ASPECTS OF THE ECOLOGY OF SPECIES REPLACEMENT IN HUMBOLDT AND MAGELLANIC PENGUINS IN CHILE

Rory P. WILSON, David C. DUFFY, Marie-Pierre WILSON and Braulio ARAYA

INTRODUCTION

Interactions between allopatric species at the edges of their ranges have been of major interest in studies of biogeography and evolution (Mayr 1963, Endler 1977) and of competition (Macarthur 1972). However, few such studies have been done on seabirds (e.g. Stresemann and Timofeeff-Ressovsky 1947, Udvardy 1963, Smith 1966, Devillers 1976, Devillers and Terschuren 1978). Seabirds are particularly appropriate for such studies as they often nest in discrete, conspicuous colonies; their distributions can be relatively easily mapped at sea, and their marine environments are often well-studied by marine biologists, fisheries scientists and oceanographers, providing objective data on environmental limits to ranges.

Unfortunately, because of the great distances involved and the resulting logistics, it is often difficult to conduct comparative research, so interferences are drawn from several studies, perhaps with differing methods, or from studies at different localities by the same author, made at different times. Differences between species may then be the result of the methods used or of different ecological conditions during the studies.

During October and November 1985, we had the opportunity to study a species-replacement, that of the Humboldt Penguin Spheniscus humboldti by the Magellanic Penguin Spheniscus magellanicus along a latitudinal gradient extending from 29°S to 53°S. We used a 'snap shot' approach of quick visits to several sites over a short period of time (cf. Ricklefs et al. 1984). Although the time we could consacrate to the study was limited, we hoped to elucidate 'seasonal' differences along the gradient of increasing latitude that might offer insight as to why the Humboldt Penguin is a subtropical/temperate species and the Magellanic Penguin temperate/sub-Antarctic. Such short term studies are likely to be inadequate where interspecific differences are minimal, but can serve to indicate species-specific environmental adaptation and competition avoidance mechanisms where interspecific differences prove to be substantial. Some of the results presented here have been presented in previous publications (Wilson et al. 1989, Wilson and Wilson 1990), in the context of other research questions.

The Humboldt Penguin breeds on the Pacific coast of South America from Isla Foca 05°12'S, Peru (Hays 1984a) south to Isla Pupuya 34°00'S Chile (Araya 1983). The Magellanic Penguin breeds from 32°35'S (Blake 1977) and exceptionally as far north 29°01'S (Araya 1983) on the Pacific coast, south through Tierra del Fuego and the Falkland Islands, and north on the Atlantic coast to approximately 42°S (Murphy 1936, Johnson 1965, Blake 1977, Boersma 1990). The two species overlap only in the Pacific, as breeders in central Chile from 32°35'S to 24°00'S and as non-breeders from approximately 32°S to 40°S (Blake 1977).

Murphy (1936) suggested that the two penguins differ in breeding season and tolerance of water temperatures; the Magellanic Penguin breeding in summer, the Humboldt Penguin breeding throughout the year. Average ocean temperatures in the breeding range of the former appear to be below 12.8°C and those in the range of the latter, well above. Johnson (1965) stated that the two species differ in nest-site preference; in areas of overlap, one species nests on one side of an island and the second species on the other side.

STUDY AREA AND METHODS

We observed Humboldt and Magellanic penguins at four sites on the Chilean coast; (1) Isla Chañaral (29°01'S, 71°50'W) (Araya and Duffy 1987), a colony of approximately 3,000 pairs
of Humboldt Penguins (study dates: 30 October - 3 November 1985), (2) Isla de Pinguinos at Algarrobo (33°39′S, 71°45′W), where there were approximately 120 pairs of Humboldt Penguins and seven pairs of Magellanic Penguins (dates: 27 October and 5-8 November 1985), (3) Islotes Pinhui (41°43′S, 74°02′W), two islands off the west coast of Isla Chiloé where one island had approximately 10 pairs of Magellanic Penguins and the other had 50 pairs of Magellanic Penguins and 20 pairs of Humboldt Penguins (dates: 13 and 16 November 1985), (4) Otway Sound (53°00′S, 71°14′W), north of Punta Arenas, a colony of approximately 200 pairs of Magellanic Penguins (dates: 18-24 November 1985).

At each breeding site, we noted nesting stages of both species, when present. We also examined the literature to determine monthly nesting activity by the two species throughout their ranges.

Adult penguins brooding small chicks were removed from their nests and fitted with autoradiographic devices that measured swimming speed and time spent swimming at each speed underwater (and therefore distance swum) (details of design and functioning in Wilson and Bain 1984, Wilson 1985a, Adams 1987, Adams and Wilson 1987, Brown 1987). Attached to feathers along the midline of the back with hoseclamps (Lishman and Croxall 1983), the devices were accurate to within 10% in determination of foraging trip duration and measured swimming speed to within 0.1 km/hr (Wilson and Bain 1984).

We also measured the maximum depth of dive during foraging, through use of capillary tubes (internal diameter 1.2 mm), coated internally with icing sugar (e.g., Adams and Brown 1983, Burger and Wilson 1988) and tapered to the outside of the speed/distance meters. Errors in the precision of the depth measurements are considered less than 10% (Burger and Wilson 1988). These devices together have a cross-sectional area approximately 2% that of Humboldt and Magellanic penguins, so that the effect of the devices was similar for both species and considered to induce a reduction of approximately 0.1 ms in mean swimming speed (Wilson et al. 1986, cf. Wilson and Culik 1992).

Overall, we fitted a total of 62 speed/distance/depth devices on Magellanic and Humboldt Penguins; 22 at Chañaral (Humboldt), 22 at Algarrobo (Humboldt) and 18 at Otway Sound (Magellanic).

Where possible, we sampled diets of adults of each species at each site, using a wet unloading stomach pump (Wilson 1984). We selected birds returning from the sea with protruding stomachs and clean beaks and plumage, conditions indicative of birds recently returned from foraging. Random sampling of adults at colonies is disruptive and usually produces stomach samples of only bile and otoliths insufficient for analysis. We sampled a total of 36 Humboldt Penguins; 17 individuals at Chañaral, 15 at Algarrobo and 4 at Chiloé, and 35 Magellanic Penguins; 16 at Chiloé and 19 at Otway Sound.

Stomach contents were strained and placed in plastic bags, then preserved, within four h, in alcohol. The samples were sorted within 24 h and prey length (fork length for fish, mantle length for cephalopods, total length for crustaceans) was measured directly when possible. All specimens were identified to the lowest possible taxonomic division possible, and voucher specimens retained for confirmation. In highly digested specimens, we removed and stored the otoliths for subsequent identification.

We determined patterns of arrival and departure of foraging birds by conducting 24-h watches of landing sites at Chañaral, Algarrobo and Otway Sound, recording all birds entering or leaving the water, as well as numbers of birds in 'beach parties' (cf. Wilson et al. 1989a, Wilson and Wilson 1990) and the number arriving or departing to inland nest sites. We could not monitor arrivals and departures at Chiloé because of limited access to the islands during bad weather. At Otway Sound, many Magellanic Penguins returned during 0500 - 0700 hr. These birds did not have protruding stomachs, suggesting that they had not fed recently and had been bathing. Similar bathing was observed at Algarrobo and Chañaral in the early morning. When birds could be identified as bathing, they were excluded from counts of arriving and departing birds.

During the 24-h watches and other observation periods, we recorded interspecific and intraspecific
interactions of penguins in 'beach parties'. We used contingency tests (Harper 1977) to examine the relative number of aggressive interactions initiated by Humboldt and Magellanic penguins. Once daily, we also scored the number of each species occupying central or peripheral positions and the species' identities of their nearest neighbours. Contingency tests were used to examine the relative proportions of the two species at the periphery and centre of groups. At Chiloé, we noted group size and species composition of penguin flocks returning to the island after foraging.

RESULTS

The literature had suggested that the northernmost site, Chañaral, would be likely exclusively occupied by Humboldt Penguins, with Algarrobo having both species, and the two most southerly sites, Chiloé and Otway Sound, being exclusively occupied by Magellanic Penguins. In fact, Magellanic Penguins were seen at Chañaral and Humboldt Penguins at Chiloé. The Chiloé site represented a 550-km southern extension of the known breeding range of the Humboldt Penguin (Araya and Millie 1986).

PATTERNS OF ARRIVAL AND DEPARTURE

Differences in foraging periods appeared to be site-specific, rather than characteristic of each species. At the three colonies where we conducted 24-h watches (Chañaral, Algarrobo and Otway Sound), most penguins left to forage just after dawn and returned during late afternoon and evening (Fig. 1).

FORAGING AND DIET

Of the 62 penguins fitted with speed/depth devices, 47 went to sea during the study periods. Thirty-eight of the devices were recovered, two birds deserted their nests, and we could not catch seven birds.

Twenty-seven of the depth gauges could be analyzed for maximum depth; four of the devices were broken by the penguins; one was lost; and six were discarded because of condensation problems within the lumen of the capillary (cf. Burger and Wilson 1988). Twenty-three of the speed/distance meters functioned well; one device was lost; two were broken, and twelve units were destroyed by seawater leaks (cf. Adams 1987).

Mean speed of Humboldt Penguins at all sites combined (x = 6.8 km/h, SD = 1.2, N = 11) was not significantly different to that of Magellanic Penguins (x = 7.6 km/h, SD = 1.3, N = 10) (t = 1.467, P > 0.05). Humboldt Penguins at Isla Chañaral did not differ (t = 0.934, P > 0.05) in their maximum depth of dive (x = 62.2 m, SD = 13.7, N = 9) from Magellanic Penguins at Punta Arenas (x = 57.6 m, SD = 7.8, N = 12), but both differed significantly (t = 7.382 and 5.442, respectively, P < 0.05) from those of Humboldt Penguins at Algarrobo (x = 27.3 m, SD = 9.2, N = 6).

Mean and median distances traveled also appeared to be site rather than species-specific. Humboldt Penguins at Isla Chañaral (x = 32.2 km, SD = 25.9, median = 22.5, N = 8) and Magellanic Penguins at Otway Sound (x = 24.8 km, SD = 28.9, median = 17.1, N = 10) had similar foraging ranges (t = 0.565). Neither was significantly shorter (t = 1.294 and 1.727, respectively, P > 0.05) than those at Algarrobo (x = 50.6 km, SD = 23.2, median = 44.1, N = 5).

DIETS

Diets varied more between sites than between species, based on both relative aggregate numerical abundance and percentage frequency of occurrence (Table 1). For example, at Chañaral, Penguins took mostly garfish (Scomberesox spp.), while their main prey at Algarrobo and Chiloé was anchovy (Engraulis ringens). Magellanic Penguins took mostly anchovy at Chiloé and herring (Sprattus đầuéni) at Otway Sound. The main prey of both species at Chiloé was anchovy, with sardines (Sardinops sagax) accounting for the rest of the Humboldt diet, and sardines and squid (Todarodes filippovae) that of the Magellanic diet.

Prey ranged from 35.6 mm (anchovy) to 270 mm (garfish) for Humboldt Penguins and 25 mm (squid) to 142 mm (anchovy) for Magellanic
Fig. 1. Patterns of (a) departure and (b) arrival of Humboldt Penguins at isla Charanai (empty bars N = 539 departures and 241 arrivals) and Algarrobo (filled bars N = 200 departures and 421 arrivals) and of Magellanic Penguins (c and d) (hatched bars N = 857 departures and 899 arrivals) at Otway Sound. Arrows show the time of dawn and dusk.
The two species took anchovy of the same size (Humboldt: $x = 109 \text{ mm}, \ SD = 15.0$, range $= 83-143, N = 19$; Magellanic: $x = 114 \text{ mm}, \ SD = 13.4$, range $= 94-142, N = 40, Z = 1.237, P > 0.05$) and pilchard (Humboldt: $x = 102 \text{ mm}, \ SD = 30.4$, range $= 55-126, N = 7$; Magellanic: $x = 97 \text{ mm}, \ SD = 20.9$, range $= 59-141 \text{ mm}, N=7, Z = 0.358, P > 0.05$) at Chiloé.

**BREEDING SEASONS**

Our field data (Table 2) showed little difference in nesting stages of Humboldt Penguins between Chanaral and Algarrobo; both had even distributions of nesting stages from eggs to large downy young. At Otway Sound, most of the Magellanic Penguin nests had very small young or hatching eggs. At Chiloé, nesting of Humboldt Penguins appeared more advanced than that of Magellanic Penguins. Half of the Humboldt nests had large downy young; none had eggs. In contrast, small downy young were the commonest contents of Magellanic Penguin nests; eggs were present and there were no large downy young.

Literature reports of nesting (Appendices 1 & 2) show that Humboldt Penguins nest throughout the year, with both winter and spring peaks, while Magellanic Penguins show a strong summer peak. Unfortunately, most of the Humboldt data come from Peru and most of the Magellanic data from Patagonia and the Falklands, with little information from the area of overlap which we studied.

**INTER AND INTRA-SPECIFIC INTERACTIONS**

Aggression rates differed significantly between Humboldt and Magellanic penguins at both Algarrobo and Chiloé ($x^2 = 16.9$ and $x^2 = 33.3$, respectively, $df = 1, P < 0.01$). At Algarrobo, in a

### Table 1. Relative abundance (Col. 1) and percentage frequency of abundance (Col. 2) of prey of Humboldt and Magellanic Penguins in central and southern Chile, November 1985.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Scomberesò</th>
<th>Engraulis</th>
<th>Sardinep</th>
<th>Sprattus</th>
<th>Squid</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chanaral</td>
<td>94</td>
<td>94</td>
<td>3</td>
<td>12</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Algarrobo</td>
<td>0</td>
<td>0</td>
<td>72</td>
<td>100</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Chiloé</td>
<td>0</td>
<td>0</td>
<td>80</td>
<td>100</td>
<td>20</td>
<td>100</td>
</tr>
<tr>
<td>Otway Sound</td>
<td>0</td>
<td>0</td>
<td>61</td>
<td>71</td>
<td>6</td>
<td>25</td>
</tr>
</tbody>
</table>

### Table 2. Nesting stages of Humboldt and Magellanic Penguins breeding at different localities on the Chilean coast during November 1985.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Species</th>
<th>Eggs</th>
<th>Small chicks</th>
<th>Medium chicks</th>
<th>Large chicks</th>
<th>Pre-fledge chicks</th>
<th>Total full nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chanaral</td>
<td>Humboldt</td>
<td>37</td>
<td>26</td>
<td>19</td>
<td>18</td>
<td>0</td>
<td>27</td>
</tr>
<tr>
<td>Algarrobo</td>
<td>Humboldt</td>
<td>31</td>
<td>23</td>
<td>27</td>
<td>19</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td>Chiloé</td>
<td>Humboldt</td>
<td>0</td>
<td>10</td>
<td>40</td>
<td>50</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Magellanic</td>
<td>15</td>
<td>44</td>
<td>41</td>
<td>0</td>
<td>0</td>
<td>34</td>
</tr>
<tr>
<td>Otway Sound</td>
<td>Magellanic</td>
<td>20</td>
<td>59</td>
<td>21</td>
<td>0</td>
<td>0</td>
<td>38</td>
</tr>
</tbody>
</table>
beach group of 96.6% Humboldt and 3.4% Magellanic penguins (N = 178). Humboldt Penguins initiated aggression against Magellanic Penguins five times more often than the reverse (total encounters = 14; Humboldt > Humboldt, 0; Humboldt > Magellanic, 10; Magellanic > Humboldt, 2; Magellanic > Magellanic, 2). Magellanic Penguins were equally aggressive to conspecific and to Humboldt Penguins, but Humboldt Penguins were not aggressive to conspecifics. At Chiloé, in a beach group of 96.4% Magellanic and 3.6% Humboldt penguins (n = 140), Magellanic Penguins were almost as aggressive to Humboldt Penguins as Humboldt Penguins were to Magellamics (ratio 0.8 to 1.0; total encounters = 38; Humboldt > Humboldt, 7; Humboldt > Magellanic, 9; Magellanic > Humboldt, 20; Magellanic > Magellanic, 16; Magellanic > Magellanic, 0).

At Chañaral and Algarrobo, Magellanic Penguins occurred significantly more frequently at the peripheries of beach parties than did Humboldt Penguins (Chañaral: χ² = 12.1, df = 1, P < 0.01; Humboldt edge, 177; middle, 272; Magellanic edge, 8; middle, 0; Algarrobo: χ² = 5.8, df = 1; P < 0.05; Humboldt's edge, 99; middle 66; Magellanic edge, 9; middle, 0) but at Chiloé, the reverse occurred: Humboldt Penguins occurred significantly more frequently at the periphery than did Magellanic (χ² = 3.9, df = 1; P < 0.05; Humboldt's edge, 8; middle, 5; Magellanic edge, 103; middle, 195). The two species tended to form monospecific groups within beach parties. Both had conspecific nearest neighbours more often than expected by chance (P < 0.01; df = 1; Algarrobo: χ² = 92.6; Humboldt - Humboldt, 236; Humboldt - Magellanic, 4; Magellanic - Humboldt, 5; Magellanic - Magellanic, 9; Chiloé: χ² = 64.4, Humboldt - Humboldt, 7; Humboldt - Magellanic, 2; Magellanic - Humboldt, 2; Magellanic - Magellanic, 97).

Of 82 groups of penguins returning to Chiloé after foraging, 55 consisted of one bird, 16 of two, five of three, three of four, and three of five. Group size was not significantly different between Humboldt and Magellanic penguins (χ² = 2.6, df = 1, P > 0.05). Although five mixed-species groups occurred, there was a strong tendency for flocks to be monospecific (e.g., of 16 flocks of two birds, 12 flocks were exclusively Magellanic and four were exclusively Humboldt. The probability of such monospecific groupings occurring by chance is less than 0.001 (based on Humbolds constituting 25% and Magellancics 75% of total individuals observed).

**DISCUSSION**

Our study encountered a much greater area of overlap in the ranges of Humboldt and Magellanic penguins than had been described in the literature. This overlap suggests that the two species do not replace each other in response to any sharp environmental gradient, such as water temperature. Relative abundance of penguins changed from Chañaral and Algarrobo, with a preponderance of Humboldt Penguins, to Chiloé with a preponderance of Magellanic Penguins. The change-over area provided a valuable opportunity to examine differences between the two species that might account for their gradual replacement of each other.

Our data showed no obvious differences in foraging rhythms or foraging behavior between the two species. All *Spheniscus* penguins studied to date seem to have a main peak in departure from the colonies around dawn with birds returning around dusk (Ross 1971, Boersma 1977, Wilson and Wilson 1990). This feature seems invariant of locality (cf. Hays 1984b, Wilson and Wilson 1990, Scolaro and Subaro 1991) and is probably due to the fact that most penguin species seem to need light in order to forage (Wilson et al. 1993). Foraging performance was similar to that of the African Penguin, *Spheniscus demersus*, a close but geographically-isolated congener (mass = 3.0 kg, Williams 1995; speed, k = 6.7 km/h, uncorrected for measurement effects, Wilson et al. 1986a; distance travelled, k = 40.2 km mean maximum depth, approximately 35 m, exceptionally to 130 m, Wilson and Bain 1984, Wilson 1986a, Wilson and Wilson 1990, Wilson and Wilson 1995) which feeds on anchovy (Wilson 1985b, Duffy and Siegfried 1986). Scolaro et al. (in press) recorded that the mean swimming speed of 30 Magellanic Penguins returning to their colony at Punta Lobos was 6.8 km/h and in a review of penguin swimming speeds in general, Wilson (1995) noted that all species travelled at very similar speeds, although there was slight trend for larger species to swim faster. Given the similarity in body masses of Magellanic and Humboldt Penguins, it is thus unlikely that species-specific differences in swim speed exist.
The general similarity of the three species suggests that Spheniscus penguins are either unable or do not need to diverge from one another in foraging techniques, either in allopatry or along the coast of Chile, in the single area of sympatry between two members of the genus. Examination of foraging performance of the geographically-isolated Galapagos Penguin (Spheniscus mendiculus) would be useful to test this assumption.

Nesting habitats also appear generally similar throughout the genus. Magellanic, Humboldt and African penguins nest in a wide variety of habitats: under bushes, in burrows, and under rocks. Unlike the other two, Humboldt and Galapagos penguins do not usually nest in the open, perhaps as a result of intense insolation at lower latitudes. La Cock (1988) has shown that surface-nesting in African Penguins is more frequent during the cooler and more overcast austral winter at 33°S, suggesting that insolation is likely to constrain surface nesting of Humboldt and Magellanic penguins at Chaharal (29°S) and Algarrobo (33°30′S), our two northern study sites.

Nesting seasons diverged sharply between Magellanic and Humboldt penguins, suggesting that this factor is partially responsible for their differences in range. The year-round breeding and winter breeding peak of the Humboldt Penguin are similar to those of the African Penguin (La Cock et al. 1987), rather than to the strictly summer-nesting regime of the Magellanic Penguin. The Galapagos Penguin, under the influence of the southern hemisphere Humboldt Current, also nests primarily during the austral winter, although nesting may occur at any time of year (Boersma 1978).

The summer breeding of the Magellanic Penguin appears an adaptation to nesting in the far south. During the austral winter at Punta Arenas, only six hours are available for diurnally foraging penguins to obtain sufficient food for themselves and their offspring. African Penguins require ca. 10 h per day to forage for large chicks (Wilson and Wilson 1990), suggesting that winter breeding would not be possible, if Humboldt and Magellanic penguins have similar foraging time demands. On the other hand, at the northern edge of the Magellanic’s range, ambient air and ground temperatures may simply be too hot to allow summer nesting by this species.

While this may explain the present situation, it does not explain why Humboldt Penguins have not evolved to be summer nesters in the southern portions of their range and why Magellanic Penguins do not breed in winter farther north. We suggest four explanations. First, winter-breeding Magellanic may in fact be common, but our field work and most visits to the area have occurred in summer, so we have underestimated the extent of Magellanic nesting activity at Chaharal and Algarrobo. Similarly, winter breeding by Humboldt Penguins may occur at Chiloé, despite the heavy winter rains (Darwin 1933, Pickard 1971) which would be expected to inhibit burrow-nesting, because of flooding (cf. Stokes and Boersma 1991).

Second, the time since the two species came into contact with one another and with new marine environments along the west coast may have been too short to allow a shift in the nesting season of the Magellanic Penguin. If we assume, based on their present ranges, that the Humboldt Penguin originated on the Pacific coast of Latin America and the Magellanic Penguin on the Atlantic coast, after being geographically isolated during one of the Pleistocene glaciations of southern Chile (cf. Devillers 1978, Devillers and Terschuren 1978, Livezey 1986, for other taxa in the area), then the two species of penguin would have come into contact only once the ice layer retreated from the coast and the Magellanic Penguin was able to expand south and west.

The last extensive glacial blockage of the Chilean coast occurred as recently as 13,000 B.P. (Mercer 1976) and contact between the two species may have occurred even later, leaving the distribution and ecologies of the two species still in flux today. Interestingly, Boersma et al. (1990) note that Atlantic populations of Magellanic Penguins are still expanding northwards, although the antiquity of this trend is unknown. The Magellanic Penguin may also be expanding its range northward on the Pacific coast.

Third, where one species is rare, it may be forced to forage under less favorable conditions than can be exploited by the more common species, because of interspecific interactions. Although Magellanic and Humboldt penguins occur together, our data suggest that interspecific aggression results in a tendency to form monospecific aggregations.
both on land and at sea. Spheniscus penguins are often gregarious at sea (Siegfried et al. 1975, Hays 1984b, Wilson et al. 1986b). Selective aggression by adult African Penguins at sea reduces the numbers of juveniles in adult foraging groups, forcing the young birds to forage less efficiently than do adults (Ryan et al. 1987). In areas where either the Humboldt or Magellanic penguin is much more abundant than do adults (Ryan et al. 1987). In areas where either the Humboldt or Magellanic penguin is much more abundant than the other, similar aggressive behaviour may exclude the rarer species from foraging groups.

Finally, competition for nesting sites may prevent shifts in breeding season. If each species is dominant where more abundant, this would provide a continuing mechanism to prevent invasion by the less-numerous species. However, while burrow use at Chiloé was heavy, so that interspecific competition could have prevented use by Humboldt Penguins, empty nest sites were common at Algarrobo, Otway Sound and Chañaal.

We cannot determine the relative importance of these four explanations because we lack data on historical constraints, the importance of competition, and on the abundance of the two species throughout the year in their area of sympatry. Further study is necessary at colonies where the relative proportions of the two species are intermediate, such as Isla Santa María 36°S and Isla Mocha 38°S.

Indirect evidence may come from comparisons with detailed ecological studies of other species pairs in southern South America, such as diving-petrels (Pelecanoides spp.) (Johnson 1965), skuas (Catharacta spp.) (Devillers 1978), cormorants (Phalacrocorax spp.) (Devillers and Terschuren 1978, Rasmussen 1991) and steamer-ducks (Tachyeres spp.) (Livezey 1986, Livezey and Humphrey 1986). Even in the absence of such studies, our work suggests that the causes of species-replacements may be complex and multiple, and that species relationships may be unstable over time, as suggested by Wiens (1977) for competitive interactions between species.

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SUMMARY

Humboldt Spheniscus humboldti and Magellanic S. magellanicus penguins exhibit a zone of sympathy along the west coast of South America. We examined aspects of their foraging ecologies at four sites (three in the zone of sympathy) along the Chilean coast between 29°S and 53°S and found that intersite differences were more pronounced than inter-specific differences. In contrast, the two species differed in their breeding seasons.

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SAMENVATTING
De Humboldt-Spheniscus humboldti, en de Magellaan penguins, Spheniscus magellanicus, komen langs de westkust van Zuid-Amerika in een groot gebied sympatrisch voor. Onderzoek werd verricht betreffende hun voedsel ecologie op vier verschillende broedplaatsen, waarvan drie gelegen zijn in de sympatrische zone langs de Chileense kust tussen 29° en 53°S. Er werd vastgesteld dat verschillen tussen de broedplaatsen meer uitgesproken waren dan de inter-specifieke. De broedseizoenen der twee soorten zijn verschillend.

RESUME
Le Marchot de Humboldt Spheniscus humboldti et le Marchot de Magellan Spheniscus magellanicus vivent en sympatie dans une large zone de la côte ouest de l'Amérique du Sud. De recherche fait sur leur écologie de nourritage dans quatre endroits de reproduction différents, dont trois sont situés dans la zone où ils vivent en sympatie entre 29° et 53°S. Les chercheurs ont constaté que les différences entre les lieux de reproduction furent plus prononcées que les inter-spécifiques. Les périodes de reproduction étaient différentes entre les deux espèces.

APPENDIX I
Available information on the breeding season of the Humboldt Penguin

<table>
<thead>
<tr>
<th>MONTH</th>
<th>EVENT</th>
<th>LOCALITY</th>
<th>SOURCE</th>
</tr>
</thead>
<tbody>
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<td>January</td>
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<td>F. Todd unpublished</td>
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<td>Islas Ballestas, Peru</td>
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<tr>
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## APPENDIX 2

Available information on the breeding season of the Magellanic Penguin

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<tr>
<th>MONTH</th>
<th>EVENT</th>
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<tbody>
<tr>
<td>January</td>
<td>Young depart</td>
<td>Punta Tombo</td>
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<td>Young depart</td>
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<td>Scolaro 1984a</td>
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<tr>
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<td>Young depart</td>
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<td>Large young</td>
<td>Punta Medanosa</td>
<td>Birabier &amp; Scott 1939</td>
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<td>Departure</td>
<td>Falklands</td>
<td>Vallentin 1924</td>
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<td>Departure</td>
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<td>Carrara 1952</td>
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<tr>
<td>August</td>
<td>Arrival</td>
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<td>Renard 1931</td>
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<tr>
<td>August</td>
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<td>Punta Tombo</td>
<td>Scolaro 1984a</td>
</tr>
<tr>
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<td>Vallentin 1924</td>
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<td>Abbot 1860</td>
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<td>September</td>
<td>Arrival</td>
<td>Ria Deseado</td>
<td>Zapata 1967</td>
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<td>Boersma et al.</td>
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<td>Argentina</td>
<td>Carrara 1952</td>
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APPENDIX 2 CONTINUED

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WILSON, Rory P., Institut für Meereskunde, Dietsenbroeker Weg 20, D-24105 Kiel, Germany.

DUFFY, David C., Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa. Current address: Alaska National Heritage Program, Environment and Natural Resources Institute, University of Alaska Anchorage, 707 A Street, Anchorage, AK 99501, Alaska.

WILSON, Marie-Pierre, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa.

ARAYA, Braulio A., Instituto de Oceanología, Universidad de Valparaíso, Casilla 13-D Viña del Mar, Chile.

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