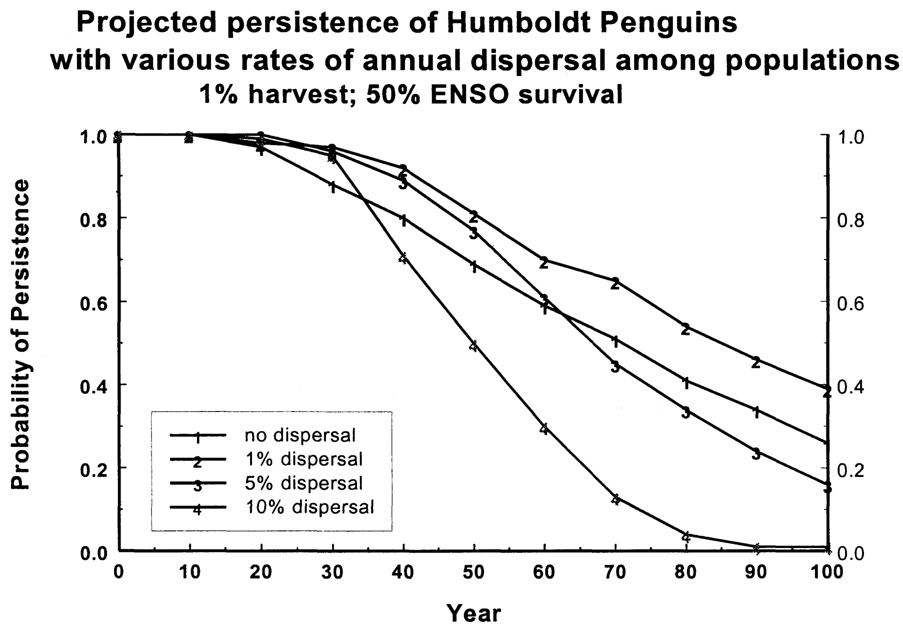

Figure 4. Probability of persistence of Humboldt penguins with 1% harvest, 50% survival during El Niño years, and 0% (line 1), 1% (line 2), 5% (line 3), or 10% (line 4) annual dispersal between populations.

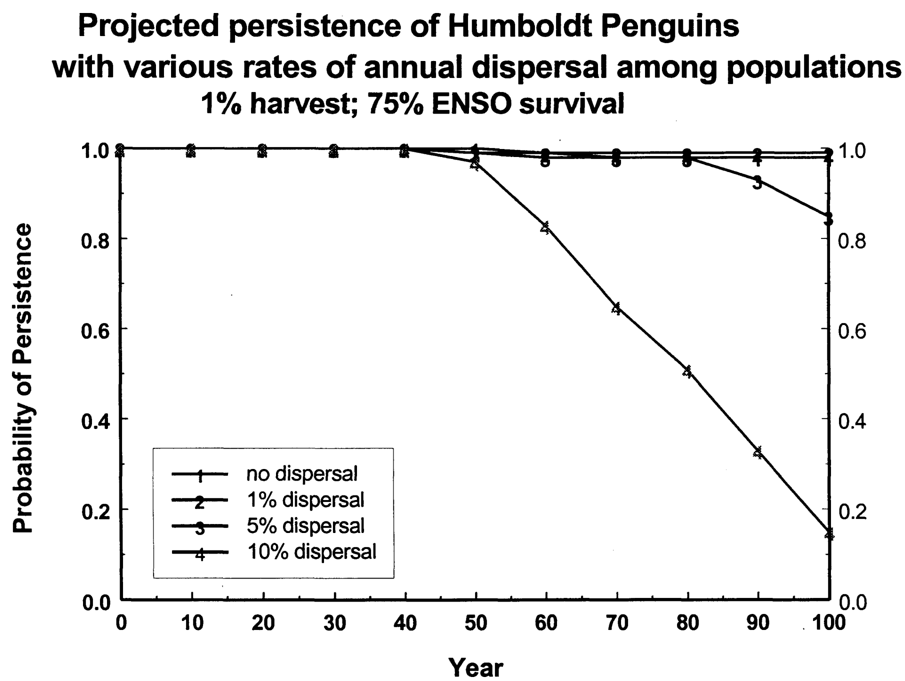

Figure 5. Probability of persistence of Humboldt penguins with 1% harvest, 75% survival during El Niño years, and 0% (line 1), 1% (line 2), 5% (line 3), or 10% (line 4) annual dispersal between populations.

The ecological carrying capacity of the habitat to support Humboldt penguins is unknown. Because there had been many more penguins along the coasts of Chile and

Peru in the past, it may be that the habitat could again support many more penguins. To test the effect of greater carrying capacity on the population projections, we examined scenarios in which the carrying capacity was increased to four times the present population levels. Table 7 shows the results for these scenarios.

Table 7. Predictions for initial N = 12 650, K = 50 600, no dispersal.

Input parameters		Simulation results			
ENSO survival	Harvest	r (SD)	PE	TE	N
50%	1%	-0.067 (.258)	0.50	58	1762
75%		0.001 (.125)	0.01	81	5134
100%		0.020 (.056)	0.00		8158
50%	3%	-0.142 (.395)	0.88	39	1858
75%		-0.040 (.191)	0.39	55	3260
100%		0.018 (.084)	0.00		6424
50%	5%	-0.243 (.519)	0.97	27	669
75%		-0.132 (.325)	0.83	37	1745
100%		-0.010 (.147)	0.16	45	4420

The higher carrying capacity only slightly improved the probability that the species would persist, but resulted in much greater average number of penguins in those simulated populations which did survive (compare Table7 with Table 2). Because the population is declining in most years of the simulation, the potential benefits of a greater carrying capacity are not usually realized, and extinction is not delayed. In those years in which the population does experience growth, however, the larger carrying capacity does allow for the populations to temporarily increase to higher numbers of penguins. The effects of increased carrying capacity on population persistence and numbers of penguins are shown in Figures 6 and 7.

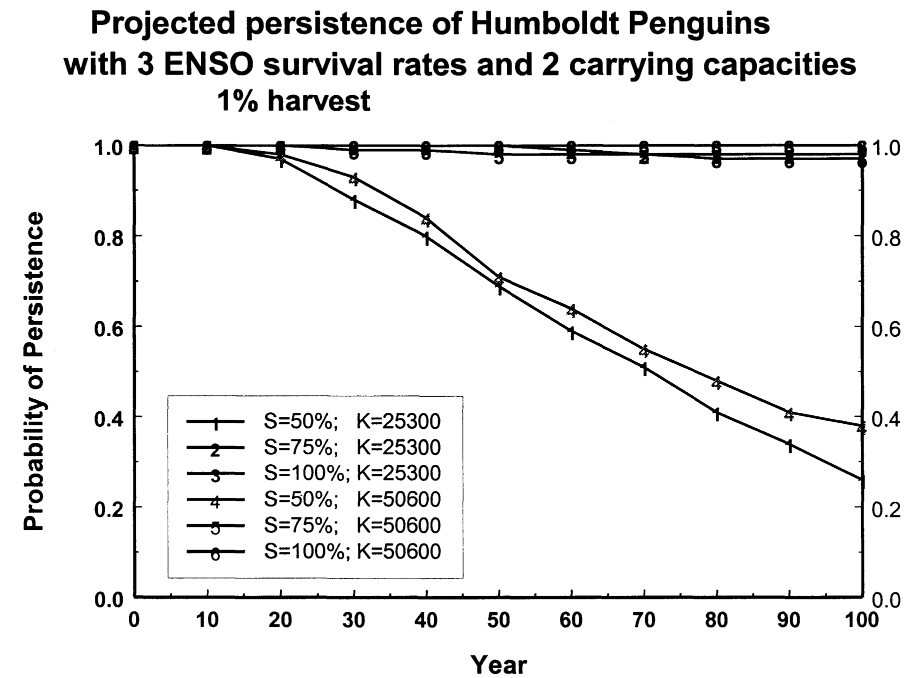

Figure 6. Probability of persistence of Humboldt penguins with 1% harvest, 50% (lines 1 & 4), 75% (lines 2 & 5), or 100% (lines 3 & 6) survival during El Niño years, no dispersal between populations, and carrying capacities of 25 300 (lines 1-3) or 50 600 (lines 4-6).

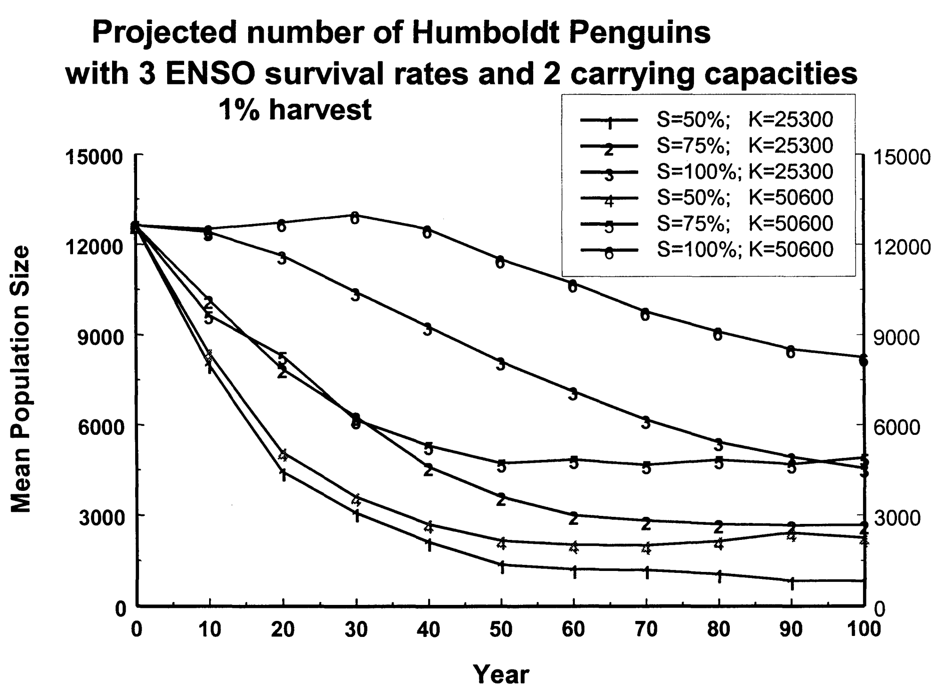

Figure 7. Projected population size of Humboldt penguins with 1% harvest, 50% (lines 1 & 4), 75% (lines 2 & 5), or 100% (lines 3 & 6) survival during El Niño years, no dispersal between populations, and carrying capacities of 25 300 (lines 1-3) or 50 600 (lines 4-6).

At the time of the PHVA workshop, it was not known what percent of the population had died in the recent ENSO event, and how many penguins remained. Preliminary observations suggested that about 50% of the penguins may have died and that current numbers may be about 12 000 to 15 000. However, it is possible that the population is substantially larger than had been estimated at the workshop. If penguins did not return to nesting sites in 1998, then a more accurate estimate of numbers would not be available until the census was completing in the following molting season. Simulations were therefore examined in which the initial numbers of penguins and the carrying capacities were set at double the levels in the initial models. Table 8 and Figures 8 and 9 show the results of these tests.

Table 8. Predictions for initial N = 25 300, K = 50 600, no dispersal.

Input parameters		Simulation results			
ENSO survival	Harvest	r (SD)	PE	TE	N
50%	1%	-0.080 (.291)	0.66	60	2338
75%		-0.004 (.121)	0.03	58	5178
100%		0.013 (.055)	0.00		9887
50%	3%	-0.170 (.423)	0.94	40	3421
75%		-0.045 (.203)	0.36	50	3140
100%		0.013 (.083)	0.00		6442
50%	5%	-0.280 (.561)	1.00	28	0
75%		-0.160 (.373)	0.89	37	1698
100%		-0.015 (.146)	0.14	59	4352

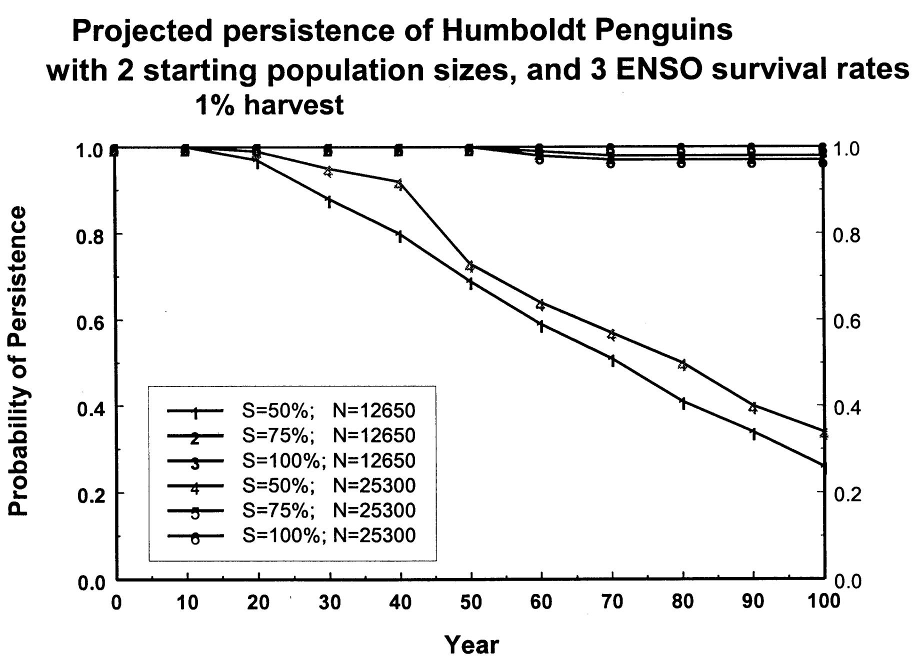

Figure 8. Probability of persistence of Humboldt penguins with 1% harvest, 50% (lines 1 & 4), 75% (lines 2 & 5), or 100% (lines 3 & 6) survival during El Niño years, no dispersal between populations, and initial population sizes of 12 650 (lines 1-3) or 25 300 (lines 4-6).

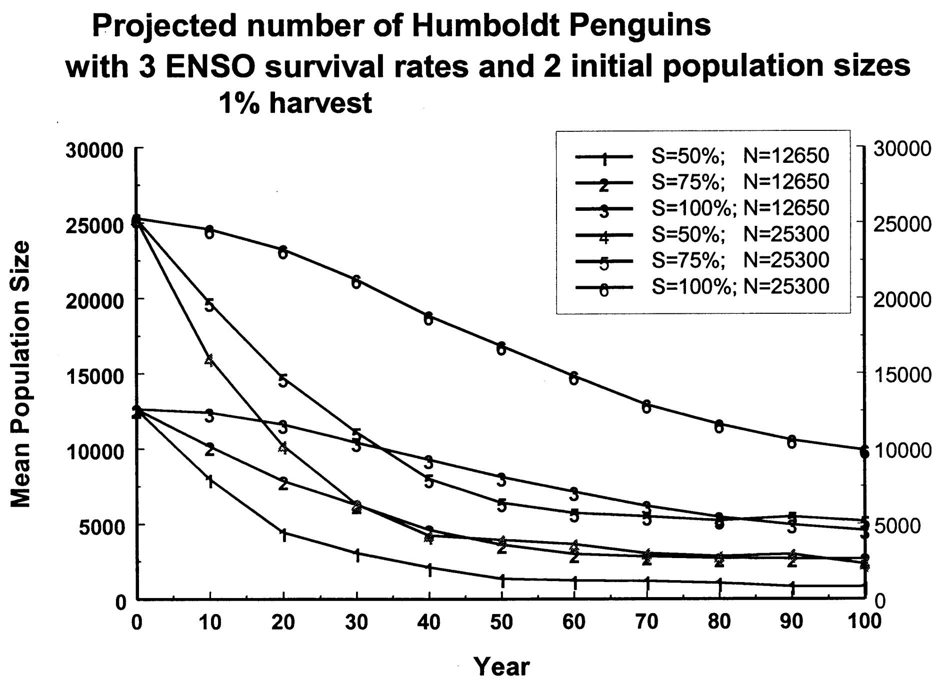

Figure 9. Projected population size of Humboldt penguins with 1% harvest, 50% (lines 1 & 4), 75% (lines 2 & 5), or 100% (lines 3 & 6) survival during El Niño years, no dispersal between populations, and initial population sizes of 12 650 (lines 1-3) or 25 300 (lines 4-6).

The higher initial numbers of penguins had little effect on the probabilities of persistence of Humboldt penguins, but did result in about double the numbers of penguins in those simulated populations which did not go extinct.

ADDITIONAL SIMULATIONS

The field studies from Peru and from Chile indicated a difference in the reproductive parameters between these populations, and the Vortex model incorporated these differences in the initial simulations. The field studies indicate that a greater percentage of the Peruvian females reproduce at least one chick each year (75% versus 50% for Chilean populations) and that the Peruvian birds were more successful at raising more than a single chick each year. As a result of these factors, the initial simulations showed that the Peruvian populations were much more likely to survive than the Chilean populations when all other factors were equal.

Testing the sensitivity of the model to changes in these reproductive factors then became important to understanding the long-term survival of the Chilean populations. In addition, another value for the impact of El Niño on adult survival was tested and a more optimistic value for the survival of the first age class was also tested.

Model Parameters for Additional Simulations:

The simulations modeled the populations using the following set of parameters:

Initial total population: 12 650. This is our best estimate of the current population and initial simulations did not indicate that this was an important factor in long-term survival of the populations.

Carrying capacity: 4 times initial population. This value leaves room for the populations to grow without exceeding the limitations of the Vortex software to track more than 62000 individuals.

Movement between populations: 0%. Field studies indicate that transfer of an adult penguin from one breeding population to another is probably an extremely rare event. Also, the initial simulations did not indicate that large movements between populations had a significant effect on population survival.

Harvest of adults (fishing net kills): 1%. While it was argued by some that the present harvest probably exceeds 1% of the population per year, this optimistic value was used simply because the initial simulations showed that the penguin populations cannot survive with a higher rate of harvest given our current best estimates of other factors.

Percentage of successful breeding females in the Chilean populations: Values of 50% and 60% were compared. Peruvian populations were unchanged (75% of female penguins produce at least 1 fledgling).

Adult Survival during El Niño: The initial population simulations had used adult survival values of 100%, 75% and 50% during an El Niño event. The pessimistic value of 50% had a severe impact on population growth. For the additional simulations, adult mortality during an El Niño event was modeled at 0%, 12.5 % and 25%. The rate of El Niño events and the impact on reproduction were left unchanged.

Mortality of first age class: Field studies have shown that mortality of fledged chicks is very high during the first year and a value of 80% mortality was used in the initial simulations. To assess the sensitivity of the population to this value, the Vortex software was also used to model populations with 75% mortality in this first age class.

Environmental variation in mortality of first age class: The last factor to be examined was the amount of variation in the mortality of the first age class. The initial simulations used a standard deviation of 10%, allowing the mortality in the first age class to randomly fluctuate over a range of values. The additional simulations included models with a standard deviation of 20%, giving more variation in the recruitment between years.

Results from Additional Simulations

The results of these additional analyses are presented in Table 9. Decreasing the average mortality in the first age class by only 5% had a very substantial positive effect on the population models. The probability of extinction dropped to zero in all the models, including those models where there was no change in breeding success of Chilean colonies and where El Niño events were associated with 25% mortality in adults. Increasing the variation in the mortality of this first age class had little effect indicating that the large amount of variation in recruitment that has been observed in field studies is probably having minimal impact on the long-term survival of this species.

Increasing the reproductive success of the Chilean populations by increasing the breeding females by 10% also made a positive difference in the population growth models. The probability of extinction was decreased compared to simulations where other factors were held constant. In general, total penguin numbers still declined over time, but for the models with the most optimistic values for adult survival during an El Niño event, the total population at 100 years was actually increased over current population estimates.

Table 9. Predictions for alternative values of percent breeding in Chilean populations, first year mortality, environmental variation in first year mortality, and survival during severe ENSO events. The % females breeding was set at 75% for the populations in Peru. Harvest rate (entanglement in fishing nets) was set at 1% for each of these scenarios.

Input parameters				Simulation results			
Chile: % breeding	1st year mortality	EV in 1st year mortality	ENSO survival	r (SD)	PE	TE	N
50%	80%	20%	75%	-0.004 (.144)	0.050	4175	79
		10%		0.002 (.127)	0.030	5434	78
		20%	87.5%	0.011 (.111)	0.000	5933	0
		10%		0.016 (.086)	0.000	6779	0
		20%	100%	0.018 (.084)	0.000	8402	0
		10%		0.021 (.059)	0.000	8158	0
60%		20%	75%	-0.006 (.144)	0.020	4601	66
		10%		0.001 (.119)	0.010	6436	69
		20%	87.5%	0.009 (.101)	0.000	8240	0
		10%		0.012 (.080)	0.000	9830	0
		20%	100%	0.020 (.070)	0.000	16581	0
		10%		0.019 (.046)	0.000	19992	0
50%	75%	20%	75%	0.017 (.138)	0.000	7497	0
		10%		0.020 (.124)	0.000	8110	0
		20%	87.5%	0.026 (.096)	0.000	13233	0
		10%		0.026 (.084)	0.000	11631	0
		20%	100%	0.029 (.062)	0.000	21751	0
		10%		0.029 (.045)	0.000	27441	0
60%		20%	75%	0.017 (.129)	0.000	13679	0
		10%		0.021 (.113)	0.000	18951	0
		20%	87.5%	0.027 (.085)	0.000	28101	0
		10%		0.026 (.076)	0.000	29819	0
		20%	100%	0.036 (.058)	0.000	40640	0
		10%		0.036 (.044)	0.000	47201	0

As would be expected, the models that combined increased reproductive success for Chilean penguins and decreased mortality in the first age class had the best predictions for the Humboldt penguin population. In all six of these models, the total number of birds at the end of the 100 year simulation was greater that the current population estimates. Whether it is possible to actually obtain these optimistic values for reproductive success and juvenile survival under the current conditions in Chile and

Peru is not known, but the evidence would indicate that population decline or growth is strongly linked to these two factors. These results must be combined with those from the initial simulations, which showed that harvesting of adult penguins (accidental deaths in fishing nets) could be a major factor in the decline of penguin populations.

DISCUSSION AND CONCLUSIONS

Populations of Humboldt penguins have been declining during the past decades. These declines could have resulted from a number of factors, including poor breeding, high nestling mortality, high rates of entanglement in fishing nets, or high mortality during El Niño years. After populations become small, it is also possible that the various processes which can destabilize small populations could cause acceleration of declines or prevent recovery. The modeling was conducted in order to help determine what factors may be contributing to the decline, to determine whether the populations are projected to continue to decline, to determine the stability of populations and vulnerability to extinction, and – most importantly – to determine what management and conservation actions might ensure the future of the species.

The analyses at the PHVA workshop found that the rates of reproductive success and survival estimated for the Chilean populations of Humboldt penguins would cause a steady decline in those populations, even in the absence impacts of ENSO events and harvest by humans (Table 1). Either increases in the percent of pairs successfully breeding each year or reduction in mortality is necessary to achieve positive population growth (Table 9). Under the better reproductive rates observed at Punta San Juan in Peru, that population would be expected to be able to grow in the absence of further threats.

If severe ENSO events cause 50% or even 25% mortality of penguins, then long-term population growth in the Peruvian populations would be slower (but still positive), the decline in Chilean populations would be faster (2.3%-4.4 % per year, in the absence of harvest by humans), and the species as a whole is projected to be in decline and vulnerable to extinction (Table 2; Figure 1). Improved breeding success would be needed to allow recovery of populations between El Niño years.

Intentional or unintentional killing of penguins by humans ("harvest") above a rate of about 1% per year was not generally sustainable in the simulated populations (Figures 2&3). Thus, at the present rates of killing which were viewed as likely by workshop participants, this human impact is projected to be causing (or accelerating) species decline, possibly leading toward ultimate extinction. If the average annual harvest is 5% or higher, the rate of species decline even in non-ENSO years is projected by be 2% per year (Table 2).

In many wildlife populations, dispersal among local breeding populations can stabilize an overall metapopulation even when some populations are not sustainable when isolated. It is believed that the rates of movement among colonies by Humboldt penguins is probably very low. Low rates of dispersal among populations had a modest benefit in some of the simulations, as penguins from growing populations (in Peru) might periodically supplement declining populations (in Chile) (Table 3&4; Figure 4). However, at rates of dispersal above 1% per year, the potentially growing populations may be depleted by losses of birds to the populations in decline, resulting in an overall decline of the species (Tables 5&6; Figures 4&5). Thus, high rates of dispersal among breeding colonies, it is occurred, would not effectively protect local populations from decline.

The number of Humboldt penguins that can be sustained with the presently available breeding and foraging habitat is not well known. However, even if there is abundant unoccupied habitat, the low reproductive success and high mortality would prevent the species from expanding to fill empty habitat (Table 7; Figures 6&7). Similarly, the actual numbers of Humboldt penguins is not precisely known, especially since the numbers that survived the recent severe ENSO event have not yet been determined. However, the simulation model shows that the species is at risk of decline and possible extinction, even if the actual numbers (and carrying capacity) are double what has been estimated (Table 8; Figures 8&9). The primary threats to the species are not random factors which can cause instability and extinction of small populations. Instead, over the long term, the present breeding rates are not sufficient to sustain population growth while there is high mortality of nestlings, of adults entangled in fishing nets, and of penguins during severe ENSO events.

In summary, predictions based on our best current estimate of various fecundity and mortality values in Humboldt penguin populations indicate a continued decline of this species with high probabilities of extinction of individual colonies and even the entire population in some cases. Reversing this trend could be best accomplished by management strategies that:

a) limit harvesting of adult penguins (accidental deaths in fishing nets) to less than 1%,
b) increase the reproductive success of Chilean penguin colonies and
c) increase survival during the first year of life.

Our ability to understand the threats to Humboldt penguins and to design effective management plans is hindered by uncertainty about breeding and mortality rates, the impacts of El Niño, the present population size, and the possible variation in demographic rates among breeding populations. While management actions are being taken to improve breeding and survival, further field surveys should be undertaken, so that future management decisions can be based on refined models of the population dynamics of the species.

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Population & Habitat Viability Assessment for the Humboldt Penguin (Spheniscus humboldti)

Olmüe, Chile
28 September - 1 October 1998

FINAL REPORT

Section 3

APPENDICES

Appendix I. Taxon Data Sheet from the Penguin CAMP (Ellis *et al.*, 1998).

Humboldt Penguin *Spheniscus humboldti*

STATUS: New IUCN Category: Vulnerable
Based on: C1, C2, E

CITES: Appendix I

Other: In Peru, governmental authorities consider that the Humboldt Penguin is in danger of extinction (Pulido 1991). In Chile the Humboldt Penguin is considered Vulnerable (CONAF 1988, Rottmann and López 1992, Araya and Bernal 1995). In the *Red List of Chilean Vertebrates* (CONAF 1988), surveys and studies for the protection of breeding islands are strongly recommended. Listed as Near Threatened in *Birds to Watch* 2, (Collar *et al.* 1994).

Taxonomic status: Species

Current Distribution:

Breeding: On the mainland coast and offshore islands of Chile and Peru mainly between Isla Foca (5°S) and Algarrobo (33° S). Araya and Todd (1987) reported a breeding site at Punihuil Islet, Chiloe Island (41° 55'S), extending the known breeding range to the south by ca. 900 kilometers.

For Peru, the most northerly breeding sites reported in 1996 were Punta Aguya (5° 41'S) and Isla Lobos de Tierra (6° 25'S). In total, there are more than 12 breeding sites in Perú.

According to Araya (1983) and Araya and Todd (1987) the northernmost known breeding site of Humboldt Penguins in Chile is located at a sea cave (Cueva del Caballo) a few kilometers north of Iquique (20° 21'S). There is information concerning a colony that existed until 1960 on Alacran island (18° 29'S), which is now connected to the mainland. There are also data suggesting 5 breeding sites between the Loa river (c. 21° S) and Caldera (c. 27° S), of which Algodonales Islet, Abtao Islet and Pan de Azúcar Island are the most important. Between Grande Island and Punihuil, a total of 12 colonies has been reported. There are no data on breeding colonies between Pupuya Islet and Punihuil islet. See Regional Populations, below, for more details.

Wintering: Humboldt Penguins occur in Chile from the Peruvian border in Arica (18° 20'S) to Punihuil. No updated information is available for Peru.

Concentrated Migration Regions: Humboldt Penguins are generally considered to be sedentary but there are recent data to refute this (Culik and Luna-Jorquera 1997a). These authors equipped non-breeding penguins from Pan de Azúcar Island with satellite transmitters and determined an extended migration route of about 700 km to northern Chile. Banding studies conducted by CONAF in 1995 indicated that juveniles from Pan de Azúcar yielded recoveries from Arica, about 750 km to the north, on the Peruvian border.

Banding studies being done at Algarrobo indicate that adult birds are dispersing to the north (50 km) and south (170 km).

Historical Distribution: The Humboldt Penguin is a "perfect example of endemism and ecological fitness. Its range is substantially the length of the coastline along which the Current (Humboldt) is in contact with the continent" (Murphy 1936). The northern limit of this species was Punta Aguja and Sechura Bay, with penguins migrating during certain seasons northward to the latitude of the Gulf of Guayaquil (ca. 3° S) (Murphy 1936). In Chile, Hellmayr (1932) and Murphy (1936) state that the breeding range of this species was from the Peruvian boundary south to Algarrobo (33° 21'S), Valparaiso, spreading in winter south to Corral (39° 50'S). Hellmayr (1932) reported a small island in Algarrobo (at present known as Isla Pájaros Niños) as the most southerly colony of this species. Johnson (1965) reported that this species occurs along the coast of Chile from Arica to Corral and nests from Pupuya islet northwards.

Extent of Occurrence: Recent studies using satellite transmitters (Culik and Luna-Jorquera 1997b) demonstrate that 90% of locations occurred within 35 km of their breeding islands (n = 5 birds). The area utilized at sea is larger than 3,800 km^2 = D

Area Occupied: Assuming that around every breeding location a 35 km radius (see Extent of Occurrence, above) may be exploited, each breeding island allows birds to exploit an area of 3800 km^2 **=** D.

Number of Locations: For Peru, the data summarized by Duffy *et al.* (1984), indicate that in 1981 there were 17 breeding sites. Today only two important breeding colonies are reported: Punta San Juan and Pachacamac. In Chile, there are at least 14 breeding sites (see table 1). Of these, 13 are islands and islets and only one is a breeding site on the mainland (a sea cave). Note that for four of these sites, there are no recent observations. For northern Chile there are about 21 non-breeding sites.

Population Trends - % Change in Years or Generations: In Peru, the population was estimated to be 9,000 birds in 1981 (Duffy *et al.* 1984). The latest estimate (1996) is of 5,500 birds (Riveros Salcedo).

In Chile, in 1982 there were 10,000-12,000 birds. After the 1982-83 El Niño, the population decreased to 3080 birds. In the last census done by Araya (unpubl. data) in 1995-96, the population was conservatively estimated to be about 7500 birds.

In general, it seems that the population is continuing to decline. Between 1980 - 81 **(**pre 1982 - 1983 ENSO event) and the present, there has been an overall drop of 35% in 15 years. There is some discrepancy in the information provided by the Contributors; this is probably due to different time of the years in which the surveys were made. An extensive data base collected by CONAF for Pan de Azúcar Islands and observations made by several researchers (B. Culik, C. Guerra, G. Luna-Jorquera), has shown that great fluctuations occurred in the numbers of birds on the colony, decreasing to c. 50% in winter with respect to the summer.

Trend over past 100 years: Murphy (1936) reported that at one time, presumably pre-twentieth century, islands off the West coast of South America had their "crusts (presumably referring to the guano cap) as full of penguins as a Cheddar is of skippers". Raimondi (1856) (cited in Murphy 1936) described how, in the middle of the nineteenth century, Humboldt Penguins abounded on the south island of the Chincha group. While neither report was able to give figures, it is clear that Humboldt Penguins once were extremely numerous in the Humboldt upwelling region. It is thus not unreasonable to assume that the Humboldt Penguin world population in the middle of the nineteenth century could have been in excess of a million birds.

By the time Murphy published his work in 1936, the population decline of penguins was already very evident. Murphy reported that the hundred or more Peruvian islets are "periodically allowed to become merely ankle-deep in new guano before they are again swept clean. The breeding penguins must resort, therefore, to precarious nesting sites." Murphy stated that by 1936 the penguin population had undergone a vast decline.

Generation Time: Humboldt Penguins need 3-4 years to reach sexual maturity (Guerra and Oyarzo 1992). The mean life span of Humboldt Penguins in the wild is unknown.

For Humboldt Penguins in captivity in North America, males breed as early as 2 years of age and 3 years of age for females. The oldest documented breeding is 30 for males and 25 for females. The average age of adults in the population in captivity is 12 years.

World Population: Consideration of the data from most recent censuses (Chile - Table 1 and Peru - Table 2), would indicate a world population of ca. 13,000 birds. NOTE: In some cases surveyors have based their numbers upon nests, and others on counts of individual birds.

Recent Field Studies:

Peru:

Carlos Zavalaga and Rosana Paredes (1997) are conducting work on the breeding biology and foraging ecology of birds from Punta San Juan.

J.C. Riveros Salcedo is conducting a long term survey on different colonies along the Peruvian coast evaluating the status of the seabirds, including the Humboldt Penguin.

Chile:

Since 1980, Braulio Araya and Mariano Bernal (1995) have been conducting a yearly census on the main Humboldt Penguin colonies along the Chilean coast.

Between 1988 and 1991 the Chilean Forest Service (CONAF, Corporación Nacional Forestal) conducted a survey on the conservation of the Humboldt Penguin at Pan de Azucar National Park (Hector Oyarzo). Final results are available (in Spanish) in the CONAF III Region (*Copiaeo*).

During August and March 1992, Yerko Vilina conducted a study on the reproductive biology of the Humboldt Penguin at Chanaral Island (Vilina 1993). Arturo Mann studied the parasite fauna of the Humboldt Penguin at Cachagua Islet. Ecto- and endoparasites were described (Mann 1992).

Since January 1995 Mariano Bernal and Alejandro Simeone (Valdivia, Chile) have been conducting a survey on dynamics and resource partitioning among Humboldt Penguins, Chilean Brown Pelicans and Kelp Gulls during the breeding season at Pájaro Niño Islet, Algarrobo.

Since 1990, Javiera Meza, CONAF V Región, Valparaiso, has been censusing the colony at Cachagua Islet. During 1990 and 1991, Carlos Guerra conducted a study on the effects of summer and winter nesting on selected life history parameters of Humboldt Penguins from Pan de Azucar Island (Guerra and Oyarzo 1992). Since 1993, Roberto Aguilar (Univerisdad de Antofagasta, Chile) has been conducting a post-doctoral study on the physiology of embryos and their growth rate in captivity.

Since 1993, Boris Culik (Kiel, Germany) and Guillermo Luna-Jorquera have been conducting ecophysiological, bioenergetic and behavioral studies of penguins at sea on birds from Pan de Azucar Island. Since 1994, E. Diebold *et al.* (1994) of the Milwaukee County Zoo together with Chilean researchers (B. Araya, A Simeone and M. Bernal) have been conducting a long term survey on the colony of penguins at Pájaros Niños Islet. The main goal is to enhance the conservation of Humboldt Penguin in the wild and in captivity (see Diebold *et al.* 1994).

Table 1. Regional populations of Humboldt Penguin in Chile (breeding individuals)

Locality	1980-82	1983	1984	1985	1986	1987	1988	1988-89	1990	1995-96	1996	Source
Cueva del Caballo (20°12'S)	-	-	-	-	-	-	16§	-	-	-	-	-
Isla Pan de Azucar (26°09'S)	6000	-	131	2500	2570	-	4000*	600	1000	1750	-	1
Isla Grande (27°15'S)	58	-	-	-	-	34§	-	-	-	40	-	1
Isla Cima Cuadrada (27°41'S)	-	180	-	-	-	-	-	-	-	-	-	1
Isla de Chañaral (29°01'S)	750	-	146	6000	1000	-	-	788	1500	2500	-	1
Isla Choros (29°15'S)	96	-	32	-	-	14§	-	-	-	50	-	1
Isla Pájaros (29°35'S)	624	-	-	-	-	54§	-	880	-	1000	-	1
Isla de los Huevos (31°55'S)	60	-	64	274	-	34§	-	-	-	120	-	1
Islote Papudo (32°30'S)	-	100	-	-	-	-	-	-	-	-	-	-
Islote Cachagua (32°35'S)	1000	-	1055	-	-	-	-	-	2030	2000	-	1
Islote Concón (32°52'S)	250-500	-	12	-	100	46§	-	12	10	20	-	1
Ex Isla Pájaro Niño (33í21'S)	-	-	530	1000	2000	-	-	-	-	200	1600	1
Islote Pupuya (34°00'S)	-	14$	-	-	-	-	-	-	-	-	-	-
Islote Puñihuil (41°55'S)	-	-	-	12	-	-	-	-	-	50	-	1
Total	9088	294	1970	9786	5670	182	4016	2280	4540	7730	1600	
Est. Total	10-12000	300	3080	10000	5-6000	200	400	3000	4500	7500	1600	

1 B. Araya and M. Bernal compiled from their data for this CAMP. Data quality 1 and 2. * Oyarzo and Correa 1988. Data quality 2. # A. Simeone (unpublished data) Data quality 1 § Araya and Todd 1987. Data quality 1 $ Araya 1983. Data quality 3.

Table 2. Regional populations of Humboldt Penguin in Peru (breeding individuals)

Localities	Mar 1981*	Jul 1981*	1996	Source
Punta Aguja (05°41'S)	-	-	10	1
Isla Lobos de Tierra (06°25'S)	900	-	100	1
Isla Macabi (07°47'S)	-	-	15	1
Isla Mazorca (11°22'S)	120	8	100	1
Isla Pachacamac (12°17'S)	750	320	800	1
Isla Chincha Centro (13°39'S)	-	-	50	1
Isla Ballestas (13°44'S)	8	9	60	1
Isla San Gallan (13°50'S)	-	111	60	1
Punta Arquillo (13°52'S)	-	-	50	1
La Vieja (14°17'S)	-	8	-	-
Pta. San Fernando (15°08'S)	-	-	500	1
Punta San Juan (15°21'S)	2220	2000	3400	2
Punta Pampa Redonda (15°50'S)	300	0	-	-
Punta La Chira (16°29'S)	-	-	300	1
Isla Hornillos (16°52'S)	-	-	60	1
Santa Rosa (19°19'S)	-	0	-	-
21 Islands and headlands	4770	-	-	-
11 Islands and Headlands	-	2608	-	-
Total	9068	5064	5505	
Estimated Total	9000	5500		

1 J.C. Riveros Salcedo compiled for this CAMP. Data quality 1 and 2.
2 C. Zavalaga and R. Paredes for this CAMP. Data quality 1. * Data from Duffy *et al.* 1984

Threats:

1. Climate. Heavy rain in some regions where it is not common, causes nest desertion with total loss of eggs and/or chicks (this is independent of rains due to El Niño).

2. Decline in prey species. over-fishing resulting in a drop in prey availability (last year in Chile the total catch was 8,000,000 metric tons).

3. Drowning. A number of Humboldt Penguin are being caught by fishermen in gill nets in some localities such as Punta San Juan, Peru (Boersma and Stokes 1995), central Chile (Simeone *et al.* 1996), and northern Chile.

4. Hunting for human consumption. Adults have been hunted and eggs collected for human consumption and baiting purposes (Schlatter 1984, Vilina *et al.* 1995). Egg collection by fishermen and tourist activities also provoke nest desertion (Araya and Todd 1987, Vilina 1993).

5. Human interference due to tourism and disruptive effects derived from scientific work and ringing activities (see Luna-Jorquera *et al.* 1996).

6. Loss of habitat due to guano exploitation.

7. Marine perturbations because of El Niño.

The following secondary threats were also detected: Interspecific competition with pelicans.

1. Predation. Araya (1983) and Schlatter (1984) have reported predation by rats. There is also an historical record from Araya and Duffy (1987) on predation by foxes introduced to Chañaral Island. At Pájaros Niños Islet, which has been linked to the mainland for about 20 years, there are some feral cats that probably prey on chicks and juveniles (Simeone, pers. obs.).

2. Pollution attributable to increasing mining, industrial activities and problems derived from urbanization and inadequate planning of growing human activities (recreation, tourism, etc.).

Trade: No current trade. Araya (1983) reported information given by local fishermen and sailors that accounts for the capture of about 40 birds from North of Chile for export (probably illegal trade). In addition, Hays (1985) estimated that 9264 Humboldt Penguins have been exported to several zoos in the world within a period of 32 years. This does not include birds that died during capture and transport. Exportation is now prohibited from Perú and Chile (Williams 1995, Simeone 1996).

Comments: El Niño must be considered a main marine perturbation for the Humboldt Penguin (Araya and Todd 1987, Arntz and Valdivia 1985). Although El Niño causes breeding failure and high mortality among the seabirds (Tovar and Cabrera 1985), there is evidence to suggest that this phenomenon exerts a selection pressure on the seabird population, favoring the ability to increase rapidly in numbers after each event (Schreiber and Schreiber 1984). Nevertheless, since the sixties, the commercial fishery for anchovies has been in competition with the guano birds and, through overexploitation, has reduced the anchovy population and its availability to the seabirds (Tovar and Cabrera 1985). Recent research suggests that Humboldt Penguins have to work hard in order to obtain food, even during non-El Niño years (Culik and Luna-Jorquera 1997b).

Recommendations:

1. Convene a PHVA Workshop in Chile in 1998 (note: planned for November 1998 in Olmüe). Strive for maximum participation from key agencies associated with wildlife management in Perú and Chile.*

2. A complete population assessment as soon as possible and the timing and methodology used for this assessment must be standardized (e.g., count molting birds).

3. Protection of breeding locations and enforcement of existing legislation where these penguins breed should be given high priority, including improved funding and support of wardens charged with enforcing regulations. In Peru, the harvest of guano must be regulated in order to preserve nesting habitat and reduce disturbance during the nesting seasons. Improved predator control at mainland sites, including maintenance of predator enclosure systems.

4. Support conservation-oriented research including patterns of reproductive success, recruitment into the breeding population, studies of foraging ecology, and studies of migratory behavior.

5. Genetic studies to determine whether Humboldt Penguins from the distributional area have the same genetic background and whether there is continuous mixing of the population.

6. Marine reserves should be created around the major breeding colonies.

7. Establish conservation education programs oriented at reducing hunting pressure and by-catch.

8. Husbandry research in order to stabilize captive populations and preclude the need to remove birds from the wild. The long term intention of captive propagation should be to reintroduce juveniles into secure sites in the wild, particularly where local extinction might occur (pending results of PHVA).

9. Investigate incidence of potential hybridization with Magellanic Penguins where the species' ranges overlap.

10. Reduce fish harvests during ENSO events.

11. Recommend enhanced industrial and mining waste treatment efforts in coastal regions where the species occurs.

*A symposium and round table discussion on the ecology and conservation of penguins in Chile was held on 13 November 1997 in Santiago, Chile, concentrating on the Humboldt penguin (Simeone 1998).

PHVA: Yes

Captive Program Recommendation - Pending. A decision regarding a captive program will depend upon further data from a PHVA. Captive programs for Humboldt Penguins already exist at several zoos and aquaria in the USA, Europe and Japan. The aim of this program must be to manage a population sufficient so as to preserve 90% or more of the genetic diversity of the overall population for a minimum of 100 years. Consequently, it is not necessary to remove new birds from the wild in the future but a complete estimation of the numbers of birds existing in captivity is highly recommended.

Level of Difficulty: There are data on aspergillosis in Humboldt Penguins maintained in captivity and problems with temperature and humidity inside the nests. Nutritional factors may affect mortality of parent-reared chicks. Consequently a moderate difficulty (level 2) is appropriate for Humboldt Penguin.

Existing Captive Population: According to Simeone (1996) there were at least 2,202 captive birds in 1994: 226 in North America, 947 in Europe, and 1029 in Japan. The members of genus *Spheniscus* have shown propensity to hybridize in captivity (del Hoyo 1992). Genetics studies should be conducted.

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Appendix III. Problems issues and themes affecting the conservation of the Humboldt Penguin in Chile and Perú. The list was compiled by the workshop participants; each problem having equal weighting. A small group organized these into the themes below.

Conservation and Habitat Management

- Guano extraction
- Protection against terrestrial predators
- Better protection of nest sites in central Chile
- Habitat protection (including ecotourism)
- Reduction of nesting habitat
- Habitat management (3)
- Habitat conservation
- Destruction of nesting habitat and the lack of adequate sites (2)
- Management of nesting habitat

Fisheries Interactions

- Incidental captures in artesanal fishing nets (3)
- Fisheries (2)
- Entanglement (3)
- Interactions with fisheries
- Interaction between fisheries actgivities and feeding behavior
- Illegal capture

Research and Monitoring

- Areas of dispersal and juvenile feeding
- Determination of causes of mortality
- Genetic exchange between colonies
- Emigration of adults and juveniles
- Increased studies of bioenergetics, and dietary requirements
- Determination of factors affecting reproductive success
- Survival/mortality of juveniles and adults (more data)
- Exahange of veterinary information to improve actions of rescue centers and to form them
- Juvenile dispersal in the sea
- Lack of studies about population dynamics
- Research into areas or factgors that limit survival
- Monitoring and census of populations
- Methods and standard techniques to census populations
- Monitoring of changes in adult mortality
- Research
- Disease
- Oiling events

Legislation

- Lack of interest by governmental authorities
- Execution/enforcement of laws that protect the Humboldt penguin (2)
- Legal means for the protection and creation of marine reserves
- legislation

Education

- Education, information, public relations
- Public sensitization
- Public education to protect penguins
- Conservation education (3)
- Education in fishing communities
- Communication of integrated research
- Sensitivity of local populations
- Education of human populations near nesting areas
- Help of NGOs in penguin protection

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Appendix IV. VORTEX REFERENCE

VORTEX: A Computer Simulation Model for Population Viability Analysis

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Abstract

Population Viability Analysis (PVA) is the estimation of extinction probabilities by analyses that incorporate identifiable threats to population survival into models of the extinction process. Extrinsic forces, such as habitat loss, over-harvesting, and competition or predation by introduced species, often lead to population decline. Although the traditional methods of wildlife ecology can reveal such deterministic trends, random fluctuations that increase as populations become smaller can lead to extinction even of populations that have, on average, positive population growth when below carrying capacity. Computer simulation modelling provides a tool for exploring the viability of populations subjected to many complex, interacting deterministic and random processes. One such simulation model, VORTEX, has been used extensively by the Captive Breeding Specialist Group (Species Survival Commission, IUCN), by wildlife agencies, and by university classes. The algorithms, structure, assumptions and applications of VORTEX are described in this paper.

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, to determine the number of progeny produced by each female each year, and to determine which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Fecundity is assumed to be independent of age after an animal reaches reproductive age. Mortality rates are specified for each pre-reproductive age–sex class and for reproductive-age animals. Inbreeding depression is modelled as a decrease in viability in inbred animals.

The user has the option of modelling density dependence in reproductive rates. As a simple model of density dependence in survival, a carrying capacity is imposed by a probabilistic truncation of each age class if the population size exceeds the specified carrying capacity. VORTEX can model linear trends in the carrying capacity. VORTEX models environmental variation by sampling birth rates, death rates, and the carrying capacity from binomial or normal distributions. Catastrophes are modelled as sporadic random events that reduce survival and reproduction for one year. VORTEX also allows the user to supplement or harvest the population, and multiple subpopulations can be tracked, with user-specified migration among the units.

VORTEX outputs summary statistics on population growth rates, the probability of population extinction, the time to extinction, and the mean size and genetic variation in extant populations.

VORTEX necessarily makes many assumptions. The model it incorporates is most applicable to species with low fecundity and long lifespans, such as mammals, birds and reptiles. It integrates the interacting effects of many of the deterministic and stochastic processes that have an impact on the viability of small populations, providing opportunity for more complete analysis than is possible by other techniques. PVA by simulation modelling is an important tool for identifying populations at risk of extinction, determining the urgency of action, and evaluating options for management.

Introduction

Many wildlife populations that were once widespread, numerous, and occupying contiguous habitat, have been reduced to one or more small, isolated populations. The causes of the original decline are often obvious, deterministic forces, such as over-harvesting,

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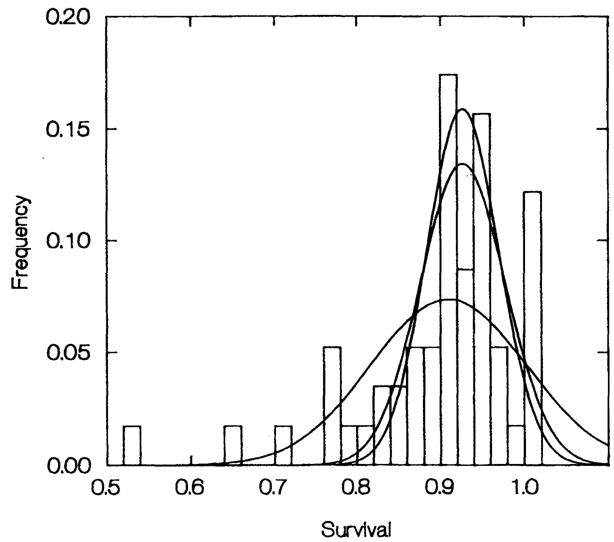

Fig. 1. Frequency histogram of the proportion of whooping cranes surviving each year, 1938–90. The broadest curve is the normal distribution that most closely fits the overall histogram. Statistically, this curve fits the data poorly. The second highest and second broadest curve is the normal distribution that most closely fits the histogram, excluding the five leftmost bars (7 outlier 'catastrophe' years). The narrowest and tallest curve is the normal approximation to the binomial distribution expected from demographic stochasticity. The difference between the tallest and second tallest curves is the variation in annual survival due to environmental variation.

hurricanes, large-scale fires, and floods are outliers in the distribution of environmental variation (e.g. five leftmost bars on Fig. 1). As a result, they have quantitatively and sometimes qualitatively different impacts on wildlife populations. (A forest fire is not just a very hot day.) Such events often precipitate the final decline to extinction (Simberloff 1986, 1988). For example, one of two populations of whooping crane was decimated by a hurricane in 1940 and soon after went extinct (Doughty 1989). The only remaining population of the black-footed ferret (*Mustela nigripes*) was being eliminated by an outbreak of distemper when the last 18 ferrets were captured (Clark 1989).

Genetic drift is the cumulative and non-adaptive fluctuation in allele frequencies resulting from the random sampling of genes in each generation. This can impede the recovery or accelerate the decline of wildlife populations for several reasons (Lacy 1993). Inbreeding, not strictly a component of genetic drift but correlated with it in small populations, has been documented to cause loss of fitness in a wide variety of species, including virtually all sexually reproducing animals in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1981; O'Brien and Evermann 1988; Ralls *et al.* 1988; Lacy *et al.* 1993). Even if the immediate loss of fitness of inbred individuals is not large, the loss of genetic variation that results from genetic drift may reduce the ability of a population to adapt to future changes in the environment (Fisher 1958; Robertson 1960; Selander 1983).

Thus, the effects of genetic drift and consequent loss of genetic variation in individuals and populations have a negative impact on demographic rates and increase susceptibility to environmental perturbations and catastrophes. Reduced population growth and greater fluctuations in numbers in turn accelerate genetic drift (Crow and Kimura 1970). These synergistic destabilising effects of stochastic process on small populations of wildlife have been described as an 'extinction vortex' (Gilpin and Soulé 1986). The size below which a population is likely to be drawn into an extinction vortex can be considered a 'minimum with extinction, undergoing modification with each application to allow incorporation of additional threatening processes. The simulation program was renamed VORTEX (in reference to the extinction vortex) when the capability of modelling genetic processes was implemented in 1989. In 1990, a version allowing modelling of multiple populations was briefly named VORTICES. The only version still supported, with all capabilities of each previous version, is VORTEX Version 5.1.

VORTEX has been used in PVA to help guide conservation and management of many species, including the Puerto Rican parrot (*Amazona vittata*) (Lacy *et al.* 1989), the Javan rhinoceros (*Rhinoceros sondaicus*) (Seal and Foose 1989), the Florida panther (*Felis concolor coryi*) (Seal and Lacy 1989), the eastern barred bandicoot (*Perameles gunnii*) (Lacy and Clark 1990; Maguire *et al.* 1990), the lion tamarins (*Leontopithecus rosalia* ssp.) (Seal *et al.* 1990), the brush-tailed rock-wallaby (*Petrogale penicillata penicillata*) (Hill 1991), the mountain pygmy-possum (*Burramys parvus*), Leadbeater's possum (*Gymnobelideus leadbeateri*), the long-footed potoroo (*Potorous longipes*), the orange-bellied parrot (*Neophema chrysogaster*) and the helmeted honeyeater (*Lichenostomus melanops cassidix*) (Clark *et al.* 1991), the whooping crane (*Grus americana*) (Mirande *et al.* 1993), the Tana River crested mangabey (*Cercocebus galeritus galeritus*) and the Tana River red colobus (*Colobus badius rufomitratus*) (Seal *et al.* 1991), and the black rhinoceros (*Diceros bicornis*) (Foose *et al.* 1992). In some of these PVAs, modelling with VORTEX has made clear the insufficiency of past management plans to secure the future of the species, and alternative strategies were proposed, assessed and implemented. For example, the multiple threats to the Florida panther in its existing habitat were recognised as probably insurmountable, and a captive breeding effort has been initiated for the purpose of securing the gene pool and providing animals for release in areas of former habitat. PVA modelling with VORTEX has often identified a single threat to which a species is particularly vulnerable. The small but growing population of Puerto Rican parrots was assessed to be secure, except for the risk of population decimation by hurricane. Recommendations were made to make available secure shelter for captive parrots and to move some of the birds to a site distant from the wild flock, in order to minimise the damage that could occur in a catastrophic storm. These recommended actions were only partly implemented when, in late 1989, a hurricane killed many of the wild parrots. The remaining population of about 350 Tana River red colobus were determined by PVA to be so fragmented that demographic and genetic processes within the 10 subpopulations destabilised population dynamics. Creation of habitat corridors may be necessary to prevent extinction of the taxon. In some cases, PVA modelling has been reassuring to managers: analysis of black rhinos in Kenya indicated that many of the populations within sanctuaries were recovering steadily. Some could soon be used to provide animals for re-establishment or supplementation of populations previously eliminated by poaching. For some species, available data were insufficient to allow definitive PVA with VORTEX. In such cases, the attempt at PVA modelling has made apparent the need for more data on population trends and processes, thereby helping to justify and guide research efforts.

Description of VORTEX

Overview

The VORTEX computer simulation model is a Monte Carlo simulation of the effects of deterministic forces, as well as demographic, environmental and genetic stochastic events, on wildlife populations. VORTEX models population dynamics as discrete, sequential events that occur according to probabilities that are random variables, following user-specified distributions. The input parameters used by VORTEX are summarised in the first part of the sample output given in the Appendix.

VORTEX simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modelled as binomial distributions. Environmental variation in carrying capacity is modelled as a normal distribution. The variance across years in the frequencies of births and deaths resulting from the simulation model (and in real populations) will have two components: the demographic variation resulting from a binomial sampling around the mean for each year, and additional fluctuations due to environmental variation and catastrophes (see Fig. 1 and section on The Dynamics of Small Populations, above).

Data on annual variations in birth and death rates are important in determining the probability of extinction, as they influence population stability (Goodman 1987). Unfortunately, such field information is rarely available (but see Fig. 1). Sensitivity testing, the examination of a range of values when the precise value of a parameter is unknown, can help to identify whether the unknown parameter is important in the dynamics of a population.

Catastrophes

Catastrophes are modelled in VORTEX as random events that occur with specified probabilities. Any number of types of catastrophes can be modelled. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors by 50% for the year. Such a catastrophe would be modelled as a random event with 0·02 probability of occurrence each year, and severity factors of 0·75 for survival and 0·50 for reproduction.

Genetic Processes

Genetic drift is modelled in VORTEX by simulation of the transmission of alleles at a hypothetical locus. At the beginning of the simulation, each animal is assigned two unique alleles. Each offspring is randomly assigned one of the alleles from each parent. Inbreeding depression is modelled as a loss of viability during the first year of inbred animals. The impacts of inbreeding are determined by using one of two models available within VORTEX: a Recessive Lethals model or a Heterosis model.

In the Recessive Lethals model, each founder starts with one unique recessive lethal allele and a unique, dominant non-lethal allele. This model approximates the effect of inbreeding if each individual in the starting population had one recessive lethal allele in its genome. The fact that the simulation program assumes that all the lethal alleles are at the same locus has a very minor impact on the probability that an individual will die because of homozygosity for one of the lethal alleles. In the model, homozygosity for different lethal alleles are mutually exclusive events, whereas in a multilocus model an individual could be homozygous for several lethal alleles simultaneously. By virtue of the death of individuals that are homozygous for lethal alleles, such alleles would be removed slowly by natural selection during the generations of a simulation. This reduces the genetic variation present in the population relative to the case with no inbreeding depression, but also diminishes the subsequent probability that inbred individuals will be homozygous for a lethal allele. This model gives an optimistic reflection of the impacts of inbreeding on many species, as the median number of lethal equivalents per diploid genome observed for mammalian populations is about three (Ralls *et al.* 1988).

The expression of fully recessive deleterious alleles in inbred organisms is not the only genetic mechanism that has been proposed as a cause of inbreeding depression. Some or

Migration among Populations

VORTEX can model up to 20 populations, with possibly distinct population parameters. Each pairwise migration rate is specified as the probability of an individual moving from one population to another. This probability is independent of the age and sex. Because of between-population migration and managed supplementation, populations can be recolonised. VORTEX tracks the dynamics of local extinctions and recolonisations through the simulation.

Output

VORTEX outputs (1) probability of extinction at specified intervals (e.g., every 10 years during a 100-year simulation), (2) median time to extinction if the population went extinct in at least 50% of the simulations, (3) mean time to extinction of those simulated populations that became extinct, and (4) mean size of, and genetic variation within, extant populations (see Appendix and Lindenmayer *et al.* 1993).

Standard deviations across simulations and standard errors of the mean are reported for population size and the measures of genetic variation. Under the assumption that extinction of independently replicated populations is a binomial process, the standard error of the probability of extinction (SE) is reported by VORTEX as

$$SE(p) = \sqrt{[p \times (1-p)/n]}\ ,$$

in which the frequency of extinction was p over n simulated populations. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Availability of the VORTEX Simulation Program

VORTEX Version 5.1 is written in the C programming language and compiled with the Lattice 80286C Development System (Lattice Inc.) for use on microcomputers using the MS-DOS (Microsoft Corp.) operating system. Copies of the compiled program and a manual for its use are available for nominal distribution costs from the Captive Breeding Specialist Group (Species Survival Commission, IUCN), 12101 Johnny Cake Ridge Road, Apple Valley, Minnesota 55124, U.S.A. The program has been tested by many workers, but cannot be guaranteed to be error-free. Each user retains responsibility for ensuring that the program does what is intended for each analysis.

Sequence of Program Flow

(1) The seed for the random number generator is initialised with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for input and output devices, population parameters, duration of simulation, and number of interations.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as

$$N_{max} = (K + 3s) \times (1 + L)$$

in which K is the maximum carrying capacity (carrying capacity can be specified to change linearly for a number of years in a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size. It is theoretically possible, but very unlikely, that a simulated population will exceed the calculated N_{max}. If this occurs then the program will give an error message and abort.

populations studied intensively have shown deleterious effects of inbreeding on a variety of fitness components (Wright 1977; Falconer 1981). Each of the two models of inbreeding depression may also be optimistic, in that inbreeding is assumed to have an impact only on first-year survival. The Heterosis option allows, however, for the user to specify the severity of inbreeding depression on juvenile survival.

(10) Years are iterated via steps 11–25 below.

(11) The probabilities of females producing each possible litter size are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percentage of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates for their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) of the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for linear changes over time. Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of breeding-age males specified to be breeding.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified sex ratio at birth. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) If the Heterosis option is chosen for modelling inbreeding depression, the genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between a new animal, A, and another existing animal, B is

$$f_{AB}=0{\cdot}5\times(f_{MB}+f_{PB})$$

in which f_{ij} is the kinship between animals i and j, M is the mother of A, and P is the father of A. The inbreeding coefficient of each animal is equal to the kinship between its parents, $F=f_{MP}$, and the kinship of an animal to itself is $f_{AA}=0{\cdot}5\times(1+F)$. [See Ballou (1983) for a detailed description of this method for calculating inbreeding coefficients.]

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If the Heterosis model of inbreeding depression is used and an individual is inbred, the survival probability is multiplied by e^{-bF} in which b is the number of lethal equivalents per haploid genome.

(4) The life-history attributes of a population (birth, death, migration, harvesting, supplementation) are modelled as a sequence of discrete and therefore seasonal events. However, such events are often continuous through time and the model ignores the possibility that they may be aseasonal or only partly seasonal.

(5) The genetic effects of inbreeding on a population are determined in VORTEX by using one of two possible models: the Recessive Lethals model and the Heterosis model. Both models have attributes likely to be typical of some populations, but these may vary within and between species (Brewer *et al.* 1990). Given this, it is probable that the impacts of inbreeding will fall between the effects of these two models. Inbreeding is assumed to depress only one component of fitness: first-year survival. Effects on reproduction could be incorporated into this component, but longer-term impacts such as increased disease susceptibility or decreased ability to adapt to environmental change are not modelled.

(6) The probabilities of reproduction and mortality are constant from the age of first breeding until an animal reaches the maximum longevity. This assumes that animals continue to breed until they die.

(7) A simulated catastrophe will have an effect on a population only in the year that the event occurs.

(8) Migration rates among populations are independent of age and sex.

(9) Complex, interspecies interactions are not modelled, except in that such community dynamics might contribute to random environmental variation in demographic parameters. For example, cyclical fluctuations caused by predator–prey interactions cannot be modelled by VORTEX.

Discussion

Uses and Abuses of Simulation Modelling for PVA

Computer simulation modelling is a tool that can allow crude estimation of the probability of population extinction, and the mean population size and amount of genetic diversity, from data on diverse interacting processes. These processes are too complex to be integrated intuitively and no analytic solutions presently, or are likely to soon, exist. PVA modelling focuses on the specifics of a population, considering the particular habitat, threats, trends, and time frame of interest, and can only be as good as the data and the assumptions input to the model (Lindenmayer *et al.* 1993). Some aspects of population dynamics are not modelled by VORTEX nor by any other program now available. In particular, models of single-species dynamics, such as VORTEX, are inappropriate for use on species whose fates are strongly determined by interactions with other species that are in turn undergoing complex (and perhaps synergistic) population dynamics. Moreover, VORTEX does not model many conceivable and perhaps important interactions among variables. For example, loss of habitat might cause secondary changes in reproduction, mortality, and migration rates, but ongoing trends in these parameters cannot be simulated with VORTEX. It is important to stress that PVA does not predict in general what will happen to a population; PVA forecasts the likely effects only of those factors incorporated into the model.

Yet, the use of even simplified computer models for PVA can provide more accurate predictions about population dynamics than the even more crude techniques available previously, such as calculation of expected population growth rates from life tables. For the purpose of estimating extinction probabilities, methods that assess only deterministic factors are almost certain to be inappropriate, because populations near extinction will commonly be so small that random processes dominate deterministic ones. The suggestion by Mace and Lande (1991) that population viability be assessed by the application of simple rules (e.g., a taxon be considered Endangered if the total effective population size is below 50 or the mation of consistency, both deterministic calculations and the simulation model project an over-wintering population of whooping cranes consisting of 12% juveniles (less than 1 year of age), while the observed frequency of juveniles at the wintering grounds in Texas has averaged 13%.

Convincing evidence of the accuracy, precision and usefulness of PVA simulation models would require comparison of model predictions to the distribution of fates of many replicate populations. Such a test probably cannot be conducted on any endangered species, but could and should be examined in experimental non-endangered populations. Once simulation models are determined to be sufficiently descriptive of population processes, they can guide management of threatened and endangered species (see above and Lindenmayer *et al.* 1993). The use of PVA modelling as a tool in an adaptive management framework (Clark *et al.* 1990) can lead to increasingly effective species recovery efforts as better data and better models allow more thorough analyses.

Directions for Future Development of PVA Models

The PVA simulation programs presently available model life histories as a series of discrete (seasonal) events, yet many species breed and die throughout much of the year. Continuous-time models would be more realistic and could be developed by simulating the time between life-history events as a random variable. Whether continuous-time models would significantly improve the precision of population viability estimates is unknown. Even more realistic models might treat some life-history events (e.g., gestation, lactation) as stages of specified duration, rather than as instantaneous events.

Most PVA simulation programs were designed to model long-lived, low fecundity (K-selected) species such as mammals, birds and reptiles. Relatively little work has been devoted to developing models for short-lived, high-fecundity (r-selected) species such as many amphibians and insects. Yet, the viability of populations of r-selected species may be highly affected by stochastic phenomena, and r-selected species may have much greater minimum viable populations than do most K-selected species. Assuring viability of K-selected species in a community may also afford adequate protection for r-selected species, however, because of the often greater habitat-area requirements of large vertebrates. Populations of r-selected species are probably less affected by intrinsic demographic stochasticity because large numbers of progeny will minimise random fluctuations, but they are more affected by environmental variations across space and time. PVA models designed for r-selected species would probably model fecundity as a continuous distribution, rather than as a completely specified discrete distribution of litter or clutch sizes; they might be based on life-history stages rather than time-increment ages; and they would require more detailed and accurate description of environmental fluctuations than might be required for modelling K-selected species.

The range of PVA computer simulation models becoming available is important because the different assumptions of the models provide capabilities for modelling diverse life histories. Because PVA models always simplify the life history of a species, and because the assumptions of no model are likely to match exactly our best understanding of the dynamics of a population of interest, it will often be valuable to conduct PVA modelling with several simulation programs and to compare the results. Moreover, no computer program can be guaranteed to be free of errors. There is a need for researchers to compare results from different PVA models when applied to the same analysis, to determine how the different assumptions affect conclusions and to cross-validate algorithms and computer code.

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EVs have been adjusted to closest values possible for binomial distribution.
EV in reproduction and mortality will be correlated.
Frequency of type 1 catastrophes: 1·000 per cent
with 0·500 multiplicative effect on reproduction
and 0·750 multiplicative effect on survival
Frequency of type 2 catastrophes: 1·000 per cent
with 0·500 multiplicative effect on reproduction
and 0·750 multiplicative effect on survival

Initial size of Population 1: (set to reflect stable age distribution)

Age	1	2	3	4	5	6	7	8	9	10	Total	
	1	0	1	1	0	1	0	0	1	0	5	Males
	1	0	1	1	0	1	0	0	1	0	5	Females

Carrying capacity = 50 (EV = 0·00 SD)
with a 10·000 per cent decrease for 5 years.

Animals harvested from population 1, year 1 to year 10 at 2 year intervals:
1 females 1 years old
1 female adults (2<=age<=10)
1 males 1 years old
1 male adults (2<=age<=10)

Animals added to population 1, year 10 through year 50 at 4 year intervals:
1 females 1 years old
1 females 2 years old
1 males 1 years old
1 males 2 years old

Input values are summarised above, results follow.

VORTEX now reports life-table calculations of expected population growth rate.

Deterministic population growth rate (based on females, with assumptions of no limitation of mates and no inbreeding depression):

r = −0·001 lambda = 0·999 RO = 0·997

Generation time for: females = 5·28 males = 5·28

Note that the deterministic life-table calculations project approximately zero population growth for this population.

Stable age distribution:

Age class	females	males
0	0·119	0·119
1	0·059	0·059
2	0·053	0·053
3	0·048	0·048
4	0·043	0·043
5	0·038	0·038
6	0·034	0·034
7	0·031	0·031
8	0·028	0·028
9	0·025	0·025
10	0·022	0·022

Ratio of adult (>=2) males to adult (>=2) females: 1·000

Population 2:

Input parameters for Population 2 were identical to those for Population 1.
Output would repeat this information from above.

Simulation results follow.

Population1

Metapopulation summaries are given at 10-year intervals.

Year 100
N[Extinct] = 79, P[E] = 0·790
N[Surviving] = 21, P[S] = 0·210
Population size = 10·38 (1·37 SE, 6·28 SD)
Expected heterozygosity = 0·600 (0·025 SE, 0·115 SD)
Observed heterozygosity = 0·701 (0·050 SE, 0·229 SD)
Number of extant alleles = 3·57 (0·30 SE, 1·36 SD)

In 100 simulations of 100 years of Metapopulation:
79 went extinct and 21 survived.
This gives a probability of extinction of 0·7900 (0·0407 SE),
or a probability of success of 0·2100 (0·0407 SE).
97 simulations went extinct at least once.
Median time to first extinction was 7 years.
Of those going extinct,
mean time to first extinction was 11·40 years (2·05 SE, 20·23 SD).
91 recolonisations occurred.
Mean time to recolonisation was 3·75 years (0·15 SE, 1·45 SD).
73 re-extinctions occurred.
Mean time to re-extinction was 76·15 years (1·06 SE, 9·05 SD).

Mean final population for successful cases was 10·38 (1·37 SE, 6·28 SD)

Age 1	Adults	Total	
0·48	4·71	5·19	Males
0·48	4·71	5·19	Females

During years of harvest and/or supplementation
mean growth rate (r) was 0·0545 (0·0128 SE, 0·4711 SD)
Without harvest/supplementation, prior to carrying capacity truncation,
mean growth rate (r) was −0·0314 (0·0021 SE, 0·1743 SD)

Final expected heterozygosity was 0·5997 (0·0251 SE, 0·1151 SD)
Final observed heterozygosity was 0·7009 (0·0499 SE, 0·2288 SD)
Final number of alleles was 3·57 (0·30 SE, 1·36 SD)

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