

Evidence of philopatry and natal dispersal in Humboldt Penguins

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Abstract. We report evidence of both philopatry and natal dispersal in Humboldt Penguins (*Spheniscus humboldti*) from a colony in central Chile. Between 1994 and 2001, we tagged 241 Humboldt Penguin chicks with subcutaneous transponder chips. Seven birds (3%) were found as adults at their natal colony: five were breeding (philopatric birds) and two were prospecting for nest-sites. Another four birds (2%) were found breeding at other colonies up to 90 km from the natal colony. Philopatric birds bred at 3.6–6.1 years old (mean \pm s.d. = 4.8 ± 1 years) at nests located 5–80 m from their natal nests (30 ± 25 m). Most philopatric and the prospecting birds used the same types of nests as their natal ones and we suggest that birds breeding for the first time may use cues of structural aspects of their natal nest when choosing a nesting site for the first time.

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Introduction

Seabirds are typically philopatric, that is individuals tend to return to breed in the colony in which they hatched (Hamer *et al.* 2002; Gaston 2004). Individuals of a wide variety of seabird families, including the Diomedidae (Gauthier *et al.* 2010), Procellariidae (Ovenden *et al.* 1991; Bradley *et al.* 1999), Spheniscidae (Dugger *et al.* 2010), Phalacrocoracidae (Schjorring 2001), Sulidae (Osorio-Beristain and Drummond 1993), Alcidae (Halley *et al.* 1995; Ibaruchi *et al.* 2011) and Laridae (Coulson and Coulson 2008), return to breed where they were hatched. Young individuals of some species return to their natal colony for one or more years before breeding for the first time, apparently to examine local environmental conditions and conspecific breeding success (Halley *et al.* 1995; Danchin *et al.* 1998; Bradley *et al.* 1999). Despite the philopatric tendency of seabirds, young birds may disperse from their natal colony and breed for the first time at a colony elsewhere (Coulson and Coulson 2008). This natal dispersal (*sensu* Greenwood 1980) involves prospecting at several colonies in the years before breeding for the first time (Coulson 2002).

The degree of philopatry and natal dispersal may vary depending on the species, year, climate, availability of food and quality of habitat (Dugger *et al.* 2010) and understanding these life-history traits is important as they affect patterns of gene flow, and genetic structure and dynamics of populations (Osorio-Beristain and Drummond 1993; Steiner and Gaston 2005; Bouzat *et al.* 2009).

The Humboldt Penguin (*Spheniscus humboldti*) breeds along the Pacific coast of Chile and Peru, foraging in the nutrient-rich waters of the Humboldt Current (Williams 1995). In central Chile, Humboldt Penguins breed twice annually: a spring event occurs

mainly between August and January and an autumn event occurs between April and June. The species has a declining world population (probably <10 000 mature individuals; BirdLife International 2013; but see Mattern *et al.* 2004). This species is also considered Vulnerable globally. Research recommendations for improving the conservation status of the Humboldt Penguin have included studies on breeding biology and life history (Araya *et al.* 2000). Despite some local efforts in providing information on these subjects (e.g. Simeone *et al.* 2002), little is still known of the age at first breeding, nest-site fidelity, philopatry and dispersal, among other relevant life-history traits. In this study we report for the first time direct evidence of both natal philopatry and dispersal of wild-ranging Humboldt Penguins tagged as chicks at their natal colony in central Chile. We also examined and report on the age at first breeding and the role of nest-site characteristics in nest-site selection of first-time breeders.

Methods

From December 1994 to December 2006 we conducted a study on the breeding biology and ecology of the Humboldt Penguin at Pájaro Niño Island (33°21'S, 71°41'W), a 3-ha island in Algarrobo, central Chile (Fig. 1). Pájaro Niño (250 pairs) and Cachagua Island (600 pairs) are the two largest colonies of Humboldt Penguins in central Chile (32–38°S) and combined comprise ~95% of the total Penguin population in this region (Simeone *et al.* 2003). During the period of study, the breeding population at Pájaro Niño fluctuated between 131 and 326 pairs (Simeone and Bernal 2000).

At the Pájaro Niño colony we established monitoring plots on three sections of the island, the area for each of the plots was 0.41,

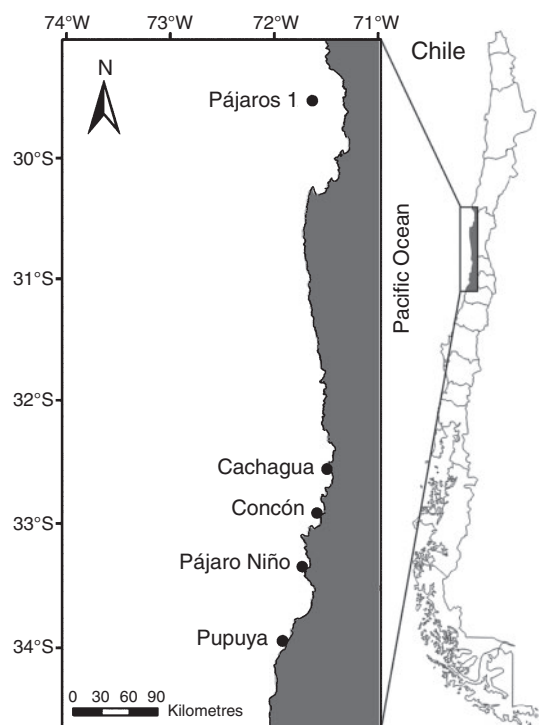


Fig. 1. Location of the Pájaro Niño colony of Humboldt Penguins (the natal colony of this study) and other colonies examined in this study in northern central Chile.

0.16 and 0.18 ha and partitioned into a 10×10 -m grid; the three plots included ~45% of the breeding population of the island. Within the gridded plots, nests were assigned a unique number (based on grid and nest) and classified into one of the following types of nest: dirt burrow, rock crevice, rock-covered and vegetation-protected. The colony was monitored twice a week during the main periods of nesting activity (April–May and October–November) and twice per month during the rest of the year. All nests within the plots were individually checked for contents and, if birds were present, bird identity was determined (see below). Additionally, once per year (normally between October and November) we did an exhaustive search for tagged Penguins around the island to check for birds that had moved from the study plots.

From December 1994 to December 2001, we tagged Penguin chicks 60–70 days old or 3.0 to 3.8 kg (i.e. before fledging) with subcutaneous transponder chips (Trovan Ltd, Douglas, Isle of Man, UK). These chips provided a unique identification code based on a combination of 10 numbers and letters. During subsequent nest inspections, we checked for tagged birds using a Trovan chip-reader LID 500, which allows detection of chips within 10 cm. Chips were placed under the skin on top of the head, approximately at the midline between the eyes, using a Trovan needle and injector. The chips were so placed for ease of reading the chip as Penguins tend to peck the chip-reader, allowing it to pick up the signal with little disturbance to the Penguin. Also, the chip tends to move less when placed on top of the head than when placed under the skin of the back where they tend to migrate caudally (R. S. Wallace, pers. obs.).

Table 1. Summary of numbers of Humboldt Penguin chicks tagged at their natal colony on Pájaro Niño Island, and numbers resighted as adults

Year	Number of chicks tagged	Number of chicks found as adults (proportion of number tagged)	
		In natal colony	Other islands
1994	8	1 (0.125)	0
1995	16	1 (0.063)	0
1996	38	1 (0.026)	0
1997	13	0	0
1998	142	4 (0.028)	4 (0.028)
1999	9	0	0
2000	0	0	0
2001	15	0	0
Total	241	7	4

In 2004, we searched for tagged birds at four other colonies: Concón Islet ($32^{\circ}53'S$, $71^{\circ}31'W$), 55 km north of Pájaro Niño, on 15 May and 25 November; Cachagua Island ($32^{\circ}35'S$, $71^{\circ}27'W$), 90 km north of Pájaro Niño, on 10–12 May and 21–23 November; Pájaros 1 ($29^{\circ}35'S$, $71^{\circ}33'W$), 420 km north of Pájaro Niño, on 6–8 November; and Pupuya Island ($33^{\circ}58'S$, $71^{\circ}53'W$), 70 km south of Pájaro Niño, on 29 May. At these colonies we did an exhaustive search of nests and checked all birds on nests using the same procedure as at Pájaro Niño. Coverage at these colonies included 80–90% of the land area and excluded nests at inaccessible sites (e.g. cliffs, sea caves).

We considered a bird to be philopatric if it returned to the natal colony and was seen on a nest attending eggs or chicks. Birds in nests, either alone or as a pair, and without confirmed eggs or chicks were considered to be prospecting (Ainley *et al.* 1983).

Because many Penguin nests in the colony disappear between years (owing to collapse, filling in with soil, drying of vegetation), it was not possible to determine directly whether Penguins selected the same type of nest as their natal one or chose a nest based on availability of sites at the time our observations were made. To overcome this problem, we used an exact binomial calculation to estimate the two-tail probability that total philopatric Penguins would use the same type of nest as its natal one ($P=0.5$) or a nest of another type ($P=0.5$) (Zar 1999).

Results

From 1994 to 2001, we tagged a total of 241 Humboldt Penguin chicks from Pájaro Niño Island (hereafter, the natal colony) with transponder chips (Table 1). These birds were ~90% of all chicks produced within the study plots during the period of study. The remaining chicks departed or died before we tagged them.

Of the 241 tagged birds, only 7 (3%) were found at least once as adults at the natal colony: 5 individuals were breeding (philopatric birds) and 2 were prospecting (Table 2). Two birds (00-01BA-D13D and 00-011D-F9B9; Table 2) were prospecting for nesting sites at 4.4 and 4.2 years old and bred for the first time 3 months and 2 years later. Two other birds (00-012A-86F8 and 00-01CA-7AFC, Table 2) were prospecting for nesting sites at 4.2 and 5.2 years old, but were not seen again at the colony. The nests of philopatric birds ranged from 5 to 80 m from their natal nests (mean \pm s.d. = 30 ± 25 m, $n=7$, note that the two birds each used two different nests, cf. Table 2); the two prospecting birds occupied nests 50 and 80 m from their natal nests (Table 2).

Table 2. Humboldt Penguins tagged as chicks at Pájaro Niño Island that were resighted as adults at their natal colony, either breeding (philopatric birds) or prospecting for nesting sites

Natal nest-type is indicated in bold. Nest-types: RC, rock-covered; CR, rock crevice; VP, vegetation-protected; DB, dirt burrow. The allocated number of each nest is given in parentheses after nest-type

Bird	Hatching date	Sighting date	Nest contents	Age (years)	Nest-type (nest number)	Distance from natal nest (m)
Philopatric birds						
00-01BA-D13D	Nov. 1994				DB (2A)	
		Apr. 1999	Pair	4.4	DB (44.3)	5
		Jul. 1999	Chicks	4.7	DB (44.3)	5
00-P012A-B25C	Dec. 1995				RC (27.8)	
		Jul. 1999	Chicks	3.6	RC (19.5)	10
		Sep. 1999	Eggs	3.8	RC (19.6)	25
		Apr. 2000	Eggs	4.3	RC (19.6)	25
00-0026-6AD0	Nov. 1996				CR (10.2)	
		Dec. 2002	Chicks	6.1	CR (3.4)	40
		Jun. 2003	Chicks	6.6	CR (3.4)	40
		Jul. 2004	Chicks	7.6	CR (3.4)	40
		Dec. 2004	Chicks	8.0	CR (3.4)	40
		Dec. 2006	Chicks	10.0	CR (3.4)	40
00-011D-F9B9	Oct. 1998				RC (31.8)	
		Dec. 2002	Pair	4.2	RC (21.11)	30
		Oct. 2004	Chicks	6.0	RC (22.9)	20
00-012A-6BC4	Nov. 1998				RC (8.2)	
		Jun. 2004	Eggs	5.5	VP (35.1)	80
Prospecting birds						
00-012A-86F8	Oct. 1998				RC (44.5)	
		Dec. 2003	Pair	5.2	RC (37.1)	50
00-01CA-7AFC	Oct. 1998				RC (8.4A)	
		Dec. 2002	Alone	4.2	RC (41.2)	80

Table 3. Humboldt Penguins tagged as chicks at Pájaro Niño that were subsequently resighted as adults at colonies other than their natal colony

Natal nest-type in bold; nest-types as Table 2

Bird	Hatching date	Colony and date where resighted	Nest contents	Age (years)	Nest-type (nest number)
00-0076-E293	Oct. 1998	Cachagua, May 2004	Eggs	5.6	DB (42.4)
		Cachagua, Nov. 2004	Eggs	6.1	RC
00-004D-847E	Dec. 1998				DB (10.3)
		Cachagua, May 2004	Eggs	5.4	DB
00-0070-CAFD	Oct. 1998				CR (18.13)
		Cachagua, Nov. 2004	Eggs	6.1	DB
00-0114-2564	Dec. 1998				CR (9.1)
		Concón, May 2004	Eggs	5.5	RC
		Concón, Nov. 2004	Chicks	5.9	RC

Of the seven philopatric and prospecting birds, six chose the same type of nest as their natal nests. Including nesting of two philopatric birds that used different nests during the study period but of the same types (see birds 00-P012A-B25C and 00-011D-F9B9, Table 2) the Penguins used the same type of nests as their natal ones in eight of nine cases ($P=0.039$).

Four birds were recorded breeding at two other colonies: Concón and Cachagua Islands (Table 3). The age of these birds ranged from 5.4 to 6.1 years (mean \pm s.d. = 5.7 ± 0.3 years). Only one of these four used a nest similar to the natal nest-type.

Discussion

The proportion of tagged birds re-sighted at the natal colony here (3%) is low but such numbers appear to be common of *Spheniscus* penguins. Whittington *et al.* (2005) estimated that, depending on year and location, 5–9% of African Penguins (*S. demersus*) banded as chicks returned to breed at their natal colony. This is likely to reflect the high mortality of most marine birds in the first year of life. During this critical period, most juveniles appear to die because they are not able to learn successfully how to feed themselves (Hamer *et al.* 2002; Gaston 2004). Rates of first-year mortality of up to 58% have been reported in first-year juvenile

Magellanic Penguins (*Spheniscus magellanicus*) (Scolaro 1987); between 31% (La Cock and Hänel 1987) and 88% (La Cock *et al.* 1987) among African Penguins; and 83% in Little Penguins (*Eudyptula minor*) (Sidhu *et al.* 2007). In our study area, incidental mortality in gill-nets is an important cause of death in Humboldt Penguins (Simeone *et al.* 1999) and this is likely to increase the already high natural rates of first-year mortality. Note, however, that most of the studies cited above used flipper-bands to mark birds, which may increase mortality in first-year birds and thus bias the results (Jackson and Wilson 2002). Effects may, however, depend largely on the types of bands (Boersma and Rebstock 2010).

To our knowledge, this is the first comprehensive attempt to estimate levels of philopatry and dispersal in free-ranging Humboldt Penguins. Previously, Schlosser *et al.* (2009) made indirect estimates of philopatry based on genetic analysis, and estimated philopatry of 75% for Penguins on Pájaro Niño and rates of dispersal of 14–22%.

We are aware of our small sample size and low numbers of resightings, but they seem representative considering the small population in the region and its current overall conservation status (BirdLife International 2013). We are reasonably confident of our estimates of philopatry, as sampling effort at the natal colony was intense and constant over time. However, it is feasible that we missed prospecting birds that came ashore for short periods or failed to find returning birds that moved outside our study plots for breeding, this despite our annual checks of nests outside the plots. Furthermore, dispersal may have been underestimated because we spent little time on the other islands visited.

Most philopatric and prospecting Penguins were seen close to their natal nests and used the same types of nests as their natal ones. It is thus conceivable that Penguins, when choosing a nest for first time, use structural aspects of their natal nest as cues for selection of their nesting site. Other seabirds (e.g. albatrosses, murre) breed for the first time close (within 50–100 m) to the nest where they were raised and explanations for this behaviour include social attraction and adaptation to microhabitat (Halley *et al.* 1995; Sagar *et al.* 1998). We suggest that first-time breeding Humboldt Penguins seek a nesting site that looks familiar to them, which is ultimately based on the single experience they have of a nest, the one in which they hatched.

We are confident that our observations of philopatric Humboldt Penguins on Pájaro Niño accurately reflects their age of first breeding because birds were tagged as chicks and our monitoring effort on the island was intense. Our results, ranging from 3.6 to 6.1 years compare well with ages of first breeding recorded for African Penguins, of 3.8–6.2 years (Whittington *et al.* 2005) and the age of sexual maturity of Magellanic Penguins, at 4 years old (García-Borboroglu and Boersma 2013). Age at first breeding in seabirds can vary widely between regions and between cohorts as a result of geographical and temporal variation in the cost of reproduction and availability of food (Croxall and Rothery 1995; Crawford *et al.* 2001; Whittington *et al.* 2005). Our data are likely to be representative of the study colony. However, we suggest similar studies be carried out at other colonies along the extensive breeding range of the species because rates of philopatry, dispersal and other relevant life-history traits may vary depending on local environmental conditions.

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