CHANGES IN ABUNDANCE AND DISTRIBUTION OF HUMBOLDT PENGUIN *SPHENISCUS HUMBOLDTI*

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SUMMARY

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Patterns of species abundance distribution (SAD) are driven by a given species' physiology, life history attributes and environmental variables, and this is true of the Humboldt Penguin *Spheniscus humboldti*. Climate variability such as El Niño Southern Oscillation (ENSO) has impacted this species and other marine fauna in the eastern South Pacific Ocean. After reviewing manuscripts and reports, we identified 80 Humboldt Penguin breeding colonies, distributed from La Foca Island (05°12′S, 81°12′W) in Peru to Metalqui Island (42°12′S, 74°09′W) in Chile, but reduced the number to 73 after fieldwork surveys in northern Chile. At least three Humboldt Penguin colonies at the southern end of the Humboldt Penguin's range also include Magellanic Penguins *S. magellanicus*. The Humboldt Penguin population of the main breeding colony in Peru, Punta San Juan, decreased 51% from 1980 to 2008, with notable decreases during El Niño. On the other hand, the population of Chañaral Island to the south increased 89% during the same period, which could be a result of irruption from more northern populations as well as past underestimation. The SAD does not follow the expected unimodal log-normal shaped model, and its shape has recently shifted significantly southward. This change is consistent with the species' pattern of long distance movement during ENSO, reduced population genetic structure and long-distance gene flow between colonies, indicating the absence of philopatry, a decrease in population size in the main colonies in Peru and an increase in population size in colonies along northern Chile. The change in SAD might result from interactions between consecutive El Niño events, human activities and climate change. To better understand this pattern, further studies are required in population genetic structure, species physiology, and environmental variables in space and time.

Keywords: Humboldt Penguin, distribution, El Niño, population size.

INTRODUCTION

At an intraspecific level, patterns of species abundance distribution (SAD) vary in space and time, especially over the largest scales. The most basic, unimodal pattern is expressed in a log-normal shape, based on the abundant-center hypothesis (Gaston *et al*. 2008). SAD patterns can be driven by environmental variables (e.g. temperature, salinity, precipitation, productivity) as well as intrinsic, species-specific factors (e.g. physiology, dispersal ability and other life-history attributes). Climate change and oscillations (e.g. El Niño, La Niña) are important variables known to influence SAD of marine species both historically and recently. Thus, when faced with climate change, a population, and ultimately a species, may have three possible biological responses: range shift, adaptation or extirpation (Holt 1990).

A strong driving force altering the distribution and abundance of marine organisms along the southern South American coast is El Niño Southern Oscillation (ENSO). The Humboldt Current System (HCS) normally exhibits cool sea surface temperatures (16°C at latitude 5°S in Peru) compared to the warmer, 25°C temperatures farther off the coast at the same latitude. The upwelling of cool waters increases biological productivity in turn, leading to great forage fish abundance. During El Niño (EN), the upwelling is interrupted, and the Chilean-Peruvian waters are invaded by warm, nutrient-depleted oceanic waters, increasing temperatures by 3°C to 5°C (Camus 1990, Thiel *et al*. 2007). As a result, biomass and the composition of phyto- and zooplankton decrease (Carrasco & Santander 1987, Thiel *et al*. 2007), affecting the population size and the distributions of anchovies and sardines (Barber & Chávez 1983, Alamo & Bouchon 1987). Several seabird species, in turn, are affected in various ways: increased mortality, nest desertions and large-scale movements (Tovar & Guillén 1987, Valle *et al*. 1987).

Humboldt Penguin *Spheniscus humboldti* is distributed along the edge of the HCS, ranging from La Foca Island (05°12′S, 81°12′W) in Peru (Paredes *et al*. 2003) to Metalqui Island (42°12′S, 74°09′W) in Chile (Hiriart-Bertrand *et al*. 2010). ENSO occurs every 3 to 8 years, causing variable impacts on the Humboldt Penguin populations along most of this range. The 1982/83 EN was responsible for a population decline of 65% in Peru, where a surviving population in 1984 was estimated to be 2100–3000 individuals (Hays 1986). The 1997/98 EN, another intense event, had a great impact in the northern end of the species' range, with populations in central Chile affected to a somewhat lesser extent. The number of breeding pairs in Ex-Pájaro Niño Island (so called because it is no longer an island) was 55%–85% lower, and the onset of nesting was delayed (Simeone *et al*. 2002). Moreover, EN also caused heavy rainfall (Rasmusson & Wallace 1983), which led to nest flooding and breeding failure (Hays 1986, Vilina 1993, Paredes & Zavalaga 1998), affecting Chilean populations at Cachagua (Meza *et al*. 1998) and Ex-Pájaro Niño Island (Simeone *et al*. 2002).

From a different perspective, a reduction in population size at a specific site may represent mortality but also temporary movement elsewhere as individuals search for better conditions. During the 1997/98 EN, individuals satellite-tracked from Pan de Azúcar Island traveled as far as 895 km as marine productivity decreased (Culik *et al*. 2000). The decrease in breeding colony sizes in Peru could have led to an increase in Chile, a phenomenon known as *irruption*: the irregular movement of great numbers of animals, in some cases for long distances from their normal range (Newton 2008) resulting in changes in SAD. To date, studies of Humboldt Penguins have evaluated changes in abundance at a specific colony or group of colonies, rather than investigating the entire species distribution.

The aims of this study are to review the numbers, location and size of Humboldt Penguin breeding colonies throughout its entire range and to analyze population trends and the effects of ENSO on these populations. We seek to better understand the factors affecting SAD in this species and discuss its possible biological response (extirpation, migration and adaptation) in the face of climate change. Humboldt Penguins are listed in Appendix I of the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES), as vulnerable according to the Red List of the International Union for the Conservation of Nature (IUCN 2012), and as endangered according to the US *Endangered Species Act*. Thus, understanding the patterns of abundance and distribution is crucial for the species' conservation in a changing world. Several breeding colonies are constantly at risk from human activities (e.g. Simeone *et al*. 1999, 2012), and the effects of climate change are also problematic.

TABLE 1
Number of penguins recorded in surveys in northern Chile

Locations	Latitude (S)	Longitude (W)	Number of penguins
Islote Algodonales	22°05′	70°13′	1450 total
Punta Itata	22°55′	70°18′	None
Punta Chacaya	22°58′	70°19′	15 adults and 7 juveniles
Islote en Punta Tames	23°01′	70°31′	3 adults[a]
Islote Abtao	23°01′	70°31′	4 adults[a]
Islote Afuera close to Punta Tal Tal	25°23′	70°30′	None[a]
Punta Tal Tal and islets	25°23′	70°30′	63 adults and 13 juveniles
Islote Blancos	25°28′	70°33′	10 adults and 4 juveniles

[a]Occupied by sea lions.

METHODS

To analyze population trends of the Humboldt Penguin, we reviewed 25 manuscripts and reports about abundance published from 1972 to 2012. We analyzed the population variation of frequently surveyed locations (Pan de Azúcar, Grande, Choros, Chañaral, Pájaros 1 and Cachagua Islands, Concon, Ex-Pájaro Niño Island) from 1980 to 2006. In addition, we completed a field survey of northern Chile, Antofagasta Region (22°05′S to 25°28′S), where data are scarce.

During December 2012 and January 2013, we visited most of the known Humboldt Penguin breeding sites between 22°S and 25°S (Table 1) to confirm the species presence. We surveyed all sites by boat, with the help of the Coast Guard, by direct observation from land using binoculars, or both. At Algodonales Islet, we disembarked for a direct survey. At Blancos Islet (25°28′S, 70°33′W), where we could only observe from the boats, we noticed that the islets were poorly covered by guano and very angular in shape, therefore appearing to provide poor penguin habitat.

RESULTS

Antofagasta field records

We found few penguins and no evidence of breeding (Table 1) in most of the eight locations surveyed. The only colony with a large number of penguins and little evidence of breeding was Algodonales Islet. A total of 1450 birds were counted from boats. We found three nests on the islet that could have been used this breeding season, as well as four molting chicks. However, it appeared that the islet

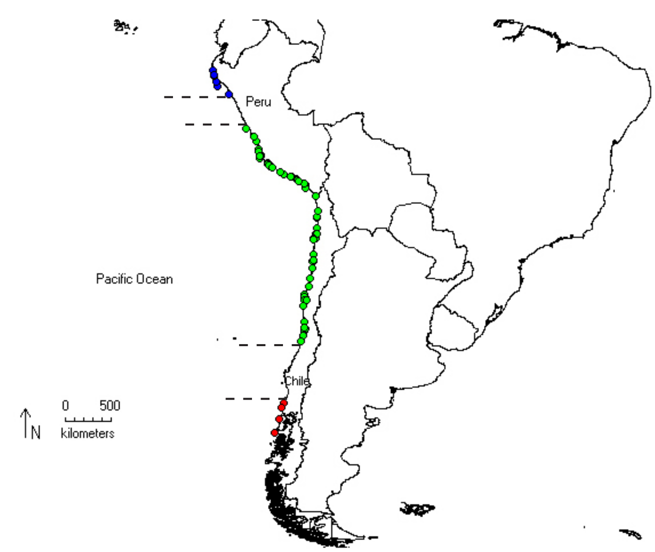

Fig. 1. Map of distribution of all 80 known and suspected Humboldt Penguin breeding colonies. Blue (north of black line) designates the northernmost breeding colonies and red (south of black line) the southernmost breeding colonies, both separated by the discontinuity areas from the other colonies (green) along the center of the species distribution.

had been well worked by humans, as we found shovels, pickaxes and bags full of guano. The amount of guano on this islet was significantly higher than at the other studied locations.

Species abundance distribution

Using information from the literature, we identified 80 colonies, 42 in Peru and 38 in Chile (Fig. 1, Appendix 1 available on the journal Web site). Upon conducting surveys, however, we reduced that number to 73 because we found no penguins breeding at eight of the colonies. Based on average numbers from 1997 to 2011, we estimated the current population to be about 36 982 Humboldt Penguins. However, this total could be an underestimate, because it was based on 59 breeding colonies with at least a single report of abundance between 1997 and 2011. Abundance could be as high as 60 295 individuals if maximum values for each colony are assumed. In Peru, penguins are found mostly between Pachacamac and Punta Coles, and mainly at Punta San Juan and San Juanito Islet (Paredes *et al*. 2003). The northernmost known breeding colony is Foca Island, Peru, confirmed in 2000 by the sighting of a penguin incubating a chick inside a cave (Paredes *et al*. 2003). The southernmost breeding location in Peru is Punta Coles (Paredes *et al*. 2003). In Chile, the largest colonies occur between 25°S and 29°S, including the colonies of Pan de Azúcar, Pájaros, Chañaral and Grande islands. In Chile, the northernmost breeding colony is a sea cave called Cueva del Caballo (Araya 1983, Araya & Todd 1987). The southernmost location was first described as Pupuya Island (34°S; Araya 1983), later Puñihuil Island (41°S; Wilson 1995) and more recently Metalqui Island (42°S, Hiriart-Bertrand *et al*. 2010).

The two main areas of abundance lie between 12°S and 17°S in Peru and between 25°S and 33°S in Chile, with three areas of low abundance (Fig. 1): 7°S to 11°S, 17°S to 20°S and 33°S to 40°S. In the first area in northern Peru, colonies at the northernmost limit of the species range are 440 km from those of higher abundance to the south. The second area of low abundance, which occurs in northern Chile, is poorly known, and the number of breeding colonies could be underestimated. The third and largest area of low abundance is found in southern Chile, about 793 km from the southernmost abundant colonies. The southern region of low abundance is similar to that of the Marine Otter *Lontra felina* (Medina-Vogel *et al.* 2008, Vianna *et al*. 2010). According to these authors, this geographical isolation has affected the genetic isolation of *L. felina*. These areas of discontinuity are consistent with extensive sandy beaches with significant human activity. The Humboldt Penguin is capable of moving large distances along the coast (Culik *et al*. 1998). However, the absence of intermediate colonies, which would otherwise facilitate a stepping stone movement, and the increase in human activities such as fisheries, could limit movement toward these southern colonies.

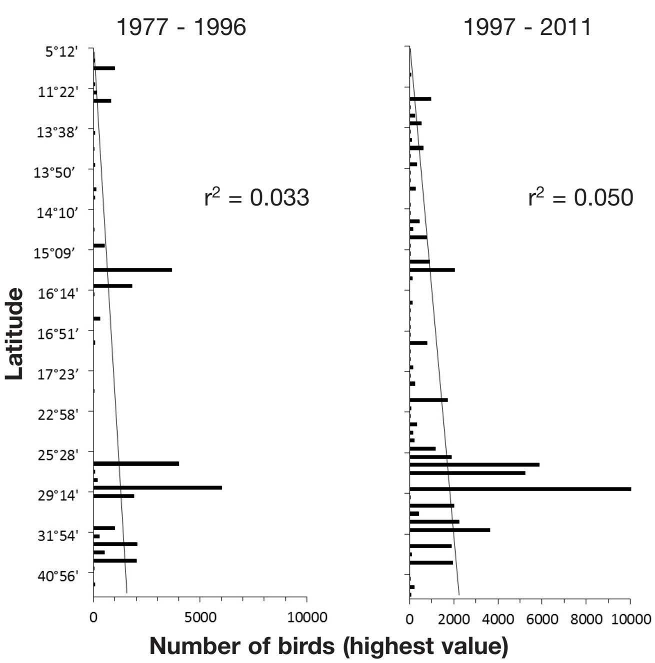

Fig. 2. Highest abundance of individuals described for all breeding colonies of Humboldt Penguin between the years 1977–1996 and 1997–2011.

Currently, 60% of the breeding colonies are distributed on islands and islets (Appendix 1). The breeding colonies recorded on the coast are either protected areas (e.g. Punta San Juan) or areas with reduced human settlements (e.g. north of Chile). Only 23 of the 73 breeding colonies (32%) are fully or partially protected, and most of these protected colonies are located on islands (n = 17; Appendix 1). Consequently, Humboldt Penguin colonies are becoming restricted to islands, which could further reduce the connectivity between colonies.

SAD distribution and ENSO effects

The species' distribution during the periods 1977–1990 and 1993–2011 did not follow the unimodal, log-normal shaped model. Between 1977–1990 and 1993–2011, the SAD completely changed from a bimodal distribution, in the earlier period, to a center of abundance lying in the southern part of the range, in the later period (Fig. 2). Within-colony changes were also observed in 1999 and 2000 at Pinguinera (15°03′S), Punta Vera (15°08′S), Sombrerillo (15°29′S) and Punta Atico (16°14′S). Humboldt Penguins were not observed in Punta Corio, Peru (17°14′S; Paredes *et al*. 2003).

In the southern portion of the Humboldt Penguin's range, the species overlaps with the Magellanic Penguin *Spheniscus magellanicus* (Simeone *et al*. 2003). Mixed colonies of both penguin species occur at Pinguino Islet (41°56′; Cursach *et al*. 2009), Puñihuil (41°55′; Simeone 2004) and Metalqui Island (42°12′S; Hiriart-Bertrand *et al*. 2010). The species ratio, Humboldt:Magellanic, at these locations is 1:5–1:7, 1:7 and 1:9, respectively. In central-north Chile, a few Magellanic Penguin pairs have been reported at Ex-Pájaro Niño Island (Simeone & Bernal, 2000; Simeone *et al*. 2003) and possibly Cachagua (Philippi 1937, Housse 1945) and Chañaral islands (Araya 1983). Humboldt Penguins have also been seen at Guafo Island (43°36′S) in a mixed-species colony, but there is no report of breeding (Reyes-Arriagada *et al*. 2009). Heterospecific pairing and hybridization have been determined by direct observation and molecular markers at Puñihuil and Metalqui islands (Simeone *et al*. 2009).

Punta San Juan, which has a fairly complete population time series, shows negative growth from 1980 to 2008 (Fig. 3). Three reductions occurred with EN 1980/81, 1996–99 and 2003–07. The most extreme EN occurred in 1983 and 1998. Although the population showed recovery after each event, it was not enough to return to historical numbers. Additionally, Humboldt Penguins were not found in 1999 and 2000 in Peru at the Pinguinera (15°03′S), Punta Vera (15°08′S), Sombrerillo (15°29′S), Punta Atico (16°14′S) and Punta Corio (17°14′) locations (Paredes *et al*. 2003).

Abundance and trends of breeding colonies

Punta San Juan showed a population decrease of 83%, from 3 680 individuals in 1980 to 630 in 2007, recovering to 1 809 in 2008; overall population reduction was 51%. This decrease may have involved irruption and not necessarily mortality. Likewise, most other main colonies in Peru (e.g. San Juanito, Tres Puertas) also exhibited decreases in 1999, 2004 and 2007 (Fig. 3). Twelve colonies in Peru were vacant after the 1990 EN. Subsequently, three recovered, three failed to recover, and recovery in the remaining six is unknown because of a lack of data. The three locations at which no population recovery was recorded are at the northern limit of the species' range (13°S to 14°S), whereas the three populations that did recover occur in a region of high abundance (14°S to 15°S). Paredes *et al*. (2003) showed a shift in the population towards the south in Peru over the last 15 years.

In contrast to Punta San Juan, Peru, the population size at Chañaral Island, Chile, showed a significant increase after 2002 (Fig. 4). From 1980 to 1995, the population at Chañaral Island never exceeded 6 000 birds (Appendix 1), changing to 10 000–22 000 individuals between 2002 and 2011. An 89% population change at Chañaral Island occurred between 1977–1996 and 1997–2011. However, this increase was attributed to a past underestimation of penguin numbers (Mattern *et al*. 2004), which is further debated below. Other populations from northern Chile (26°S to 29°S) — Pan de Azúcar, Grande, Choros, Chañaral and Pájaros 1 islands — also showed positive growth (Fig. 4). On the other hand, populations from central Chile (32°S to 33°S) show a stable or slightly negative trend (e.g. Cachagua, Concón, and Ex-Pájaro Niño islands; Fig. 4). Those three populations occur in the most densely human populated areas on the Chilean coast, which could have negatively affected penguin abundance. These data sets indicate that populations from northern Chile (e.g. Pan Azúcar, Chañaral, and Choros islands) were also affected by the two strong EN; however, the populations might have been able to recover as a result of irruption from more

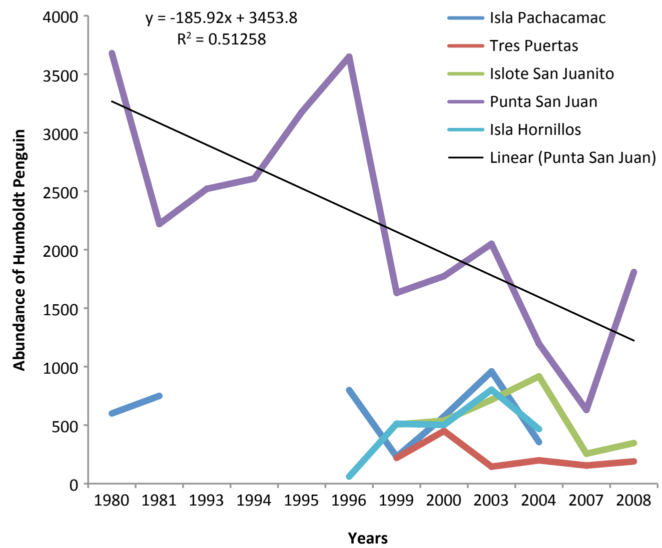

Fig. 3. Abundance fluctuation (number of individuals) of Humboldt Penguins from the main breeding colonies from Peru.

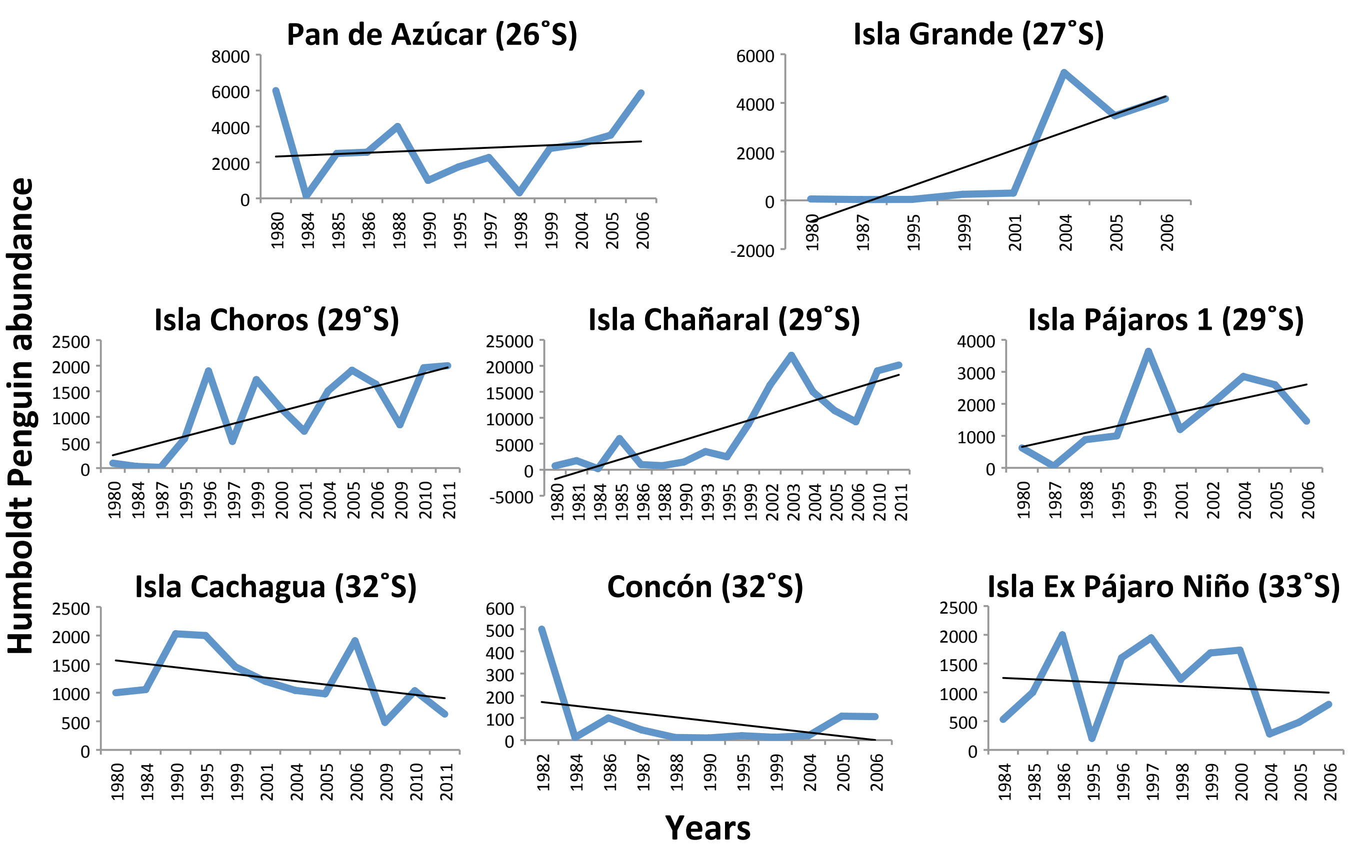

Fig. 4. Abundance fluctuation (number of individuals) of Humboldt Penguins of eight breeding colonies from Chile.

northern populations (see discussion below). In central Chile colonies, such as Ex-Pájaro Niño Island, the number of breeding pairs became significantly lower during EN 1997/98, and the onset of nesting was delayed (Simeone *et al*. 2002).

DISCUSSION

Irruption or population underestimation at Chañaral Island?

Population size significantly increased at Chañaral Island after 2002, and the increase was mostly attributed to past underestimations (Mattern *et al*. 2004). However, the shift of Humboldt Penguin SAD from 1977–1990 to 1993–2011 southward after consecutive EN years provides other evidence. The growth of the Chañaral population (89%) and other colonies in northern Chile appears to be associated with the negative growth (51%) of the main breeding colony in Peru, Punta San Juan. Moreover, after the last strong EN, no penguins were found in some colonies in Peru that are usually stable. However, EN is not the only factor accounting for this change of SAD. There has also been an increase in human presence and activities along the central coast of Peru (INEI 1999), mainly a progressive growth of local fisheries (Paredes *et al*. 2003). Another factor is the fluctuation of sardine and anchovy abundance associated with varying ocean temperature, leading to a decrease in seabird populations (Chávez *et al*. 2003). Lastly, latitudinal trends that could be associated with climate change should be further evaluated: Humboldt Penguin distribution could be gradually shifting to higher latitude, following the distribution of prey (e.g. Perry *et al*. 2005, Last *et al*. 2011).

The Humboldt Penguin has been described as a species with strong adult philopatry (Araya *et al*. 2000) and extreme nest site fidelity (Teare *et al*. 1998). If this were correct, the species should have a strong population genetic structure, but this is not corroborated by recent results. Studies of microsatellite loci among four colonies (Punta San Juan, Cachagua Island, Ex-Pájaro Niño Island-Algarrobo and Puñihuil Islet) showed a pattern of isolation by distance, but a lack of or reduced population structure — the pairwise *Fst* value ranged significantly from 0 in the closest colonies to 0.01 in the farthest (Schlosser *et al*. 2009). These authors also found high levels of heterozygosity (0.69–0.74) among all four locations. Although in Peru some of the colonies have decreased in size (Zavalaga & Paredes 1997), the species' current population is still large enough to maintain a high genetic diversity (Schlosser *et al*. 2009). Moreover, these authors suggest that Punta San Juan serves as a source population, with irruption into the three populations to the south.

In addition, several studies have shown that Humboldt Penguin is not a sedentary bird and can move long distances, especially when marine productivity is low. In 1994 and 1995, 19 penguins were banded in Ex-Pájaro Niño Island in Algarrobo, of which 18 were later recovered (dead) in different locations up to 592 km away (Wallace *et al*. 1999). One penguin was found alive in Cachagua Island in 1998, about 88 km from Algarrobo. Culik & Luna-Jorquera (1997) studied five Humboldt Penguins satellite-tracked from Pan de Azúcar Island during the winter, one of which moved 640 km to Iquique (20°S). During EN 1997/98, the birds satellite-tracked from Pan de Azúcar Island moved 895 km. The authors related this movement to a decrease in marine productivity (Culik *et al*. 2000).

Why is Chañaral Island currently the main breeding colony for Humboldt Penguins? Following a collapse in the fish stock in the late 1980s, in 1991 new fishery legislation was approved in Chile (Fishery & Aquaculture Law No 18 892 [FAL]), defining the right to fish for the industrial and artisanal sectors (Gelcich *et al*. 2010). The FAL established recognition of artisanal fishers, assigning exclusive access rights within five nautical miles of shore, and excluding the industrial fleet from this area. This regulation led to a continuous and sustained increase in landing by the artisanal fleet (Gelcich *et al*. 2010). This could have had contrasting impacts on Humboldt Penguin populations: an increase of food supply in coastal waters but an increase in penguin mortality due to gill nets. Although the implementation of the law is a benefit for marine conservation along the entire coast of Chile, protecting areas of high productivity could be even more beneficial.

Although irruption from more northern populations might have occurred, the hypothesis that the Chañaral Island population was underestimated (Mattern *et al*. 2004) cannot be completely rejected. The number of individuals at Chañaral apparently increased more than the population in Peru decreased. However, there is a lack of historical records of population abundance from northernmost Chile. In addition, the recovery of the population at Chañaral could not be due exclusively to immigration or high breeding success, given the species' low fecundity (Paredes *et al*. 2002, Simeone *et al*. 2002, Hennicke & Culik 2005).

To completely elucidate this SAD change, further studies are required, such as remote sensing to evaluate different marine environmental variables along the species' range, including during EN; studies of the species' physiology and its thermal tolerance; and population genetic studies sampling more breeding colonies (including Chañaral Island) than sampled to date, to evaluate direction of gene flow (southward) and possible founder effects on the southern limit of the species' range.

Humboldt Penguin conservation

Our data indicate a shift in Humboldt Penguin SAD in space and time, and the impact of EN on this change, which is affected as well by the increase in human settlements and activities along the coast. The major threats are mortality by gill nets, over-fishing, competition with humans for the same resources, introduced species, industrial activities and intensive tourism (Hays 1984, Williams 1995, Simeone *et al*. 1999; Simeone & Luna-Jorquera 2012). Climate change is another threat, assuming that EN will become more frequent and intense. Therefore, we suggest that action plans include an integrated program of management and conservation for Humboldt Penguins in its entire range. The maximum number of breeding colonies should be protected, with the population at Chañaral Island being crucial. Connectivity between breeding colonies must be maintained to avoid local extirpation; to facilitate future displacement of distribution and colonization due to EN, climate change or human activities; and to maintain genetic diversity. The colonies at the extreme limits of the species' range should also be protected, as they may be most sensitive to changing local conditions, as well as to large-scale climate change.

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