

Gentlemen first? 'Broken stick' modelling reveals sex-related homing decision date in migrating seabirds

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Abstract

Technical progress in animal-borne tracking and movement data analysis has facilitated the understanding of the interplay between successive periods in the life cycle of migratory animals. We investigated how sex differences on the constraints of homing may influence migration to breeding areas in crested penguins (genus *Eudyptes*). We used a novel approach to infer homing decision date, a precise point in time that translates statistically as a change point in the current distance of the animal to its colony ('broken stick' modelling approach, R codes provided here). We applied this approach to geolocation tracking data on migration in three *Eudyptes* species, from three localities in the southern Indian Ocean (five populations). Sex had a subtle and consistent influence on the temporal activity of the 66 animals during their migratory journey. Males began migration to the breeding localities earlier than females, by an average of 9.1 (range: 4.5–13.5) days. This difference was statistically significant in 4 of 5 populations, and occurred among all species, sites and years surveyed. Our study shows an original application of a recent modelling approach to detect change point in movement data. Our results suggest that sex-specific constraints related to breeding in migrating animals may also modify activity schedules well before breeding commences.

Introduction

Understanding the interplay between successive periods of the life cycle in migratory animals has long been constrained by our inability to track individuals across different phases (Sorensen *et al.*, 2009). To track migrating animals' movements over their complete non-breeding phase is difficult indeed, especially marine species such as seabirds, which are generally inaccessible when not breeding (Hamer, Schreiber & Burger, 2002). Consequently, our knowledge about their non-breeding phase has long remained poor (Warham, 1975; Stahl *et al.*, 1985; Williams, 1995). However, over the last two decades, both animal-borne tracking and movement data analysis techniques have considerably improved and unravelling the behavioural adjustments taking place at sea may now be feasible (Wilson & Vandenabeele, 2012).

In this study we therefore used some of the latest developments in both tracking and data analysis to investigate how the sex-specific adjustments on arrival date in their upcoming breeding season may affect migration patterns in penguins. We focused on the crested penguins (genus *Eudyptes*). This is the most diverse penguin genus, and their complete non-breeding phase while at sea is now well described for several species, thanks exclusively to the

use of recently developed, ultra-miniaturized light-based geolocation loggers (GLSs).

Penguins are very sensitive to instrumentation (Bannasch, Wilson & Culik, 1994), which precludes the use of large archival tags for extended periods at sea for both technical and ethical reasons. However, the size, shape and logging capacity of GLSs allowed us to collect data during their entire period of 5–7 months at sea, without major ethical considerations.

Eudyptid penguins can venture thousands of kilometres from their colonies to reach their wintering areas, travelling ~50 km per day (see Bost *et al.*, 2009; Thiebot *et al.*, 2011, 2012). Among studies on crested penguin species over the non-breeding season, no significant sex differences in foraging areas have been reported (Pütz *et al.*, 2002, 2006; Raya Rey, Trathan & Schiavini, 2007; Bost *et al.*, 2009; Thiebot *et al.*, 2011, 2012). Yet, male *Eudyptes* penguins typically arrive at the colony *c.* 1 week prior to females in order to occupy nesting places (Warham, 1975; Williams, 1995). It is unknown whether this difference in arrival date between sexes is due to the fact that males may leave their offshore wintering site and start their pre-breeding migration earlier than females. Alternatively, both sexes may leave the wintering area concurrently, but that males travel faster than females, or that

females remain at sea near the shore while males occupy their nests, remains to be measured.

To identify the date when male and female penguin started to migrate back from their wintering site to their breeding site (the ‘homing decision date’), we relied on an innovative ‘broken stick’ modelling method. A method for unambiguously and clearly identifying this event is necessary because (1) light-based geolocation precludes direct inference of homing date from visual inspection of the location estimates because of their low spatial accuracy; (2) inference from the single farthest location may lack support from objective criteria of general animal movement and (3) in seasonal environments, migration activity may coincide with solar cues such as the equinox (Hamer *et al.*, 2002), a period when latitude estimation is unreliable (Wilson *et al.*, 1992; Hill, 1994). Our underlying hypothesis was that contrasts between sexes in arrival date for breeding may be reflected in shifts in pre-breeding migration timing. We applied the modelling method to a previously acquired large dataset on the complete migration in three *Eudyptes* species, the macaroni *E. chrysolophus*, the eastern rockhopper *E. filholi* and the northern rockhopper *E. moseleyi* penguins, from three localities in the southern Indian Ocean (Bost *et al.*, 2009; Thiebot *et al.*, 2011, 2012).

Materials and methods

Datasets were collected at three localities in the southern Indian Ocean: Crozet (46°24’S, 51°45’E), Kerguelen (49°20’S, 69°20’E) and Amsterdam (37°50’S, 77°31’E) islands. Penguins were equipped with leg-mounted miniaturized light-based geolocation loggers (GLSs, model: BAS MK4, British Antarctic Survey, Cambridge, UK) in 2006 and 2007. These loggers (mass: 6 g) record ambient light level every 10 min, thus geographic location can be estimated from local day/night duration and sun zenith time (Wilson *et al.*, 1992; Hill, 1994). This light-based geolocation approach allows location to be estimated twice a day, that is, at mid-day and midnight, with a mean spatial error of tens to hundreds km for diving animals (*c.* 120–130 km on average, Staniland *et al.*, 2012). In addition, these loggers also record ambient sea temperature with a resolution of 0.06°C and an accuracy of ±0.5°C. Temperature records were incorporated in the location estimation process, together with a land mask precluding terrestrial locations and specific movement parameters (mean, variance and

distribution of movement speed) for the animals, following a Bayesian approach (Sumner, Wotherspoon & Hindell, 2009; Thiebot & Pinaud, 2010). This approach enabled the determination of the most probable location estimates. In total, 66 individual tracks were collected from the three sites: 12 in 2006 (*E. chrysolophus* from Kerguelen only) and 54 in 2007 (both *E. chrysolophus* and *E. filholi* species on both Crozet and Kerguelen islands, and *E. moseleyi* on Amsterdam; Table 1).

From these tracks, we calculated the great-circle distance of each location to the corresponding colony of origin. To infer the dates of change in migration pattern, we used a ‘broken stick’ modelling approach (e.g. Authier *et al.*, 2012), described below. Specifically, we used the distance to the colony to estimate when birds started to migrate back to their rookeries. This metric was normalized to the interval 0–1 (excluding boundaries) by dividing by the observed maximum distance to the colony for each bird. We analyzed these data with beta regression (Cribari-Neto & Zeilis, 2010). This regression technique bypasses the need to transform the original data to meet the normality assumption of residuals while intrinsically taking into account the heteroskedasticity and skewness typical of continuous data ranging from 0 to 1 (Cribari-Neto & Zeilis, 2010). We let $y_{i,t}$ denote the distance ratio of the i th bird on day t :

$$y_{i,t} \sim \text{beta}(\mu_{i,t}, \tau) \tag{1}$$

where $\mu_{i,t}$ is the mean distance ratio:

$$\text{logit}(\mu_{i,t}) = \beta_{1,i} + \beta_{2,i} \times \text{day}_t, \tag{2}$$

and τ^{-1} is a dispersion (variance) parameter.

We were interested in testing a broken stick model, where two periods can be distinguished: first a migration away from the breeding colony followed by a return journey to the colony. The break point T_i is the date at which a bird started its back migration (i.e. the homing decision date):

$$\text{logit}(\mu_{i,t}) = \beta_{1,i} + \begin{cases} \beta_{2,i} \times (\text{day}_t - T_i), & \text{if date} \leq T_i \\ \beta_{3,i} \times (\text{day}_t - T_i), & \text{if date} > T_i \end{cases} \tag{3}$$

To estimate T_i , we used a profile likelihood approach: the likelihood for the model described by the equation above was computed for each location date spanning the interbreeding period of penguins (see Fig. 1 for an example). The value of T_i

Table 1 Summary of the penguin groups studied (species, locality, year and number of individuals of each sex), homing decision date (HD date: median ± standard deviation in days, format: dd/mm) and average 95% confidence interval width (CI: mean ± standard deviation in days) for male and female penguins in each group surveyed between successive breeding periods

Species	Locality	Year	Males			Females		
			<i>n</i>	HD date	95% CI	<i>n</i>	HD date	95% CI
<i>E. chrysolophus</i>	Crozet	2007	4	04/10 ± 5.3	7.4 ± 4.1	7	12/10 ± 8.9	10.4 ± 5.8
	Kerguelen	2006	7	27/08 ± 10.8	6.6 ± 1.3	5	07/09 ± 7.4	7.2 ± 2.9
	Kerguelen	2007	3	21/08 ± 7.7	5.7 ± 1.2	4	02/09 ± 6.5	7.3 ± 1.3
<i>E. filholi</i>	Crozet	2007	5	22/09 ± 4.6	7.7 ± 3.1	6	26/09 ± 7.6	6.9 ± 2.4
	Kerguelen	2007	9	15/09 ± 7.1	5.4 ± 1.9	5	29/09 ± 12.9	5.5 ± 0.7
<i>E. moseleyi</i>	Amsterdam	2007	7	16/05 ± 6.5	5.8 ± 2.1	4	22/05 ± 3.8	5.6 ± 1.1

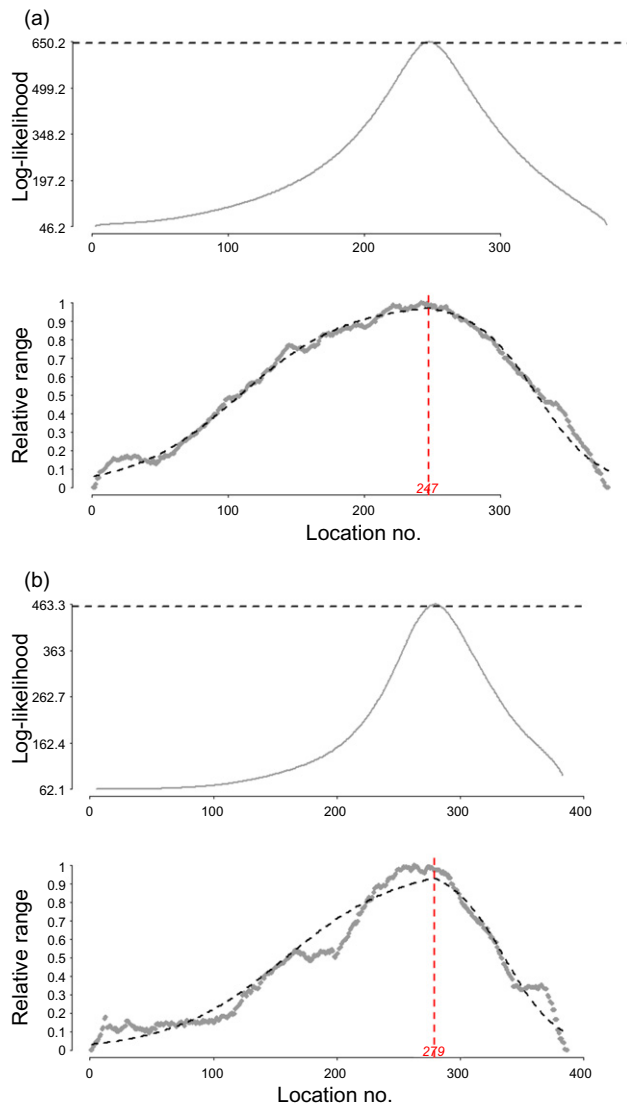


Figure 1 Two examples (a, b) of a 'broken stick' determination process for homing decision date, based on the log-likelihood for existence of a change point (upper panel) in the relative distance reached from the colony, at each location (lower panel): grey thick line shows the relative distance from the colony reached by the penguin, dashed black curve shows the beta regression fitted and vertical dashed line shows the change point inferred. The two examples shown refer to a male (a) and a female (b) *Eudyptes filholi* from Kerguelen; homing decision date was determined for location estimates no. 247, that is, on 15 September 2007, and no. 279, that is, on 28 September 2007, respectively.

that maximized the likelihood was thus evaluated, and an approximate confidence interval for T_1 was computed with a likelihood ratio test with 1 d.f. From the individual homing decision dates identified by this method, we then measured the difference in these dates between males and females in each group or between groups using Student's *t*-test after systematic validation of normality distribution of data with

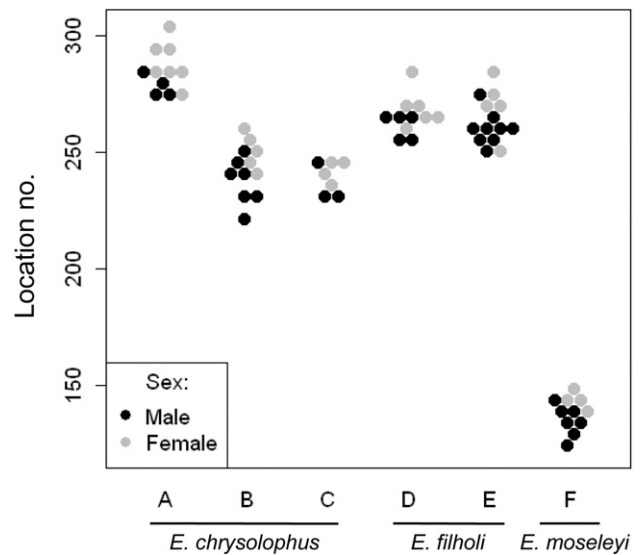


Figure 2 'Bee swarm' plot showing the homing decision date inferred for each individual penguin surveyed in the different groups of species/locality/year available: A: *Eudyptes chrysolophus* Crozet, 2007; B: *E. chrysolophus* Kerguelen, 2006; C: *E. chrysolophus* Kerguelen, 2007; D: *E. filholi* Crozet, 2007; E: *E. filholi* Kerguelen, 2007; F: *E. moseleyi* Amsterdam, 2007.

Shapiro–Wilk normality test. In all tests, statistical significance was set at 5%.

Computations were performed with the software R (R Development Core Team, 2012) with the *betareg* package (Cribari-Neto & Zeileis, 2010); the *beeswarm* package was also used to draw figures. The R code used is provided as electronic supplementary material (Supporting Information Appendix S1 and S2) with an example to run.

Results

For each of the 66 migrating penguins, the broken stick model found a date of change in the individuals' distance to the colony likely reflecting homing decision date (Table 1). The 95% confidence intervals around these dates averaged 6.8 days. Regarding macaroni penguins, at Crozet, the date of the change detected was significantly earlier by 8 days in males than in the corresponding females ($t_{8,87} = 2.29, P = 0.048$, Fig. 2). On Kerguelen, between two successive years studied, the homing decision dates were not significantly different, for each sex (males, 2006 vs. 2007: $t_{5,46} = 0.30, P > 0.7$; females, 2006 vs. 2007: $t_{6,91} = 1.49, P = 0.2$). Therefore, we pooled both years. As for Crozet, males from Kerguelen had a homing decision date that was significantly earlier on average than that of females ($t_{16,64} = 2.60, P = 0.019$), with a difference of nearly 12 days observed in both years. In eastern rockhopper penguins, males started their inbound migration significantly earlier (of 4.5 days) than females ($t_{8,44} = 2.44, P = 0.039$) on Crozet. On Kerguelen, the greatest difference between sexes was observed (13.5 days) but was not statistically significant

($t_{5.36} = 1.72$, $P = 0.143$). Finally, male northern rockhopper penguins from Amsterdam started to return back to the colony 5.4 days earlier than females, and this difference was significant ($t_{8.97} = 2.57$, $P = 0.03$).

Discussion

Previous colony-based studies have shown that male *Eudyptes* penguins arrive first on the breeding sites; our survey of penguins' at-sea movements before breeding shows that this is not because they travel faster than females, but because they leave their wintering areas earlier. Sex had a measurable and consistent influence on the onset of migration in each of the three penguin species. Despite unbalanced sample sizes, males consistently started their return to their breeding localities earlier than females by an average of 9.1 (range: 4.5–13.5) days among the five groups of penguins. This pattern of earlier homing decision date in males occurred for all three species, on three localities and for both years surveyed, and hence seems general to the genus.

Male penguins typically exhibit strong territorial activity on their arrival at the breeding site, both when occupying their former nest site and when competing for a new nest site (Williams, 1995). Therefore, competition among males to access prime nesting locations seems a key determinant in the timing of return to the colony as a better nesting site will improve their chances of mating (Warham, 1975; Coulson, 2002). In this context, our results suggest that availability of good nesting locations on the colony would be a limiting factor driving penguins' activity schedule at sea and operating within all three study species.

The approach used here widens the scope of GLS dataloggers in seabirds. These devices are increasingly used because they are small enough to be leg-mounted (Bost *et al.*, 2009) and apparently do not modify foraging of diving seabirds (Ropert-Coudert *et al.*, 2009). This is a great advantage over back-mounted satellite tags, which may have non-negligible impacts (Bannasch *et al.*, 1994), especially over prolonged periods (Bost *et al.*, 2004). Nevertheless, one drawback of data collected from GLS loggers is their relatively low accuracy in the spatial dimension (Staniland *et al.*, 2012). Here, we show that fine details in seabirds' behaviour can be obtained from these loggers when considering data in the temporal dimension.

Acquiring these data was only possible because of the fertile cross-pollination between cutting-edge techniques: advanced light-based geolocation for prolonged tracking and a novel use of discontinuous (broken stick) beta regression with movement data. Though no cross-validation with *in situ* measurements could be carried out, our study on oceanic migrants could objectively determine the homing decision date for each tagged individual. Importantly, this method is better than choosing a single estimate of geographic location. Single estimates may be erroneous because of the low spatial accuracy of each GLS location (especially during vernal and autumnal equinoxes), or because of erratic movements of the tracked animal, whatever the tracking device used. Our approach is therefore preferable because it takes a broader view of the

animal's movement, and is not dependent upon a single location. It also suggests that valuable information can be extracted from equinoctial locations, and for this reason that studies should aim at refining them rather than discard them.

Previous use of this modelling technique in behavioural ecology has focused on estimating change points for ontogenetic shifts with stable isotope data in seals (Authier *et al.*, 2012). Determining a change point in biological data is a very broad requirement in ecology and this method is particularly relevant in this context because it also provides a confidence interval around the estimated value (see also Roth *et al.*, 2012). We recognize that we applied this method in the context of a relatively simple, though fairly general, case of migration: penguins moved relatively directly to their wintering area, and then came back to their colony in a straightforward manner. In the case of animals performing more complex migration schemes (such as other seabirds, e.g. Shaffer *et al.*, 2006), it might be necessary to conduct this analysis on a truncated portion of the track where the looked-for change point is likely to occur, or to enhance the model to account for the possibility of several change points in the dataset.

Further research to understand why male eudyptid penguins are able to forgo 9 days of foraging at sea to return to land earlier than females, would require monitoring energetics at sea throughout the wintering period, possibly using heart rate recording (Green *et al.*, 2009). Such data would help inform as to whether males are more efficient in the manner that they utilize their wintering areas. Indeed, male macaroni penguins tend to dive deeper than females during winter (Green *et al.*, 2005), which may confer male eudyptids a slightly higher potential foraging ability than females at that time.

Specializations in behavioural traits between males and females may lead to spatially and/or temporally skewed distribution of the individuals (Cook *et al.*, 2007; Catry *et al.*, 2012). Our results developed this theory further: behavioural correlates of sexes during the breeding season may indeed change an individuals' activity schedule well before breeding commences.

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Appendix S1. R code used to perform broken stick modelling.

Appendix S2. Example of time-series of distance to the penguin colony, to be run with the code provided.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site: