A Space Oddity: Geographic and Specific Modulation of Migration in Eudyptes Penguins

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Abstract

Post-breeding migration in land-based marine animals is thought to offset seasonal deterioration in foraging or other important environmental conditions at the breeding site. However the inter-breeding distribution of such animals may reflect not only their optimal habitat, but more subtle influences on an individual’s migration path, including such factors as the intrinsic influence of each locality’s paleoenvironment, thereby influencing animals’ wintering distribution. In this study we investigated the influence of the regional marine environment on the migration patterns of a poorly known, but important seabird group. We studied the inter-breeding migration patterns in three species of Eudyptes penguins (E. chrysolophus, E. filholi and E. moseleyi), the main marine prey consumers amongst the World’s seabirds. Using ultra-miniaturized logging devices (light-based geolocators) and satellite tags, we tracked 87 migrating individuals originating from 4 sites in the southern Indian Ocean (Marion, Crozet, Kerguelen and Amsterdam Islands) and modelled their wintering habitat using the MADIFA niche modelling technique. For each site, sympatric species followed a similar compass bearing during migration with consistent species-specific latitudinal shifts. Within each species, individuals breeding on different islands showed contrasting migration patterns but similar winter habitat preferences driven by sea-surface temperatures. Our results show that inter-breeding migration patterns in sibling penguin species depend primarily on the site of origin and secondly on the species. Such site-specific migration bearings, together with similar wintering habitat used by paraspatrics, support the hypothesis that migration behaviour is affected by the intrinsic characteristics of each site. The paleo-oceanographic conditions (primarily, sea-surface temperatures) when the populations first colonized each of these sites may have been an important determinant of subsequent migration patterns. Based on previous chronological schemes of taxonomic radiation and geographical expansion of the genus Eudyptes, we propose a simple scenario to depict the chronological onset of contrasting migration patterns within this penguin group.

Introduction

Migration is a widespread behaviour in the animal kingdom and is generally understood to be an adaptive mechanism in seasonal environments, by which individuals may compensate for locally unfavourable conditions outside the breeding period (review in [1,2]). Migrating individuals may exploit other environments with supplementary gain (i.e., survival) compared with resident species. However, in the case of land-based marine species, migration after the breeding period may also reflect the release from breeding constraints, allowing inter-breeders to forage in more optimal habitats that may not be seasonal, but which are too distant for adults to use while raising their offspring on land (e.g. [3]). These scenarios prompt questions about what factors influence inter-breeding area location and hence migration direction in land-based marine species. Other factors known to promote the emergence of migration behaviour relate to memories of favourable sites and to the inherent historical factors individuals may carry [1,4,5]. Indeed, memories of profitable sites strongly decrease migration cost [1,4,6] and hence are likely to facilitate migration in animals such as seabirds that commonly exhibit high wintering-site philopatry [5,7,8]. By contrast, the role of historical influences on migration patterns has been little investigated in seabirds (but see [9]).

Seabird migration has mostly been considered for flying species [5,10,11], whereas migration movements of swimming/diving species have been little studied (but see [9,12,13]), mainly because of methodological issues [14]. Diving, flightless birds such as penguins are much more constrained in their large-scale movements than are volant seabirds because of their slower locomotion mode [6], so they may better integrate environmental modulation and reflect the influence of the site of origin on
Migration in *Eudyptes* Penguins

**Materials and Methods**

**Ethics Statements**

All scientific procedures at the French Islands were approved by the ethics committee of the French Polar Institute (IPEV) and were conducted according to its guidelines and under permits of the Réserve Naturelle des Terres Australes Françaises and of the Comité de l’Environnement Polaire. On South-Africa’s Marion Island, a permit (SE11-07) was granted by the South Africa’s Department of Environmental Affairs. The greatest care was taken to minimize stress while handling animals, which lasted less than 20 min in all cases.

**Study Sites and Species**

The study took place in the southern Indian Ocean (Fig. 1), an oceanic region strongly influenced by the Antarctic Circumpolar Current (ACC), flowing eastwards. Circulation of the ACC in the western part of the study region is impacted by the warm southward flowing Agulhas Current [29]. Penguins were studied at four sites that together represent all the geological formations existing in the study region. From west to east these are: Marion, Crozet, Kerguelen and Amsterdam Islands, among which Marion and Amsterdam are the youngest in age, while Crozet and Kerguelen are much older (Table 1, [30–33]).

The genus *Eudyptes* diverged from the other penguins about 15 Ma ago and in turn speciated within about the last 8 Ma in the New Zealand area [34]. Extant species are aged at approximately 3–8 Ma [34–36]. Today *Eudyptes* is the penguin genus with the highest species richness, with 8 extant species, despite the recent extinction of an eudyptid in New-Zealand, *Eudyptes chathamensis* [37]. These medium-size penguins are commonly found on Southern Ocean islands between 37°S and 62°S, where they breed annually in large colonies [16]. Three *Eudyptes* species were investigated in this study. We first focused on one of the largest eudyptids, the macaroni penguin *E. chrysolophus*, which is the greatest consumer of marine prey among all seabirds and the most numerous penguin [38,39]. Secondly, we studied the smallest eudyptid, the rockhopper penguin, which was recently divided taxonomically into three species [40]. Two rockhopper penguins breed in the southern Indian Ocean, namely the eastern species *E. moseleyi*, a common subantarctic penguin, and the northern species *E. moseleyi*, which is restricted to the sub-tropics. We studied *E. chrysolophus* and *E. filholi* at the subantarctic Marion, Crozet and Kerguelen islands, where they breed sympatrically but with a 3-week difference in their breeding phenology [41]. In contrast, *E. moseleyi* has an earlier and longer breeding cycle [42], and was studied at subtropical Amsterdam Island (see details on migration schedule at each locality in Table S1 and [8,13,18,43,44]).

**Tracking Techniques**

Penguins were instrumented with one of the two following tracking devices when moult was complete on land, i.e., before the birds’ departure for migration during the inter-breeding period at sea (Table 2). Animals from Marion (n = 24) were equipped with ARGOS Platform Terminal Transmitters (PTTs) that emit signals to satellites allowing the calculation of their position [45]. These PTTs were fitted medially to the lower back to reduce drag, and fixed to the back feathers using cyanoacrylate glue (Loctite 401) and plastic cable ties. Devices used in 2005, 2006 and 2007 measured 91*48*21 mm (45 g) and in 2008 90*34*24 mm (30 g). They were duty-cycled to transmit for 8 hours with a transmission rate of 60 s and to switch off for the next 16 hours. Penguins from Crozet (n = 40), Kerguelen (n = 57) and Amsterdam (n = 20) were equipped with miniaturized light-based geolocation positioning...
devices (GLSs, British Antarctic Survey, Cambridge, UK). These devices were leg-mounted using specially designed flexible leg bands, following [13]. GLS loggers record ambient light level and time, allowing the estimation of latitude and longitude twice a day [46,47]. GLS tags also recorded ambient sea temperature, once during every 20 min period of continuous immersion, with a resolution of 0.0625 °C and an accuracy of ±0.5 °C. After the GLSs were recovered, logged data were analyzed following previously published methods [48], using the package ‘tripEstimation’ in R 2.9.0 [49] and assuming a mean daily travelling speed of 2 km h−1 [50] in order to estimate the most probable track. Location estimates in this case are not as accurate as for PTTs (tens to hundreds kms versus 1 km in the best cases, respectively [51,52]), and GLSs need to be recovered in order to collect the data, unlike in the case of satellite linked PTTs. However, the larger satellite tags with their antennae are more likely to produce adverse effects such as additional hydrodynamic drag on the foraging efficiency of these streamlined diving birds, especially over prolonged periods [14,53]. The total number of animals instrumented amounted to 141, with most of these (104 individuals) tracked during the same year (2007) from the four sites. Detailed information about the winter habitat used by penguins from Crozet, Kerguelen and Amsterdam Islands is provided for each species in published papers [8,13,18].

Analytic Tools Used
For all analyses we used R 2.9.0 [49]. Unreliable Argos locations were removed using the algorithm from the ‘argosfilter’ R package [54], with an upper-threshold speed of 2.1 m s−1 according to previous measurements [55]. In order to standardize the frequency of locations available along the tracks, we resampled the tracks obtained and made linear interpolations to conform to the 12 h frequency of GLS-derived estimates, using R packages ‘sp’ and ‘trip’. Locations received from the PTTs were thereafter analysed in the same way as GLSs to standardise interpretation of all the tracks.

Bearing was calculated between the point of origin at the colony and the farthest point reached for each animal studied, using

Table 1. Coordinates, environment and age of the four islands in the southern Indian Ocean from where the penguins were studied.

| Island       | Geographic coordinates | Oceanographic situation | Age (Ma) | Eudyptes species breeding          |
|--------------|------------------------|-------------------------|----------|-----------------------------------|
| Marion       | 46°54′S, 37°44′E       | Subantarctic            | 0.45     | E. chrysophalus, E. filholi       |
| Crozet       | 46°24′S, 51°45′E       | Subantarctic            | 8.1      | E. chrysophalus, E. filholi       |
| Kerguelen    | 49°20′S, 69°20′E       | Subantarctic            | 40       | E. chrysophalus, E. filholi       |
| Amsterdam    | 37°50′S, 77°31′E       | Subtropical             | 0.40     | E. moseleyi                       |

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Table 2. Summary of tracking devices used to study inter-breeding movements of Eudyptes chrysolophus, E. filholi and E. moseleyi penguins.

| Species tracked | Locality       | Year | Animals instrumented n (––) | Colony at locality | Device used (weight) |
|-----------------|----------------|------|-----------------------------|--------------------|---------------------|
| E. chrysolophus | Marion         | 2005 | 2 (1–1)                     | Macaroni Bay North | PTT – Telonics ST-10 (45 g) |
|                 |                 |      |                             |                    | FT – Sirtrack Kiwisa (30 g) |
| E. chrysolophus | Marion         | 2007 | 6 (4–2)                     | Swartkop, Bullard North | PTT – Telonics ST-10 (45 g) |
|                 |                 |      |                             |                    | FT – Sirtrack Kiwisa (30 g) |
| E. chrysolophus | Marion         | 2008 | 6 (3–3)                     | Swartkop, Bullard North | PTT – Sirtrack Kiwisa (30 g) |
|                 |                 |      |                             |                    | FT – Sirtrack Kiwisa (30 g) |
| E. chrysolophus | Crozet         | 2007 | 18 (9–9)                    | Jardin Japonais    | GLS - BAS MK4 (6 g) |
|                 |                 |      |                             |                    | FT – Sirtrack Kiwisa (30 g) |
| E. chrysolophus | Kerguelen      | 2006 | 21 (11–10)                  | Cap Cotter         | GLS - BAS MK4 (6 g) |
|                 |                 |      |                             |                    | FT – Sirtrack Kiwisa (30 g) |
| E. chrysolophus | Kerguelen      | 2007 | 16 (8–8)                    | Cap Cotter         | GLS - BAS MK4 (6 g) |
|                 |                 |      |                             |                    | FT – Sirtrack Kiwisa (30 g) |
| E. filholi      | Marion         | 2006 | 2 (1–1)                     | Trypot             | PTT – Telonics ST-10 (45 g) |
|                 |                 |      |                             |                    | FT – Sirtrack Kiwisa (30 g) |
| E. filholi      | Marion         | 2007 | 2 (?–7)                     | Trypot             | PTT – Telonics ST-10 (45 g) |
|                 |                 |      |                             |                    | FT – Sirtrack Kiwisa (30 g) |
| E. filholi      | Marion         | 2008 | 6 (?–7)                     | van den Boogaard, Swartkop | PTT – Sirtrack Kiwisa (30 g) |
|                 |                 |      |                             |                    | FT – Sirtrack Kiwisa (30 g) |
| E. filholi      | Crozet         | 2007 | 22 (11–11)                  | Pointe Basse       | GLS - BAS MK4 (6 g) |
|                 | Kerguelen      | 2007 | 20 (10–10)                  | Île Mayes          | GLS - BAS MK4 (6 g) |
|                 |                 |      |                             |                    | FT – Sirtrack Kiwisa (30 g) |
| E. moseleyi     | Amsterdam      | 2007 | 20 (14–6)                   | Entrecasteaux      | GLS - BAS MK4 (6 g) |

Kerguelen 2007 21 (11–10) Cap Cotter 2007 16 (8–8) Cap Cotter

‘circstat’ package. This was expressed as a circular measurement in degrees, with 0° equivalent to a northwards direction. We used circular analysis of variance with ‘high concentration F-test’ in R package ‘circular’ to compare bearings between sites or species. We excluded from these analyses the shortest tracks from Marion Island (duration <15 d; 1 E. chrysolophus and 2 E. filholi) that were probably caused by early battery failure. As a consequence, we assumed that bearings inferred from tracks over 15 d indicated the directions of wintering destination of the penguins, which seems to be the case in these species, which typically migrate directly towards population-specific wintering areas [8,13,18].

As GLS-derived location estimates are less precise than PTTs to depict wintering destination of the penguins, we also analyzed monthly average temperature records to compare seawater temperature used, possibly reflecting a latitudinal shift, between species. We carried out Student’s t-tests to compare these monthly-averaged temperature records between species. For the three sites where two species of Eudyptes penguin breed sympatrically, all locations available for the inter-breeding period of each species were also binned by degree of latitude. From this dataset, Student’s t-test was again used to examine for statistical differences in the latitudinal distributions of species. In all tests the threshold for significant differences was set at p = 0.05.

Habitat suitability for the penguins during the wintering period (as defined below) was modelled using Mahalanobis Distances Factor Analysis (MADIFA, [56]) in R package ‘adehabitat’. This method is appropriate for building habitat suitability maps from presence-only data, such as tracking data (as a comparison of methods see [57]). In the MADIFA, two principal components analyses (PCAs) successively summarize available information comprising: (a) the environment described by spatial variables; and (b) the relationship between the locations of animals and the environment. Environmental variables used were bathymetry (BATHY) and its gradient (BATHYG), sea-surface temperature (SST) and its gradient (SSTG), SST anomalies (SSTA), sea-surface chlorophyll a concentration (CHLA), mixed-layer depth (MLD) and eddy kinetic energy (EKE). MLD was a mean of annual data obtained since 1941. Previous studies have shown that these variables can be used to model at-sea movements of penguins [see [58–60]]. The temporal resolution selected for dynamic variables was one month, and the spatial grid 1° in accordance with the geolocation technique accuracy. The spatial data were obtained from the NOAA’s ETOPO (http://www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html?dbase = GRDE72), the Bloomwatch 180 (http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW180.jsp), the LOCEAN (http://www.locean-ipsl.upmc.fr/˜cdblod/mld.html) and the AVISO [http://las.aviso.oceanobs.com/las/servlets/dataset] websites. We modelled winter at-sea distribution of the two species that were studied at more than one site (that is, E. chrysolophus and E. filholi). We focused on the year 2007 when most of the tracking data were collected and all sites were sampled. The habitat model was based on the at-sea distribution of the birds from Crozet, and the model predictions were projected on the whole study area in order to compare predictions with the actual locations of the birds from all sites. We chose Crozet as a reference site for habitat modelling since it has an intermediate longitudinal location between the two other sites. The time window for modelling wintering habitat was one month, according to seasonality in this oceanic region [61], and taking into account the minimum mobility of the birds (that suggests intensive use of a wintering area, see [13]), which occurred in July for E. chrysolophus [8,13], September for E. filholi and May for E. moseleyi [18].

Results

From the 141 animals instrumented in the four sites we obtained 87 tracks, with 62 from the 2007 inter-breeding season.

Satellite-tracking from Marion Island

PTTs transmitted locations for 11 E. chrysolophus individuals from Marion, over periods from 14.7 d to more than 205 d
(mean±SD: 90.6±73.5 d). Among these, devices used in 2008 transmitted considerably longer (171.5±32.4 d). For E. filholi, 10 animals were followed, from 4.9 to 120.8 d (60.9±45.9 d all years pooled, and 99.8±20.6 in 2008). One PTT was recovered from E. chrysolophus in spring 2008.

Archival Tags from Crozet, Kerguelen and Amsterdam Islands

For GLS-equipped animals, 36 E. chrysolophus (65.5%) and 26 E. filholi (62%) were recaptured on Crozet and Kerguelen Islands, and 14 E. moseleyi (70%) on Amsterdam Island. Data which could be downloaded comprised 30 GLSs from E. chrysolophus, 25 from E. filholi and 11 from E. moseleyi.

General Inter-breeding Migration Patterns for the Study Birds

Tracked Eudyptes penguins performed long-range inter-breeding movements (Fig. 1), travelling thousands of km. These penguins concentrated in two areas: firstly to the west of Crozet, comprising penguins of the western sector (i.e. from Crozet and Marion), and secondly east of Kerguelen, with penguins from Kerguelen and Amsterdam. All penguins remained in the study region for the complete inter-breeding period, except a few individuals from Marion that reached the southern Atlantic Ocean (at least three E. chrysolophus and one E. filholi, with maximum ranges of 1993, 2239, 1772 and 1588 km, respectively). Penguins from Marion, and to a lesser extent from Crozet, showed higher angular variance in bearing (0.84 and 1.06 versus 0.62 and 0.77 for E. chrysolophus and E. filholi, respectively) than those from Kerguelen and Amsterdam, which typically migrated in a very narrow range of directions (0.01, 0.04 and 0.01 for E. chrysolophus, E. filholi and E. moseleyi, respectively, Fig. 2). When pooled together by site, Eudyptes penguins at each site had significantly different average bearings to those from all other sites (Table 3).

Comparisons between Sympatric Species

Bearings at maximum range were not significantly different between sympatric species, for all three sites studied with more than one species (Fig. 2, Table 4). For each site where they occurred together, E. chrysolophus dispersed significantly more southerly than E. filholi (t\(_{490}\) = 65.7, t\(_{544}\) = 51.1, t\(_{1119}\) = 69.5 for Marion, Crozet and Kerguelen, respectively, all p<0.00001, Fig. 3). This was confirmed by the ambient sea temperature records from the GLSs of the animals from Crozet and Kerguelen, with E. chrysolophus distributing in colder waters than E. filholi, except during the end of their at-sea period, when birds of both species were distributed close to their breeding localities (Fig. 4).

Comparisons between Parapatric Populations

In both E. chrysolophus and E. filholi, outbound migration bearings were significantly different between penguins from one site to any other one (Table 5).

Eudyptes chrysolophus. Winter habitat modelling of E. chrysolophus from Crozet, based on location data from July 2007, showed the primary importance of SST on the first axis of the first PCA and of BATHYG on the second axis (Table S2). The second PCA showed the highest scores for SST and SSTG on the first axis (Table S3). On the second PCA, variance was almost entirely captured on the first principal component, revealing the primary influence of SSTG on the winter distribution of E. filholi. Mapping of habitat suitability showed in this case a latitudinal band of more suitable habitat around 45°S, that separated into two branches east of 80°E (Fig. 6). Between these two branches occurred very low levels of suitability (0–20%), where the deepest values of MLD were found in the study area. The locations of E. filholi from Crozet in winter matched high suitability levels (97.9±2.1%) just north of Crozet, while for the Kerguelen birds, locations fell along the edges of the expected suitable habitat (66.2±25.6%). However, Kerguelen birds closely followed the dichotomic pattern predicted for habitat suitability (Fig. 6). No data from Marion were available for September 2007.

Discussion

Our investigation generates new insights into the inter-breeding period and winter biology of Eudyptes penguins at both species and population levels [13,17,62]. First, eudyptids (all species pooled) showed site-specific migration bearings. Second, at each site similar compass bearings were observed between sympatric species, though E. chrysolophus was consistently distributed in colder waters than E. filholi. And third, within each species we found different migration patterns for populations from different sites, although individuals foraged in similar environments. These results show that inter-breeding migration patterns in a group of sibling seabird species depend primarily on the site of origin and secondly on the species. Such site-specific migration bearings, together with similar wintering habitat used by parapatrics, support the hypothesis that migration behaviour is affected by the intrinsic characteristics of the originating site [63]. In this study two kinds of positioning devices were used to track penguin migration: Argos PTTs and GLS loggers, with the former providing better spatial accuracy (see Methods section). However, compared to the ocean-wide scale of our study the different instruments used will not impact our conclusions, especially since we accounted for the low accuracy of GLSs in the habitat modelling resolution.

Main Environmental Factors Driving the Eudyptes Distribution

The MADIFA approach showed the general importance of SST, SSTG, BATHYG and CHLA as the main environmental factors affecting Eudyptes penguin distributions during the inter-breeding period. High levels of MLD appeared negatively to affect habitat suitability for E. filholi: birds from Kerguelen were distributed at the periphery of the area where the highest levels of MLD (over 200 m) were found. For both species, predictive maps produced for the habitat used by individuals from Crozet corresponded well with observed distribution patterns of animals from Kerguelen. For both species also, the model predicted suitable habitat at more southerly latitudes in the Marion region than in the Crozet region, which is consistent with water mass circulation in this sector [29]. Finally, E. chrysolophus tracked from Crozet during July 2007 logically matched high levels of suitability (92.2±7.6%, Fig. 5) and importantly so did those from Kerguelen (74.2±16.9%), albeit some locations fell south of the areas predicted as the most suitable (50.0±20.6%). No E. chrysolophus locations were available in July 2007 from Marion.
Marion in 2008 appeared to distribute according to the model predictions (see Fig. 1 and Fig. 6), though the model was based on 2007 data. These results add support to the notion of low inter-annual variability in winter feeding grounds for eudyptid penguins [8] and hence the validity of our habitat modelling approach [3]. At a finer scale, penguins from Marion exhibited the largest variance in migration bearing, but we could not test for a potential effect of the colony of origin at this island because too few individuals were sampled from each colony (Table 2). However the small size of the island (area: 290 km²) argues against this potential effect because at the much larger Kerguelen Island (area: 7215 km²), the different species tracked from distinct colonies showed similar bearings. Finally, we recall that rockhopper penguins from Amsterdam Island (*E. moseleyi*) are now considered to belong to a separate species than *E. filholi* [40], which precluded including the former in the habitat suitability modelling of the latter. In any case, it would have been necessary to carry out such analyses separately for penguins from Amsterdam owing to the time shift in their migration schedule compared to rockhopper penguins from the other sites.

**Population-based Strategies: Evolutionary Implications**

Our large-scale study shows clear site-specific migratory patterns among the 4 islands. The fact that 96% of seabirds breed in colonies probably favours emergence of such site-specific migration patterns in these organisms: the possibility of individuals communicating and sharing information within the colony has been debated for a long time [25–27]. The existence of such strategies in our study reveals a major selective advantage to migrate to and exploit certain marine areas according to an

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**Table 3. Statistical comparison of migration bearings for *Eudyptes* penguins from their respective breeding sites.**

| Localities compared (no. individuals) | Circular Analysis of Variance |
|--------------------------------------|-------------------------------|
| Marion (18)/Crozet (22)              | \( F_1 = 24.8, p < 0.01 \) |
| Marion (18)/Kerguelen (33)           | \( F_1 = 18.7, p < 0.01 \) |
| Marion (18)/Amsterdam (11)           | \( F_1 = 5.3, p = 0.03 \) |
| Crozet (22)/Kerguelen (33)           | \( F_1 = 89.6, p < 0.01 \) |
| Crozet (22)/Amsterdam (11)           | \( F_1 = 106.7, p < 0.01 \) |
| Kerguelen (33)/Amsterdam (11)        | \( F_1 = 13.8, p < 0.01 \) |

Maximum distances from breeding localities were used to determine bearings. The number of individuals compared is indicated in brackets. doi:10.1371/journal.pone.0071429.t003

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**Figure 2. Outbound migration bearings of each sampled *Eudyptes* population.** Geographical direction of the farthest point reached from the colony for all individuals tracked was used to determine bearing. doi:10.1371/journal.pone.0071429.g002
Figure 3. Latitudinal distributions of the two sympatric *Eudyptes* species. Penguins from (A) Marion, (B) Crozet and (C) Kerguelen Islands. doi:10.1371/journal.pone.0071429.g003
animal’s origin, thereby maximizing winter food gains at an individual scale. Synchronized departure and return in eudyptids, together with highly coherent at-sea distribution, at-sea observations of flocks of individuals and possible synchronized dives between individuals [8,18,64,65] all suggest that penguins are strongly influenced by group dynamics in their foraging strategies in general. Such characteristics favour indeed the emergence of population-based foraging strategies [66]. Further, this site-specific migration behaviour suggests that the spatial heterogeneity of favourable habitats in the southern Indian Ocean is not recent, and may be significant in shaping penguin populations’ evolution (and possibly population trend, [17]). Recently, segregation of populations outside the breeding period has been identified as a strong barrier to gene flow in seabirds, and especially in penguins [67]. These behavioural mechanisms thus potentially drive genetic divergence in *Eudyptes* populations, with implications for subspeciation and eventually speciation through reproductive isolation [68].

**Species Segregation in Winter**

At the species level, winter tracking showed that macaroni penguins consistently wintered in colder, more southerly waters (the ‘Polar Frontal Zone’, see [8]) than did the sympatric rockhopper penguins (the ‘Subantarctic Zone’, see [18]), thus confirming previous inferences from dietary stable isotopes analyses [62]. Hence, spatial segregation is the main mechanism involved in resource partitioning between these closely-related species. Previous studies conducted during the breeding period showed only partial if any segregation of sympatric eudyptids on every ecological axis investigated: breeding chronology [41], foraging range and habitat [55,69], diving behaviour [70] and diet [71,72]. However, it has often been emphasised that sympathy in eudyptids involves no more than two species that include the smallest (the rockhoppers), in low numbers, together with one of the largest species (Macaroni, Royal *E. schlegeli* or Erect-crested *E. sclateri* penguins) [16]. Knowing the importance of size and body mass on penguins’ diving behaviour [73], this suggests that coexistence is probably also related to the vertical component of the birds’ foraging behaviour. Therefore, we can assume that during the breeding season, sympatric penguins are more constrained to return frequently to their colonies, and thus cannot segregate at a large spatial scale, their respective niches may be separated by the conjunction of all partial segregating mechanisms in time, space (horizontal and vertical components) and trophic resources, as it is the case in other congeneric penguins [74]. Outside the breeding period, the situation seems more straightforward, since the birds may distribute on a larger scale at that time without returning to the colonies and thus display clear-cut spatial segregation. Further, the small delay in the migration schedule may even be viewed as an adaptive mechanism allowing

![Figure 4. Mean temperature recorded by the GLS devices fitted on penguins from Crozet and Kerguelen. Values are mean±SD for *E. filholi* and mean - SD for *E. chrysolophus*. Different letters indicate significantly different (p<0.05) monthly means between the two species; for letters that are the same there was no significant difference. doi:10.1371/journal.pone.0071429.g004](image)

**Table 4.** Statistical comparison of migration bearings for sympatric species of *Eudyptes* penguins from their respective breeding sites.

| Locality   | *E. chrysolophus/E. filholi* (no. individuals) | Circular Analysis of Variance |
|------------|-----------------------------------------------|-------------------------------|
| Marion     | (10)/(8)                                      | *F*₁ = 2.2, *p* = 0.16        |
| Crozet     | (11)/(11)                                     | *F*₁ = 2.7, *p* = 0.12        |
| Kerguelen  | (19)/(14)                                     | *F*₁ = 3.6, *p* = 0.07        |

The number of individuals compared is indicated in brackets.

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a decrease in inter-specific competition for food [55] by decreasing the at-sea overlap between both species during the departure period, when birds have poor body condition after their moulting fast [20,21].

Evolutionary Inertia of the Migration Program

The locations of the breeding grounds and of suitable winter feeding habitat must have an important influence on migration bearings. However, in mammals, some populations migrate to a specific geographic destination even though the targeted habitat may have been strongly altered [75], suggesting that there may be elements of evolutionary inertia in the inherited migration program [1]. For some birds, expanding populations may have retained their original, but modified or apparently sub-optimal, winter quarters and migration routes [22]. Interestingly, all such cases have been reported for species whose juveniles migrate independently from the adults [76,77]. This evolutionary inertia suggests that migration patterns that are observed at a given time are not necessarily optimal at an evolutionary time scale and supports the hypothesis of a strong influence of paleoenvironments on site-specific migration patterns. In most seabirds, including penguins, emancipation of juveniles is generally not synchronous with the post-breeding migration of adults [15,78]. Thus, inter-generational learning may be limited in these animals and evolutionary inertia for migration programmes would be strong in adults, an idea supported by the strong inter-annual fidelity observed in their wintering areas [5,7,8]. Moreover, eudyptid penguins are associated with well-defined habitats during the inter-breeding period, notably regarding SST as revealed by our study and delimited by oceanographic fronts [8,18]. It is probable that large-scale shift of these boundaries over geological time scales towards or away from a breeding location, and the resulting changes in food available within the swimming range of penguins [16], have had an influence on their inter-breeding migration

Table 5. Statistics comparison of migration bearings between parapatric populations of *Eudyptes* penguins.

| Species      | Localities compared (no. individuals) | Circular Analysis of Variance |
|--------------|---------------------------------------|-------------------------------|
| *E. chrysolophus* | Marion (10)/Crozet (11)               | F₁ = 9.4, p < 0.01            |
| *E. chrysolophus* | Marion (10)/Kerguelen (19)            | F₁ = 29.9, p < 0.01           |
| *E. chrysolophus* | Crozet (11)/Kerguelen (19)            | F₁ = 162.2, p < 0.01          |
| *E. filholi*    | Marion (8)/Crozet (11)                | F₁ = 12.3, p < 0.01           |
| *E. filholi*    | Marion (8)/Kerguelen (14)             | F₁ = 6.8, p = 0.02            |
| *E. filholi*    | Crozet (11)/Kerguelen (14)            | F₁ = 11.3, p < 0.01           |

Maximum distances from sites were used to determine bearings. The number of individuals compared is indicated in brackets.

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Figure 5. Outputs of MADIFA habitat suitability modelling for *E. chrysolophus*. Map of winter habitat suitability predicted, with observed winter distribution of conspecifics. The model was based on the distribution of animals from Crozet only, during the month with minimum mobility (July). Locations of the colonies are indicated: Marion (grey circle), Crozet (white triangle) and Kerguelen (black triangle). Locations of the animals from Crozet (white) and Kerguelen (black) during the corresponding month are shown; no data available from Marion in July 2007.

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patterns. This inertia may explain why in our study the penguins from Crozet appear to behave paradoxically in the current situation. Indeed, the vast majority of these eudyptids from Crozet swam against the main flow of the ACC at the onset of their winter migration, while (1) such movements are expected to be costly, particularly after the prolonged fasting period spent on land during moult [20,21], and (2) suitable habitats must be available for both species at only moderate distances eastwards (Figs. 5 and 6). In contrast, other penguin species have been shown to have migration facilitated by currents [9].

A Scenario for Site-specific Onset of Eudyptes Migration

Here we propose a simple, plausible scenario based on previous work on taxonomic radiation [34,35] and molecular biogeography [36] of the genus *Eudyptes*, that may explain the site-specific migrating schemes observed in our study. We recall here that a fundamental assumption is that *Eudyptes* penguins’ current ecological optimum in terms of winter habitat remains similar over the entire period considered (see [8,18], this study). Since our results pointed out the influence of SST on penguins’ habitat, this scenario also integrates the historical latitudinal movements of the water masses in the southern Indian Ocean that have been depicted from analysis of sediments in the Southern Ocean seafloor [79,80].

In the southern Indian Ocean the first sites which could have been colonised by *Eudyptes* penguins were probably Kerguelen and Crozet, the oldest ones. This colonisation may have taken place as early as 5 Ma ago (separation of the clades “macaroni” and “rockhopper”), but more probably later, owing to subsequent speciation within this group (3 Ma ago, [35]) with geographic range extension around the Southern Ocean along the ACC pathway and away from their New-Zealand origin. It is likely that Kerguelen penguins developed an inter-breeding migration strategy directed with the main flow of the ACC (i.e., eastwards), due to the lower energetic cost of this strategy (Fig. S1A). However, Crozet penguins would have developed an opposite strategy, because in the early Pleistocene (from 1.9–1.3 to 0.9–0.42 Ma ago) there was a prolonged period of intense cooling [79,80] that may have driven penguins from Crozet to migrate towards the northwest to reach the closest warmer, optimal wintering waters advected by the Agulhas Current. This cooling period lead surface isotherms to be located at more northerly latitudes (by nearly 10°) than those occupied today [80]. At that time, Kerguelen penguins likely also adjusted the latitudinal component of their inter-breeding migration but keeping their eastwards longitudinal component (Fig. S1B). Then, from 0.9–0.42 Ma ago, climate warmed during the mid-Pleistocene transition and caused the Southern Ocean water masses to shift southwards. Owing to the importance of SST to these species’ habitat suitability, we assume penguins would have modified their migration routes in response to this phenomenon. More recently (0.45–0.40 Ma ago), Marion and Amsterdam Islands emerged: Marion centred on the eudyptid’s wintering habitat and Amsterdam to the north of it. Therefore, *Eudyptes* penguins that colonized Amsterdam from subantarctic islands [36] would have developed a migration route directed south-eastwards, accounting both for optimality to reach more southerly habitats, and to travel with the main flow of the ACC (Fig. S1C). Penguins colonizing Marion Island would have been less constrained in the direction towards which they migrate, because of the location of this island in the favourable habitat exploited by the penguins.

Conclusions and Perspectives

Our study suggests an influence of paleoenvironments in the different inter-breeding migration patterns for populations of seabirds such as penguins. To our knowledge, only one other study
attributed the divergent winter migration patterns observed in penguins to such possible historical influences. Our putative scenario is probably much simplified compared with the successive environmental events and other ecological factors, which all have led to the different strategies that are currently observed. Nevertheless, our proposed scheme explains how these strategies may be more site-specific than species-specific for this homogeneous penguin group. Importantly, this scenario supports the hypothesis that the longitudinal component of large-scale movements seems to be a deep, site-specific life-history trait, as it is shaped by the paleoenvironmental conditions governing the site. Conversely, the latitudinal component seems much more variable as populations would be able to finely adjust this component given local variation in the environment. However, limits to this plasticity may be reached in case of rapid changes in the environment, as seems to be the case today [60,81].

Our study also emphasizes the benefit of the comparative approach in tracking survey analyses. Comparison of winter migration patterns from multiple sites (e.g., [82]) and/or species (e.g., [10], this study) provides an understanding of ocean-scale movements of animals that is invaluable for conservation purposes. In our study, E. moseleyi was the species suffering the worst conservatism status (listed as ‘endangered’, [83,84]). Yet, it was also the only species in our study for which we could not compare parapatrics. In order to investigate fidelity in its environmental niche and promote conservation of this threatened species, it is urgently needed to track birds from the Tristan da Cunha group in the southern Atlantic Ocean, the only other region where it is distributed.

Supporting Information

Figure S1 Illustration of the chronological scenario proposed from the paleoenvironments to explain the *Eudyptes* penguins’ contrasted inter-breeding migration patterns. Cool period during early Pleistocene (A, from 1.9–1.3 to 0.9–0.42 Ma ago), with penguins at Crozet and Kerguelen Islands and putative migration routes (yellow arrows); then (B) warming during the mid-Pleistocene transition (from 0.9–0.42 Ma ago); and (C) emergence of Marion and Amsterdam Islands from 0.45–0.40 Ma ago, with putative migration routes for penguins from these islands (white arrows). Shaded areas symbolize supposedly suitable winter habitat for each period. Warm Agulhas (orange arrow) and cool Antarctic Circumpolar (blue arrow) currents are also indicated. (TIF)

Table S1 Migration schedule (peak departure/return dates from the colony) and tagging period of the three species surveyed (the macaroni *Eudyptes chrysolophus*, the eastern *E. filholi* and the northern *E. moseleyi* rockhopper penguins) on the four localities (Marion, Crozet, Kerguelen and Amsterdam Islands). References: *, this study, 8. Thiebot JB, Cherel Y, Trathan PN, Bost CA (2011) Inter-population segregation in the wintering areas of macaroni penguins. Mar Ecol Prog Ser 421:279–290. 13. Bost CA, Thiebot JB, Pinaud D, Cherel Y, Trathan PN (2009) Where do penguins go during the interbreeding period? Using geolocation to track the winter dispersion of the macaroni penguin. Biol Lett 5:473–476. 18. Thiebot JB, Cherel Y, Trathan PN, Bost CA (2012) Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. Ecology 93:122–130. 43. Crawford RJM, Cooper J, Dyer BM (2003) Population of the Macaroni Penguin *Eudyptes chrysolophus* at Marion Island, 1994/95–2002/03, with Information on Breeding and Diet. Afr J Mar Sci 25:475–486. 44. Crawford RJM, Cooper J, Dyer BM, Greynolds MD, Klages NTW, Nel DC, Nel JL, Petersen SL, Wollaardt AC (2003) Decrease in Numbers of the Rockhopper Penguin *Eudyptes chrysocome filholi* at Marion Island, 1994/95–2002/03. Afr J Mar Sci 25:487–498. (DOC)

Table S2 Summary of the MADIFA model for wintering *Eudyptes chrysolophus* from Crozet and Kerguelen Islands. Values indicate % of variance explained by the three first principal components of the PCAs and scores of the variables on those components. Abbreviations used for the variables: BATHY: bathymetry; BATHYG: gradient of bathymetry, SST: sea-surface temperature, SSTG: gradient of SST, SSTA: SST anomaly, MLD: mixed-layer depth, CHLA: sea-surface chlorophyll a concentration, EKE: eddy kinetic energy. (DOC)

Table S3 Summary of the MADIFA model for wintering *Eudyptes filholi* from Crozet and Kerguelen. Values indicate % of variance explained by the three first principal components of the PCAs and scores of the variables on those components. Abbreviations used for the variables: BATHY: bathymetry, BATHYG: gradient of bathymetry, SST: sea-surface temperature, SSTG: gradient of SST, SSTA: SST anomaly, MLD: mixed-layer depth, CHLA: sea-surface chlorophyll a concentration, EKE: eddy kinetic energy. (DOC)

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Author Contributions

Conceived and designed the experiments: CAB YC RJMC ABM. Performed the experiments: CAB JBT RJMC ABM. Analyzed the data: JBT. Contributed reagents/materials/analysis tools: CAB RJMC PNT DP. Wrote the paper: JBT YC.

References

1. Alerstam T, Hedenstrom A, Akesson S (2003) Long-distance migration: evolution and determinants. Oikos 103: 247–260.
2. Dingle H, Drake VA (2007) What is migration? Bioscience 57: 113–121.
3. Thiebot JB, Lescrocé A, Pinaud D, Trathan PN, Bost CA (2011) Larger foraging range but similar habitat selection in non-breeding versus breeding sub-Antarctic penguins. Antarct Sci 23: 117–126.
4. Mueller T, Fagan WF (2008) Search and navigation in dynamic environments - from individual behaviors to population distributions. Oikos 117: 654–664.
13. Bost CA, Cherel Y, Trathan PN, Bost CA (2011) Inter-population segregation in the wintering areas of macaroni penguins. Mar Ecol Prog Ser 421: 279–290.

14. Ballard G, Toniole V, Ainley DG, Parkinson CL, Arriaga KR, et al. (2010) Responding to climate change: Adélie Penguins confront astronomical and ecologically unprecedented challenges. Ecology 91: 2066–2089.

15. González-Sols J, Felisicimo A, Fox JW, Afanasev V, Kolbeinsson Y, et al. (2009) Influence of sea surface winds on shearwater migration detours. Mar Ecol Prog Ser 391: 221–230.

16. Pinet P, Jaeger A, Cordier E, Potin G, Le Corre M (2011) Colonialization of tropical seabird behavior. PLoS ONE 6: e27693.

17. Wilson RP, Calik B, Kousinou P, Adelung D (1998) The overwinter movements of a chimera type. Polar Rec 34: 107–112.

18. Bouvet DN, Thiebot JB, Pirin D, Cherel Y, Trathan PN (2009) Where do penguins go during the interbreeding period? Using geolocation to track the winter dispersion of the macaroni penguin. Biol Lett 5: 473–476.

19. Williams TD (1995) The Penguins. Oxford: Oxford University Press. 295 p.

20. Warman J (1975) The Crested Penguins. In: Stonehouse B, editor. The biology of penguins. London: Macmillan. 189–269.

21. Patz K, Raya Rey A, Schiavini A, Clausen AP, Lutz BH (2006) Winter migration of rockhopper penguins (Eudyptes chrysocome) breeding in the Southwest Atlantic: in utilisation of different foraging areas reflected in opposing migration trends. Polar Biol 29: 735–744.

22. Thiebot JB, Cherel Y, Trathan PN, Bost CA (2012) Coexistence of oceanic predators on wintering penguins explained by population-scale foraging segregation in space or time. Ecology 93: 122–130.

23. Caires DK (1989) The regulation of seabird colony size—a Hinterland model. Mar Biol 113: 141–146.

24. Cherel Y, Charrassin JB, Challet E (1994) Energy and protein requirements for molt in the king penguin Aptenodytes patagonicus. Am J Physiol 266: R1182–R1188:

25. Green JA, Boyd II, Woakes AJ, Warren NL, Butler PJ (2009) Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin Eudyptes chrysocome. J Avian Biol 40: 59–58.

26. Weimerskirch H, Bertrand S, Silva J, Marques JC, Goya E (2010) Use of social information in seabirds: compass rafts indicate the heading of food patches. Ibis 115: 517–534.

27. Weimerskirch H, Bertrand S, Silva J, Marques JC, Goya E (2010) Use of social information-centers for food-finding. Ibis 115: 517–534.

28. Gonza´lez-Solı´s J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration of tropical seabird behavior. PLoS ONE 6: e27663.

29. Clarke JA, Ksepka DT, Stucchie M, Urbina M, Giannini N, et al. (2007) Estimation of presence-only methods for modeling species distribution. Diversity 8: 169–185.

30. Banks J, Van Buren A, Cherel Y, Whitfield JB (2006) Genetic evidence for three species of rockhopper penguins, Eudyptes chrysolophus. Polar Biol 30: 61–67.

31. Stahl JC, Derenne P, Jouventin P, Moguil J, Teulières L, et al. (1985) Le cycle reproduction du goéland de l’archipel Crozet: Eudyptes chrysocome, le Goéland macaroni, et Eudyptes chrysolophus, le Goéland sauteur. Oiseau Rev Fr Ornithol 55: 27–43.

32. Giret A, Weis D, Gre´goire M, Mattielli N, Moine B, et al. (2003) L’Archipel de l’île Crozet. Chronique des 137 années de recherches géologiques 137: 15–23.

33. Giret A, Weis D, Zhou X, Cottin JY, Tourpin S (2003) Ge´ologie des ıˆles Crozet. Revue Franc¸aise d’Ichtyologie. 199–202.

34. Bourdon C, Weimerskirch H, Bost CA (2012) Projected poleward shift of king penguins Eudyptes chrysocome from the Southern Ocean. Mar Ecol Prog Ser 330: 283–295.

35. Crossin GT, Trathan PN, Crawford RJM (2013) The macaroni penguin and rookery (E. chrysolophus) penguins: an assessment of techniques and species comparison. Wildl Res 26: 789–803.
70. Hull CL (2000) Comparative diving behaviour and segregation of the marine habitat by breeding Royal Penguins, *Eudyptes schlegeli*, and eastern Rockhopper Penguins, *Eudyptes chrysoceorus filholi*, at Macquarie Island. Can J Zool 78: 333–345.

71. Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar Ornithol 22: 1–192.

72. Hull CL (1999) Comparison of the diets of breeding royal (*Eudyptes schlegeli*) and rockhopper (*Eudyptes chrysoceorus*) penguins on Macquarie Island over three years. J Zool Lond 247: 507–529.

73. Wilson RP (1995) Foraging Ecology. In: Perrins CM, Bock WJ, Kikkawa J, editors. The Penguins. Oxford: Oxford University Press. 81–106.

74. Wilson RP (2010) Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. Pume Ecol 24: 646–657.

75. Andersen R (1991) Habitat deterioration and the migratory behavior of moose (*Alces alces*) in Norway. J Appl Ecol 28: 102–108.

76. Berthold P, Helbing AJ, Mehr G, Querner U (1992) Rapid microevolution of migratory behavior in a wild bird species. Nature 360: 668–670.

77. Berthold P (1999) A comprehensive theory for the evolution, control and adaptability of avian migration. Ostrich 70: 1–11.

78. Hamer KC, Schreiber EA, Burger J (2002) Breeding biology, life histories, and life history-environment interactions in seabirds. In: Schreiber EA, Burger J, editors. Biology of Marine Birds. Boca Raton: CRC Press. 217–261.

79. Becquery S, Gersonde R (2002) Past hydrographic and climatic changes in the Subantarctic Zone of the South Atlantic - The Pleistocene record from ODP Site 1090. Palaeogeogr Palaeoclimatol Palaeoecol 182: 221–239.

80. Kemp AES, Grigorov I, Pearce RB, Naveira Garabato AC (2010) Migration of the Antarctic Polar Front through the mid-Pleistocene transition: evidence and climatic implications. Quat Sci Rev 29: 1993–2009.

81. Cresswell KA, Wiedenmann J, Mangel M (2008) Can macaroni penguins keep up with climate- and fishing-induced changes in krill? Polar Biol 31: 641–649.

82. Frederiksen M, Moe B, Daunt F, Phillips RA, Barrett KT, et al. (2012) Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. Diversity Distr 18: 530–542.

83. IUCN (2012) IUCN Red List of Threatened Species. Version 2012.2. Available: http://www.iucnredlist.org. Accessed 05 November 2012.

84. Robson B, Glass T, Glass N, Glass J, Green J, et al. (2011) Revised population estimate and trends for the Endangered Northern Rockhopper Penguin *Eudyptes moseleyi* at Tristan da Cunha. Bird Conserv Int 21: 454–459.