Universiteit Antwerpen

This item is the archived preprint of:

Mates but not sexes differ in migratory niche in a monogamous penguin species

Reference:

1 **Mates but not sexes differ in migratory niche in a monogamous penguin species**

2

3 Jean-Baptiste Thiebot[1], Charles-André Bost[2], Nina Dehnhard[3], Laurent Demongin[3], Marcel

4 Eens[3], Gilles Lepoint[4], Yves Cherel[2] and Maud Poisbleau[3]

5

6 [1]National Institute of Polar Research, 10-3 Midori-cho, Tachikawa, 190–8518 Tokyo, Japan

7 [2]Centre d'Études Biologiques de Chizé, UMR 7372 du CNRS-Université de La Rochelle,

8 79360 Villiers-en-Bois, France

9 [3]University of Antwerp, Department Biology - Ethology, Campus Drie Eiken,

10 Universiteitsplein 1, 2610 Antwerp (Wilrijk), Belgium

11 [4]University of Liège, MARE Center, Laboratory of Oceanology, 15 allée du 6 août, 4000

12 Liège, Belgium

13 **Author for correspondence:** Jean-Baptiste Thiebot; e-mail: jbthiebot@gmail.com

14

15

16   Strong pair bonds generally increase fitness in monogamous organisms, but may also underlie

17   the risk of hampering it when re-pairing fails after the winter season. We investigated whether

18   partners would either maintain contact or offset this risk by exploiting sex-specific favourable

19   niches during winter in a migratory monogamous seabird, the southern rockhopper penguin

20   *Eudyptes chryscocome*. Using light-based geolocation we show that although the spatial

21   distribution of both sexes largely overlapped, pair-wise mates were located on average 595 ±

22   260 km (and up to 2500 km) apart during winter. Stable isotope data also indicated a marked

23   overlap between sex-specific isotopic niches (δ^{13}C and δ^{15}N values) but a segregation of the

24   feeding habitats (δ^{13}C values) within pairs. Importantly, the tracked females remained longer

25   (12 d) at sea than males, but all re-mated with their previous partners after winter. Our study

26   provides multiple evidence that migratory species may well demonstrate pair-wise

27   segregation even in the absence of sex-specific winter niches (spatial and isotopic). We

28   suggest that dispersive migration patterns with sex-biased timings may be a sufficient

29   proximal cause for generating such a situation in migratory animals.

30

31   **Keywords:** pair bonds, winter, monogamy, geolocation (GLS), seabird, stable isotopes

32

1. Introduction

In 1758, the Swedish taxonomist Carl Linnaeus named the passerine bird chaffinch *Fringilla coelebs* (meaning 'bachelor finch') because he would mainly observe males throughout winter, while females migrated to lower latitudes (in [1]). For monogamous species, such sex-based segregation increases the risk of failure to re-unite partners in the subsequent breeding season, and may therefore considerably reduce fitness [2]. It is generally assumed that this potentially risky strategy would be offset by the exploitation of sex-specific, specialised niches, in which each partner may increase foraging gains and/or adjust timing of return compared to a shared-niche situation [3].

In seabirds, which can mate for life [4], it is unknown whether partners maintain close contact while at sea until the next breeding season. Recent surveys showed that partners may migrate to similar wintering areas, but without providing evidence for either close contact or segregation once there [5]. Here we focused on the southern rockhopper penguin *Eudyptes chryscocome*. Eudyptid penguins are serially monogamous [6], despite undertaking long-range migrations during winter [7,8]. Recent progress made in miniaturized archival light-level geolocators has enabled the tracking of penguins at sea over the complete non-breeding season, with minimal disturbance [7,8]. We combined this spatial approach with stable isotope analysis to provide explicit inferences regarding pair bonds throughout winter.

2. Material and methods

Study birds originated from a colony on New Island, Falkland Islands/Islas Malvinas (51.7°S; 61.3°W), where individuals of known sex have been surveyed since 2006 through systematic reading of individual, sub-cutaneous transponders [9]. We deployed leg-mounted global location sensing (GLS) loggers (weighing ≤ 6 g) on each mate of 10 penguin pairs when moulting was complete (24 March – 6 April 2012). These loggers record light level,

58   immersion and seawater temperature. Birds were recaptured and blood-sampled in October

59   when they returned to breed. Their movements were estimated following a maximum-

60   likelihood approach including latitude correction by seawater temperature, in the R package

61   'tripEstimation' [10] (see the electronic supplementary material, S1). Light-based geolocation

62   provides two daily location estimates, with an expected spatial error of ~120–130 km for non-

63   flying migrants tracked with the loggers we used [11]. Kernel utilization distribution contours

64   were computed from location estimates, using 'adehabitat' in R with a search radius *of* 2

65   degrees of latitude/longitude.

66   Stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) were measured on red blood

67   cells (see S2). Three additional pairs (six birds) were blood-sampled at the same time to

68   increase our sample size. Isotopic half-life for δ^{15}N in red blood cells of rockhopper penguins

69   was assumed to amount to 14.3 days, following experimental work on another penguin

70   species of comparable body mass [12]. Since turnover rates are similar for δ^{13}C and δ^{15}N in

71   endotherms [13], almost all blood C and N was renewed after ~57 d (corresponding to four

72   half-lives). Hence, the time integration of blood δ^{13}C and δ^{15}N corresponded to a two months

73   period before sampling, i.e. to the end of the winter tracking period. Isotopic niches were

74   compared between sexes from Bayesian standard ellipses computed in the package 'SIAR'

75   [14].

76   Paired and non-paired *t*-tests were used to investigate whether niche components differed

77   between sexes and partners, respectively. Differences were considered as significant for $p <$

78   0.05.

79

80   **3. Results**

81   Sixteen birds (7 males and 9 females, composing 7 pairs from the previous season) were

82   recaptured at their return on 7–21 October 2012. In all 7 pairs, partners remained together for

83   the new breeding season. Of the 16 retrieved loggers (80% of deployed GLSs), 13 were

84   downloaded successfully (6 from males and 7 from females, composing 5 complete pairs).

85   The loggers indicated that females left the colony ~6 d earlier than males (t_{12} = -3.08, p =

86   0.01; paired data: t_4 = 2.90, p = 0.04), and returned ~6 d later (t_{12} = 3.60, p = 0.004; paired

87   data: t_4 = -6.74, p = 0.0025; table 1).

88   Geolocation data showed wide-range (37.2–58.2°S; 32.8–72.3°W), dispersive migration of

89   the penguins, mainly over the Patagonian Shelf (figure 1*a*). Although females seemed to

90   distribute over a wider area than males, especially in the north, the distribution of both sexes

91   overlapped markedly and no statistical difference in maximum range reached or total distance

92   travelled was found between sexes (t_{12} = 1.64, p = 0.13 and t_{12} = -0.28, p = 0.78, respectively)

93   or partners (t_4 = -1.94, p = 0.12 and t_4 = -1.10, p = 0.33, respectively). Nevertheless, partners

94   were systematically segregated over a large spatial scale: inter-mates distance averaged 595 ±

95   260 km across the non-breeding period and peaked at 885 km in August (range 216–1351 km

96   among pairs, figure 1*b*). In one pair this distance approached 2500 km in June, when the

97   female moved to the Argentine Basin.

98   The birds' isotopic signatures showed a continuum of values, with a marked overlap

99   between both sexes: the females' niche overlapped by 42% with that of males (figure 2*a*, see

100   S3). Within pairs, isotopic niches differed in $\delta^{13}C$ (t_9 = 2.30, p = 0.047) but not significantly

101   in $\delta^{15}N$ (t_9 = 1.90, p = 0.089). Similarly, the recorded temperatures overlapped for both sexes

102   during each month (all p values > 0.05; figure 2*b*, but the paired females exploited

103   significantly warmer waters than their partners, on average (April–October, t_{34} = -2.38, p =

104   0.023).

105

106   **4. Discussion**

5

107   Our results provide multiple evidence that throughout their winter migration, paired male and

108   female penguins were spatially segregated over a larger scale than the expected error range of

109   geolocation estimates. That partners were located hundreds of km apart over most of the year

110   did not prevent our study birds from re-pairing with their previous mates for breeding.

111   Besides the 7 pairs that re-united, two birds returned but mated with a new partner as the

112   previous one did not return. Thanks to our individual long-term monitoring data [9], we are

113   confident that the remaining four birds that were not detected did not return to the colony but

114   either dispersed to another colony or died at sea during winter.

115   Over their annual cycle, penguin mates seem to spend only limited time together. During

116   the breeding period, colony-based observations ([6]; authors' pers. obs.) indicate that partners

117   reunite for ~20–30 d (day and night) from courtship to egg laying periods, ~2–3 d during the

118   incubation, and at night only during chick-rearing (over ~70 days). During the 3 weeks of

119   moult spent ashore, partners may or may not re-unite at the nest ([6]; authors' pers. obs.).

120   Partners then spend winter apart (this study). Overall, partners are together only during ~23%

121   of the annual cycle. The high pair fidelity in these penguins thus cannot be explained by a

122   prolonged time spent in close vicinity. However, these periods spent together occur at the nest

123   exclusively, where the amount of elaborate pair-formation behaviour might affect mate

124   retention [15]. In this respect, it is noteworthy that penguin species that do not build a nest

125   have lower mate-fidelity (in [4]).

126   In our study, the segregation of partners did not originate from a sex-based differential

127   migration leading to exclusive winter niches (as opposed to other species [1,3]). Rather, our

128   data showed that although females tended to distribute in warmer (i.e., more northerly)

129   waters than males, the habitats exploited by each sex overlapped markedly, as depicted by the

130   isotopic niches (figure 2a, see also [16]) at the end of the winter period. Stable isotope

131   analysis showed that (1) there is a continuum of isotopic niches exploited by male and female

132   penguins in winter, (2) the isotopic niche of both sexes overlapped extensively at that time,

133   (3) for a given $\delta^{13}C$ value, both sexes had similar $\delta^{15}N$ values, suggesting that they fed on the

134   same type of prey, and (4) paired males and females segregate in their isotopic niche, at least

135   at the end of the winter period. That migratory animals may well demonstrate pair-wise

136   segregation even in the absence of distinct, sex-specific winter niches brings the question of

137   the proximate cause underlying this pattern. One mechanism may be the dispersive migration

138   mode of the southern rockhopper penguin. This observation from our dataset is consistent

139   with the large variation in individual routes shown by winter satellite tracking in this species

140   [17]. Such dispersive migration, together with females leaving the colonies before the males,

141   would hence result in partners being segregated *de facto*, without any exclusion mechanism.

142   Given that parapatric populations over-winter in the same area [8,17], while sibling

143   rockhopper species in the Indian Ocean conversely show directed migrations to population-

144   specific wintering areas [7], this dispersive migratory behaviour may minimize potentially

145   high levels of local intra-specific competition. Hence, overlapping winter niches between

146   sexes do not preclude segregation within pairs in monogamous migratory animals, and

147   dispersive migration with sex-biased timings may yet be a sufficient proximal cause for

148   generating this pattern.

149

161 **Data accessibility.** The penguin tracks are available on BirdLife International's seabird

162 tracking database (http://www.seabirdtracking.org/?q=Sphenisciformes).

163 **Authors' contributions.** Study conception and design: M.P., L.D. and C.-A. B.; data

164 acquisition, analysis and interpretation: all authors, manuscript draft and revision: all authors.

165 All authors approved the publication. We have no competing interests.

166

References

1. Cristol DA, Baker MB, Carbone C. 1999 Differential migration revisited: latitudinal segregation by age and sex class. In *Current ornithology*, vol. 15 (eds. VJ Nolan, ED Ketterson, CF Thompson), pp. 33–88. New York: Kluwer/Plenum.

2. Rowley I (1983) Re-mating in birds. In *Mate choice* (ed. P Bateson), pp. 331–360. Cambridge University Press.

3. Catry P, Phillips RA, Croxall JP. 2005 Sexual segregation in birds: patterns, processes and implications for conservation. In *Sexual segregation: ecology of the two sexes* (eds. KE Ruckstuhl, P Neuhaus). Cambridge University Press.

4. Bried J, Jouventin P. 2002 Site and mate choice in seabirds: an evolutionary approach. In *Biology of marine birds* (eds. EA Schreiber, J Burger), pp. 263–305). CRC Press.

5. Müller MS, Massa B, Phillips RA, Dell'Omo G. 2015 Seabirds mated for life migrate separately to the same places: behavioural coordination or shared proximate causes? *Anim. Behav.* **102**, 267–276.

6. Warham J. 1975 The Crested Penguins. In *The biology of penguins* (ed. B Stonehouse), pp. 189–269. London: Macmillan.

7. 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.

8. Ratcliffe N, Crofts S, Brown R, Baylis AMM, Adlard S, Horswill C, Venables H, Taylor P, Trathan PN, Staniland IJ. 2014 Love thy neighbour or opposites attract? Patterns of spatial segregation and association among crested penguin populations during winter. *J. Biogeogr.* **41**, 1183–1192.

9. Poisbleau M, Dehnhard N, Demongin L, Parenteau C, Quillfeldt P, Eens M. 2013 Females paired with new and heavy mates reduce intra-clutch differences in resource allocation. *PLoS ONE* **8**, e72136.

10. Thiebot JB, Pinaud D. 2010 Quantitative method to estimate species habitat use from light-based geolocation data. *Endang. Species Res.* **10:** 341–343.

11. Staniland IJ, Robinson SL, Silk JRD, Warren N, Trathan PN. 2012 Winter distribution and haul-out behaviour of female Antarctic fur seals from South Georgia. *Mar. Biol.* **159**, 291–301.

12. Barquete V, Strauss V, Ryan PG. 2013 Stable isotope turnover in blood and claws: a case study in captive African penguins. *J. Exp. Mar. Biol. Ecol.* **448**, 121–127.

13. Thomas SM, Crowther TW. 2015 Predicting rates of isotopic turnover across the animal kingdom: a synthesis of existing data. *J Anim Ecol* **84**, 861–870.

14. Jackson AL, Inger R, Parnell AC, Bearhop S. 2011 Comparing isotopic niche widths among and within communities: SIBER – stable isotope Bayesian ellipses in R. *J. Anim. Ecol.* **80**, 595–602.

15. Ainley D, Le Resche R, Sladen W. 1983 *Breeding biology of the Adélie Penguin.* Berkeley, CA: University of California Press.

16. Dehnhard N, Voigt CC, Poisbleau M, Demongin L, Quillfeldt P. 2011 Stable isotopes in southern rockhopper penguins: foraging areas and sexual differences in the non-breeding period. *Polar Biol.* **34**, 1763–1773.

17. Pütz K, Ingham RJ, Smith JG, Lüthi BH. 2002 Winter dispersal of rockhopper penguins *Eudyptes chrysocome* from the Falkland Islands and its implications for conservation. *Mar. Ecol. Prog. Ser.* **240**, 273–284.

214 **Table 1.** Winter migration metrics (n = 13 birds, 6 males and 7 females) for southern

215 rockhopper penguins surveyed from New Island. Values are mean ± SD.

216

Bird group	Departure date	Return date	Time at sea (d)	Maximum range (km)	Total distance travelled (km)
All	4 April ± 5 d	14 October ± 5 d	194 ± 7	999 ± 476	17219 ± 6470
Males	7 April ± 3 d	11 October ± 4 d	187 ± 3	793 ± 134	17781 ± 6291
Females	1 April ± 4 d	17 October ± 3 d	200 ± 4	1176 ± 599	16737 ± 7081

217
218

219 **Figure 1.** Winter migration of 13 southern rockhopper penguins surveyed from New Island

220 (white circle) using GLS loggers. *(a)* Distribution area (95% kernel distribution contours) of

221 males (*n* = 6) and females (*n* = 7) are shown with blue and red curves, respectively, and an

222 example of one pair is detailed (blue dots circled in black : male ; red dots circled in white :

223 female). Background greyscale symbolizes bathymetry (darker for deeper areas), and black

224 dotted lines show the 200 m isobath. *(b)* Monthly distance between location centroids of five

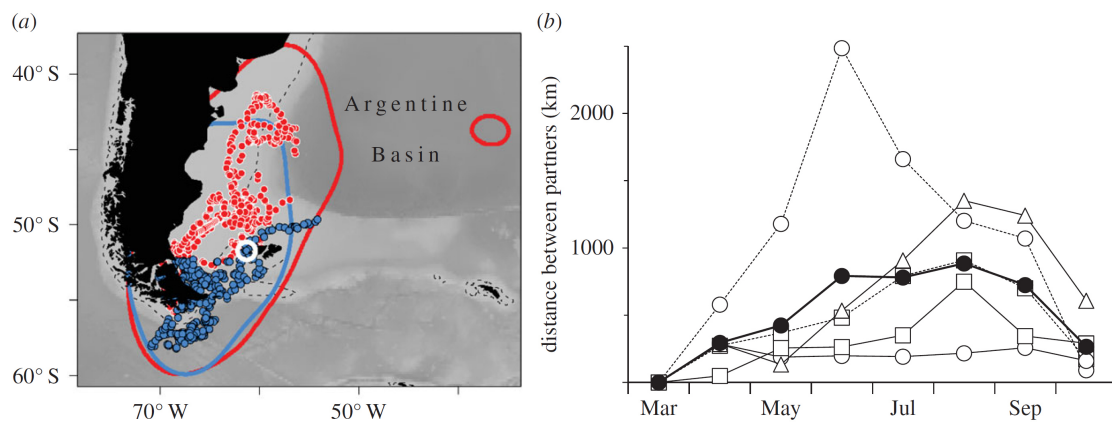225 penguin pairs (average of all pairs is shown in bold); values are mean ± s.d.

226

227
228
229

230   **Figure 2.** Southern rockhopper penguins' winter niche. *(a)* Blood $\delta^{13}C$ and $\delta^{15}N$ values of

231   male (triangles) and female (circles) penguins from the seven GLS-fitted and three additional

232   sampled pairs (pair mates share same colour). Standard Bayesian ellipse areas corrected (solid

233   line) and uncorrected (dashed line) for small sample sizes are shown for males and females

234   (black and grey lines, respectively). *(b)* Monthly seawater temperature recorded by loggers

235   from males (n = 6; filled symbols) versus females (n = 7; open symbols); values are mean +

236   s.d. for females and mean – s.d. for males.

237
238

239