

1 **Did the animal move? A cross-wavelet approach to**
2 **geolocation data reveals year-round whereabouts of**
3 **a resident seabird**

4 **Amédée Roy · Karine Delord ·**
5 **Guilherme T. Nunes · Christophe**
6 **Barbraud · Leandro Bugoni · Sophie**
7 **Lanco-Bertrand**

8 Received: date / Accepted: date

9 **Abstract** Considerable progress in our understanding of long-distance migra-
10 tion has been achieved thanks to the use of small lightweight geolocator devices
11 (GLS). Errors of geolocation are however important, difficult to estimate, have
12 a complex structure leading to poor precision and accuracy. Thus, the study of

A. Roy
Institut de Recherche pour le Développement (IRD)
MARBEC (Univ. Montpellier, Ifremer, CNRS, IRD)
Avenue Jean Monnet 34200 Sète, France E-mail: amedee.roy@ird.fr

K. Delord
Centres d'Etudes Biologiques de Chizé UMR7372 Centre National de la Recherche Scien-
tifique 79360 Villiers en Bois, France

G. T. Nunes
Centro de Estudos Costeiros, Limnológicos e Marinhos Universidade Federal do Rio Grande
do Sul (FURG), Campus Litoral Norte Avenida Tramandaí, 976 95625-000 Imbé, RS, Brazil

C. Barbraud
Centres d'Etudes Biologiques de Chizé UMR7372 Centre National de la Recherche Scien-
tifique 79360 Villiers en Bois, France

L. Bugoni
Biological Sciences Institute and Seabirds and Sea Turtles Laboratory Universidade Federal
do Rio Grande (FURG) Avenida Itália, km 8, Carreiros 96203-900 Rio Grande, RS, Brazil

S. Lanco-Bertrand
Institut de Recherche pour le Développement (IRD)
MARBEC (Univ. Montpellier, Ifremer, CNRS, IRD)
Avenue Jean Monnet 34200 Sète, France

13 short-distance migrants or resident birds remains challenging. Here we aimed
14 at elucidating the sex-specific marine space uses of a resident tropical seabird,
15 the masked booby (*Sula dactylatra*) over the full annual life cycle at the Fer-
16 nando de Noronha archipelago (Brazil), using GLS and synchronicity analyses
17 between movement and saltwater immersion data. Masked boobies ($n = 31$)
18 showed a resident behaviour over their entire annual cycle. We inferred from
19 the wavelet analysis that birds traveled way and back from the colony on
20 consecutive trips of short length (~ 2 -4 days) and short range (~ 100 -300
21 km) from the east of the colony. Duration and range of trips depended on
22 the sex of the individual and on the time of the year. Trip duration increased
23 gradually from the end of the breeding period to the post-breeding period,
24 probably due to the release of the central-place breeding constraints. During
25 the pre-breeding period, females had farther ranges eastward and spent more
26 time in water than males. Despite inherent limits of light-based geolocation,
27 synchronicity analysis of geolocation data revealed year round whereabouts
28 of the resident tropical masked booby and sex-specific movement behaviour,
29 which could be used more broadly to investigate resident or short-migrants
30 animal movement based on GLS data.

31 **Keywords** activity pattern · breeding constraints · GLS · masked boobies ·
32 saltwater immersion · sexual dimorphism · *Sula dactylatra*

33 **Introduction**

34 Animals move to feed, to find mates, to avoid risks such as predation or ad-
35 verse climatic conditions, or to locate breeding areas, within the range of
36 their motion and navigation abilities (Bowler and Benton, 2005; Nathan et al.,
37 2008). Birds in particular, including seabirds have great mobility and naviga-
38 tion skills, and many migratory birds are able to travel over long distances,

39 to occupy distant areas at different seasons, returning repeatedly to the same
40 localities from year to year (Egevang et al., 2010; González-Solís et al., 2007;
41 Shaffer et al., 2006; Stenhouse et al., 2012; Weimerskirch and Wilson, 2000;
42 Wilson et al., 1998). In opposition, other seabirds can be referred as resident
43 (or sedentary) when their distribution and center of distribution remain more
44 or less the same all year round, and from year to year (Newton, 2008; Schacter
45 and Jones, 2018).

46 Resident behaviour might be explained by a reliable supply of food avail-
47 able locally all year, and/or if there are territorial advantages to regular year-
48 round visits to their breeding site (Newton, 2008). It therefore might be related
49 to an energy-saving strategy, where birds avoid metabolic costs associated with
50 migration, but rather invest energy in remaining in seasonally less favorable
51 habitats (Garthe et al., 2012). In particular, numerous tropical seabirds are
52 identified as resident species such as petrels, shearwaters, tropicbirds, boobies
53 and noddies (Ballance et al., 2006; Diamond, 1978). Indeed, in the tropics
54 seasonality is generally less pronounced and food resources have smoother
55 variation than in temperate and polar regions (Ashmole, 1971; Longhurst and
56 Pauly, 1987).

57 Migration may have evolutionary consequences at the species level, as it
58 increases the probability of encountering individuals from other populations
59 and, consequently, of gene flow. Therefore, being resident can have important
60 consequences on gene flow disruption between populations and on population
61 genetic structures (Friesen et al., 2007), which in the end conditions the evo-
62 lutionary resources populations may rely on in changing environments. Resi-
63 dency behaviour is thus of great interest for future investigations into the topic
64 of population resilience. Current knowledge of seabird residency is however
65 principally based on direct observations (Jaquemet et al., 2004; Olson et al.,
66 2001), and to our knowledge few studies aimed at confirming or elucidating

67 year-round behaviour in a resident seabird using tracking devices (Schacter
68 and Jones, 2018).

69 Masked booby (*Sula dactylatra*) is a pan-tropical seabird found in every
70 ocean on or off nearly every coast except the eastern Atlantic, northern In-
71 dian Ocean and the central-eastern Pacific (Nelson, 2005). This species has
72 been the subject of a relatively large number of movement-based studies dur-
73 ing breeding period (Lerma et al., 2020; Wilkinson et al., 2020). Yet, masked
74 boobies' movements during the non-breeding period remain unclear. Adults
75 would stay in the vicinity of the colony and would eventually disperse widely
76 (thousands of km from the colony), post-breeders returning back to the colony
77 intermittently (Del Hoyo et al., 1992; Nelson, 2005). Apart from the uncer-
78 tainties related to masked boobies post-breeding whereabouts, other questions
79 remains, particularly concerning their reversed sexual dimorphism (hereafter
80 RSD, when females are heavier and larger than males). Several studies have
81 expected a sex-related differences in the foraging strategies of masked boobies,
82 assuming that the challenges related to foraging in tropical ecosystems charac-
83 terized by low productivity presumably exert strong selection pressure for the
84 body size differences in tropical seabird species (Lewis et al., 2005; Weimer-
85 skirch et al., 2009). However, if some studies suggested a higher foraging effort
86 by females (Weimerskirch et al., 2009), most of them did not demonstrate dif-
87 ferences between sexes in foraging trips (Poli et al., 2017; Sommerfeld et al.,
88 2013; Young et al., 2010).

89 Yet, it is very challenging to accurately track year-round resident seabirds
90 such as masked boobies. Due to attachment and power limitations, the use
91 of tracking devices such as GPS loggers and Argos transmitters is most often
92 limited to short time periods (from hours to months) (Ropert-Coudert et al.,
93 2004; Wakefield et al., 2009; Wilson et al., 2002). Light-level data loggers or
94 global location sensors (GLS) remains a preferred option for studying seabird

95 spatial behaviour perennially since they are small enough to be attached on a
96 plastic ring, energy-efficient to be deployed for up to several years, and with
97 reduced costs. The main idea to infer position from light data relies on the
98 analysis on twilights derived from highly frequent light intensity records (Hill,
99 1994; Lisovski et al., 2019). However, light signals may be subject to errors
100 due to physical features (e.g. shade from vegetation or animal body covering
101 the device), weather (e.g. cloud cover), and behaviour of animals (individuals
102 nesting in burrows or being sat on the logger). As a consequence, positions
103 derived from light records remain much less precise than positions estimated
104 from GPS (Ekstrom, 2007; Lisovski et al., 2012; Phillips et al., 2004). For such
105 reason, GLS and associated analytical methods are particularly relevant for
106 elucidating migratory movements, as well as for movements that are in the
107 order of magnitude of geolocation errors (e.g. 65 ± 54 km in longitude and
108 358 ± 499 km in latitude, as estimated in our study Fig. 1). In the latter case,
109 the stumbling block remains in distinguishing movements from geolocation
110 error to detect animal movements. Hopefully, many GLS also record external
111 data such as saltwater immersion and sea surface temperature, which is crucial
112 for improving geolocation estimations and/or interpreting GLS data (Guilford
113 et al., 2009; Merkel et al., 2016).

114 Wavelet analyses have been widely used in ecology (e.g. Bertrand et al.,
115 2008; Cazelles et al., 2008; Fablet et al., 2013; Jenouvrier et al., 2005) since
116 this method is highly appropriate to analyze periodic patterns in biological
117 time series that are often noisy, non-linear and non-stationary (Cazelles and
118 Stone, 2003). Wavelet analysis provides appropriate tools for comparing the
119 frequency contents of time-series, drawing conclusions about series' synchronic-
120 ity at certain periods and across certain ranges of time. Therefore, it could be a
121 relevant tool for investigating behavioural patterns from noisy GLS data. The
122 overarching hypothesis being that significant synchronicity between saltwater

123 immersion time-series and light-based position estimations reveals with higher
124 confidence if the position deviation to the colony is related to real movement
125 rather than geolocation error.

126 In this study, we used GLS to understand year-round at-sea movements of
127 the masked booby. Objectives were to elucidate the post-breeding movements
128 of masked boobies and sex-specific non-breeding behaviours, and to demon-
129 strate the relevance of wavelet analysis as an analysis tool for GLS data derived
130 from short-migrants or resident species.

131 **Material and Methods**

132 Study site

133 Fernando de Noronha (hereafter FdN, 03°50'S, 32°30'W) is an offshore archipelago
134 (21 islands and islets, 18.2 km²) lying at 360 km east from the mainland city
135 of Natal, Brazil. FdN is a clear priority for biodiversity conservation at the
136 Brazilian federal state level (through the Ministry of Environment, ICMBIO)
137 and scientific data are critical for improving the design of conservation policies.
138 This archipelago hosts the highest diversity of seabirds in Brazil, with eleven
139 species reported to breed there (Mancini et al., 2016). In order to elucidate
140 the year-round whereabouts of masked boobies breeding on the archipelago,
141 fieldwork was conducted on one of the secondary island, Meio island, which
142 hosts one of the main masked booby breeding colony with 388 active nests (i.e.
143 with eggs or chicks) censused in April 2018 (Antas, 1991, authors unpublished
144 data).

145 GLS data analysis

146 *GLS deployment*

147 Breeding adults raising two to seven weeks old chicks were caught on 4-6 May
148 2017 and fitted with GLS attached to a plastic ring. In total, 34 individuals
149 were caught (16 females and 18 males) and two types of GLS were deployed
150 (n = 20 MK3006 and n = 14 MK3005 models from Biotrack Ltd., Wareham,
151 UK). GLS weighted 2.5 g and were fixed to the plastic ring (2 g) with cable
152 ties, the entire equipment corresponding to less than 0.4% of the body mass.
153 All loggers recorded daylight level intensity, saltwater immersion (i.e. activity
154 data) and sea surface temperature data.

155 Loggers measured daylight level intensity every 60 s and recorded the max-
156 imum light intensity for each 10 min for MK3006 and each 5 min for MK3005.
157 For MK3006 wet/dry status is sampled every 3 s and the sum of immersion
158 events for each 10 min receives a score between 0 and 200 (wet; immersion
159 data > 0) and is stored. Temperature is recorded after 20 first minutes contin-
160 uously wet, temperature wet timer resets anytime the device goes dry for > 3
161 s. For MK3005, wet/dry status is sampled every 3 s and the sum of wet/dry
162 duration is stored. Temperature is recorded after 25 minutes continuously wet,
163 temperature wet timer resets anytime device goes dry for > 6 s.

164 *Light-based geolocation*

165 Twilight times (i.e. sunrise and sunset) were determined using an arbitrary
166 light intensity threshold of 2.5. A good choice for light threshold is often the
167 lowest value that is consistently above any noise in the nighttime light lev-
168 els, slightly above complete darkness (Pollet et al., 2014). The selection of
169 the threshold was performed through the existing R library TwGeos (Lisovski

170 et al., 2016). *In situ* calibration was done following Lisovski et al. (2019) rec-
171 ommendations. Relying on our knowledge of the phenology of masked boobies
172 based on in situ observations, we assumed that birds stayed at their breeding
173 place at least from 10 May 2017 to 15 June 2017. A sun elevation angle was
174 computed for each tag using the Hill-Ekstrom calibration (i.e. minimization of
175 latitude error variance), and used for the estimation of birds' geographic posi-
176 tions over the whole deployment. This was performed through the existing R
177 library SGAT (Wotherspoon et al., 2016). Then, we assigned to each position
178 mean temperature and proportion of time in water calculated between two
179 twilights.

180 Finally, for each individual we evaluated the deviation between all observed
181 twilight times and theoretical twilight at FdN with respect to the calibrated
182 sun elevations (Fig. 1). The OSTIA global sea surface temperature reprocessed
183 product provided by the Copernicus Marine Service was also used to compute
184 the deviation between mean temperature recorded by the tags and the sea
185 surface temperature from satellite observations ¹.

186 *Utilization distributions and maps of geolocation errors*

187 Utilization distributions were estimated by applying a two-dimensional Kernel
188 Density Estimation (KDE) on observed positions from all GLSs with grid of
189 mesh 0.5° and a bandwidth of 2° (Fig. 2). Percentage of presence within the
190 Exclusive Economic Zone (EEZ) was also computed of each map, defined as
191 the proportion of positions laying within the EEZ. The impact of measurement
192 errors on geolocation estimates was illustrated by a map of geolocation error
193 (Fig. 2). This map was estimated by sampling positions likely to be observed
194 from a fixed GLS at FdN and by applying a two-dimensional KDE with same

¹ [https://resources.marine.copernicus.eu/
\(product_identifier_SST_GLO_SST_L4_REP_OBSERVATIONS_010_001\)](https://resources.marine.copernicus.eu/(product_identifier_SST_GLO_SST_L4_REP_OBSERVATIONS_010_001))

195 parameters. In our case, a twilight error structure was defined by fitting a
 196 gamma distribution on all twilight times deviation estimated during the cali-
 197 bration period (Fig. 1). Twilight times observations were then simulated and
 198 used to estimate geolocations. Positions associated to deviation in tempera-
 199 ture over 0.5°C were removed, based on the theoretical sensor accuracy given
 200 by the archival tag provider (Biotrack Ltd., Wareham, UK). Bhattacharyya
 201 coefficient was used for estimating quantitatively the dissimilarities between
 202 these distributions.

203 *Cross-wavelet analysis*

204 Wavelet analysis consists in a local scale decomposition of a signal through
 205 the computation of the wavelet coefficient:

$$W_y(a, \tau) = \int_{-\infty}^{+\infty} y(t)\Psi_{a,\tau}(t) \quad (1)$$

206 where $\Psi_{a,\tau}$ is the mother wavelet in its conjugate form, τ represents time,
 207 and a is the scale of the wavelet (Fig. 3). The wavelet coefficient represents the
 208 contribution of a scale a (i.e. the time periods on vertical axis in Figs 3 and
 209 4) in the observed signal at time τ (i.e. the absolute time on horizontal axis in
 210 Figs 3 and 4). In other words, the more the signal $y(t)$ at time has a pattern
 211 with the same period as $\Psi_{a,\tau}$, the higher is $W_y(a, \tau)$. In practice, the Morlet
 212 wavelet is the most widely used mother wave, and is known for performing a
 213 good trade-off between temporal and scale resolutions (Torrence and Compo,
 214 1998).

215 The cross-wavelet transform of two time series $x(t)$ and $y(t)$, with respective
 216 wavelet transforms W_x and W_y is finally defined by:

$$W_{x,y}(a, \tau) = \frac{1}{\tau} \cdot W_x(a, \tau) \cdot W_y(a, \tau) \quad (2)$$

217 The evaluation of the statistical significance of power cross-wavelet coef-
218 ficients is then critical for interpreting them correctly (Cazelles et al., 2014;
219 Rouyer et al., 2008). The significance test involves a null hypothesis of "no
220 joint periodicity", and performs simulations of random time series in order
221 to estimate the cross-wavelet coefficients range under the null hypothesis. By
222 fixing a level of significance it is therefore possible to determine statistically
223 significant correlation between the two observed time-series.

224 In our study, we evaluate cross-wavelet coefficient with the time-series of
225 mean time in saltwater immersion, and longitude, since longitude is more
226 accurately estimated than latitude (Hill, 1994). Thus, as a null hypothesis
227 we simulated time-series by random sampling longitude and mean time in
228 saltwater immersion. One out of two samples was sampled only from day data
229 and the other only from night data. Analysis were conducted with the help of
230 the WaveletComp R library (Rosch and Schmidbauer, 2018).

231 Results

232 Light-based geolocation

233 GLS were recovered ($n = 31$ loggers, i.e. 91% recovery rate) during the follow-
234 ing breeding season during the second half of April 2018, and the light-based
235 geolocation approach revealed that no masked booby had shown any migra-
236 tory or wide-range movement (Fig. 2). The estimation of twilight deviations
237 between observed and expected times at FdN over a year-round deployment did
238 not differ much from deviations estimated during the calibration period (Fig.
239 1). The estimation of global error twilight structure lead to a gamma distribu-
240 tion of scale 2.66 and rate 0.32, which corresponds to detection of dawn and
241 dusk with about 10 min deviation in average and 20 min in worst cases, while
242 maximal deviations over the whole deployment were about 30 min. Similarly,

243 the distribution of temperature deviations over the deployment was very simi-
244 lar with the deviations observed during the calibration period with most value
245 between -0.5°C and $+0.5^{\circ}\text{C}$. Spatially, the associated error range estimation
246 and utilization distribution were thus very similar with a Bhattacharyya coef-
247 ficient of 0.97 and 0.95 when comparing estimated maps respectively without
248 and with filtering coordinates with respect to temperature data (Fig. 2). How-
249 ever, important deviations both in twilight times and temperature occurred
250 when masked boobies spent more than 75% of the time in water between two
251 consecutive twilights (Fig. 1), and associated to a slight deviation eastward in
252 the utilization distribution (Fig. 2).

253 Wavelet analysis

254 The cross-wavelet analysis revealed local significant joint-periodicities (i.e. syn-
255 chrony) between longitude and saltwater immersion time-series for every indi-
256 vidual ($p < 0.01$). This synchronicity appeared for different couple of specific
257 periods and times and they are discernable in matrixes of cross-wavelet power
258 coefficients (Fig. 3). The average matrixes of cross-wavelet power coefficient
259 for all individuals show global patterns of joint synchronicity, and a strong
260 relationship with the phenology of masked boobies (Fig. 4). Periods with al-
261 most no significant periodicity occurred mostly between March and July which
262 correspond to the first stage of the breeding period (i.e. incubation: laying to
263 hatching). In contrast, from July to March, which corresponds to the last
264 stage of the breeding season until the end of the non-breeding season, signifi-
265 cant joint-periodicity can be observed for both females and males. During this
266 period, eastward movement (longitude increasing) corresponded to an increase
267 of time spent on water, and equally westward movement (longitude decreasing)
268 corresponded to a decrease of proportion of time spent on water. Interestingly,

269 these joint-periodicities occurred mainly for periods of 2 to 8 days, with a
270 modal period that increases from 2 days in July to 5 days in November. We
271 could also observe specific period where all birds seem to stop showing joint-
272 periodicity such as in the end of September or in mid-December. Differences
273 by sex appeared when breeding is over, i.e. after fledging with higher power
274 coefficient for females (Fig. 4).

275 These joint-periodicity illustrated that the tagged birds traveled way and
276 back from the colony on consecutive trips of short length with (\sim 2-4 days)
277 to the east of the colony, with length and range depending on the sex and on
278 the time of the year (Figs. 4 and 5). Trips had increasing average duration
279 from the end of the breeding season to the pre-breeding period (Fig. 4) and
280 associated increasing range (Fig. 5). In particular, during the pre-breeding
281 period (January–March), females travelled significantly further to the east
282 (Welch Two Sample t-test: $p < 0.001$) and spent more time in water than
283 males (Fig. 5).

284 Discussion

285 GLS data and resident behaviour

286 Data from 31 GLS showed that masked boobies from FdN archipelago stayed
287 in the vicinity of their breeding site both during breeding and non-breeding
288 season. The cross-wavelet analysis revealed their short round trip of few days
289 eastward to their breeding site.

290 GLS data have been only rarely used to demonstrate resident behaviour
291 (Schacter and Jones, 2018). Existing studies have dealt with staging behaviour
292 and most of them have estimated home range by applying KDE on a scatter
293 of light-derived positions (Bächler et al., 2010; Stenhouse et al., 2012). Travel-
294 ling periods are usually discriminated from resting periods by fixing empirical

295 thresholds on distance to the colony (Leal et al., 2017) or on change in lon-
296 gitude (Guilford et al., 2009). Nevertheless, all insisted to be cautious when
297 interpreting such data. Due to inherent limits of light-based geolocation accu-
298 racy, utilization distribution derived from GLS data often leads to a scatter
299 of coordinates extended in latitude. In this study, we estimated maps of er-
300 ror range, and year-round utilization distribution of FdN’s masked boobies,
301 suggesting that masked boobies are resident at FdN. One could argue that it
302 would be impossible to detect wide range movements in case seabirds would
303 have changed of breeding location or simply skipped the breeding season. In-
304 deed, because birds with archival tags needed to be recaptured, we only re-
305 covered tags that have been deployed on birds that bred at the same place for
306 two consecutive years. However, previous observations (Kepler, 1969), as well
307 as our own with recovery rate around 90

308 Our study reveals joint-periodicity between longitude and saltwater im-
309 mersion time-series. One could think that these periodicities result from bias
310 in the measure of light-level intensity when masked boobies sit on water and
311 that they have not travelled eastward to FdN. This is however unlikely since
312 shading due to immersion could explain a positive twilight deviation, but it is
313 unlikely that it could explain the negative twilight deviation observed in Fig.
314 1. Indeed negative twilight error are theoretically impossible with GLS data,
315 especially in environments with no artificial lights. Finally, GPS tracking of
316 masked boobies in the same colony during the breeding season conducted in
317 every April between 2017 and 2019 revealed that masked boobies from FdN
318 forage almost exclusively at the east of the archipelago, and that they occa-
319 sionally spent one night at sea, eastward of their breeding locations (8 out of
320 130 recorded trips, S. Bertrand, unpubl. data). Such nights at sea should be
321 observable in GLS data, and in April few males showed indeed a joint period-
322 icity of period 48 h, which could correspond to trips lasting about 24 h (Fig.

323 4). Based on our analysis, we are thus confident that masked boobies travelled
324 way and back to the colony during the non-breeding season and beginning of
325 breeding season, and that the eastward deviation consisted in real movements
326 of about 150 km eastward to FdN.

327 Masked boobies' year-round residency

328 The year-round residence of masked boobies and the fact that they forage
329 eastward of the archipelago might be related to the presence of twice more
330 productive areas at the north-east of FdN due to the island effect of São
331 Pedro São Paul offshore archipelago, which is known to trigger a local enrich-
332 ment in the surrounding waters through an upwelling island effect (de Santana
333 Campelo et al., 2019), which also support a resident population of Brown boo-
334 bies *Sula leucogaster* there (Nunes et al., 2018). The intermittent way back
335 to the colony is also in line with the territorial behaviour of masked boobies,
336 known to come back to the colony intermittently during post-breeding period
337 (Nelson, 2005).

338 Most previous studies on seabirds at FdN relied on colony-based sightings
339 (Antas, 1991; Mancini et al., 2016; Sazima and de Almeida, 2008) and stable
340 isotope analyses for trophic ecology (Mancini et al., 2013, 2014). Studies un-
341 derlined the need for going further in the study of the ecology of seabirds at
342 FdN, especially on their movement and the definition of their habitat, so as
343 to improve conservation strategies (Mancini et al., 2016). This work provides
344 a first answer on masked boobies year-round behaviour, inferring their non-
345 migratory behaviour and estimating their home range. In particular, masked
346 boobies stay within the Brazilian Exclusive Economic Zone throughout the
347 year, which brings valuable information for developing relevant conservation
348 strategies such as designing Marine Protected Areas.

349 Stage-related and sex-specific activity patterns

350 If some uncertainties remain on the exact home range of masked boobies, our
351 study brings new insights on temporal, year-round, variation of their space
352 use. In particular, we show a strong relationship between the duration of trips
353 outside FdN and breeding constraints. Laying, incubating and hatching peri-
354 ods were associated with no joint periodicity, suggesting that the range and
355 duration of foraging trips during these periods are below the error threshold of
356 the signal provided by light and activity. These breeding stages are character-
357 ized by substantial thermal and energetic constraints linked to reproduction,
358 since adults need to incubate or to brood and feed their chick. They mostly
359 share time between defending the nest site or their chick and foraging at sea.
360 Therefore, they are not expected to spend time resting at the sea surface
361 for long periods during breeding (e.g. within the timeframe of two locations
362 per day derived from GLS). Even if they forage far from their colony they
363 have to come back frequently, and are likely to be observed at FdN. When
364 chicks are older and can survive without the protection of their parents (i.e.
365 rearing to fledging), the release of the thermal constraints was evidenced by
366 joint-periodicity with gradually increasing periods.

367 Interestingly, when there was no constraint related to reproduction (i.e.
368 no strict obligation to return to the nest), males and females showed slight
369 differences in cross-wavelet power, particularly the few months prior breeding.
370 During this specific period (January to March), the cross-wavelet analysis
371 revealed higher power coefficients for females, which can be explained by longer
372 trips and longer time spent on water. This confirms the fact that for this
373 species, attendance at site prior to mate is larger for males than for females.
374 Males are territorial and work at conquering and defending a nest place at that
375 period (Nelson, 2005). By travelling further eastward and resting on water for

376 longer period, females may reach and stay in more productive area (de Santana
377 Campelo et al., 2019), at a period where they need to accumulate energy for
378 the ovogenesis. Sexual differences in space use and activity patterns in the pre-
379 breeding period (which is not observed during the breeding period) provides
380 a new light on reversed sexual dimorphism (RSD) of masked boobies. One
381 of the functions proposed for RSD is niche segregation, especially to avoid
382 intersexual competition and optimize the use of resources (Serrano-Meneses
383 and Székely, 2006). Where many studies have failed to demonstrate differences
384 in foraging behaviours of masked boobies in order to explain masked boobies'
385 RSD, our own study provide relevant sex-specific activity patterns during the
386 pre-breeding period i.e. pre-laying (Poli et al., 2017; Sommerfeld et al., 2013;
387 Young et al., 2010).

388 Wavelet analysis of geolocation data

389 When dealing with GLS data deployed on resident or other non-migratory
390 animals, the question might not be "where is the animal?" but rather "did
391 the animal move?". In this situation, we might need external data in order to
392 determine movement based on a relevant correlation. This is the case in our
393 study, where we aimed at determining masked boobies' movements by studying
394 the relationships between saltwater immersion and longitude. Our analytical
395 framework could easily be used in order to investigate the space-uses of other
396 resident seabirds, but also for elucidating if high deviations in position are
397 due to shading caused by clouds (Lisovski et al., 2018). Indeed, it is a conve-
398 nient and powerful tool for studying the sequentiality of noisy time-series such
399 as light-derived positions, and for exploring significant synchronicity between
400 such time-series, coupled with any other relevant external data (e.g. weather
401 data, behavioural data).

402 Despite the inaccuracy of GLS geolocation, our study shows it is appro-
403 priate for revealing year-round whereabouts of a resident tropical seabird over
404 long periods, such as during the non-breeding season. Indeed, thanks to time-
405 series with higher precision and reliability recorded by GLS such as tempera-
406 ture and saltwater immersion we can extract more out of GLS data, particu-
407 larly by elucidating activity patterns, and saltwater immersion periodicity. We
408 brought new insights on masked booby movement patterns related to breeding
409 constraints, and we revealed pre-breeding sex-specific movements that had not
410 been observed to date. Finally, we demonstrated that wavelet analysis is a rel-
411 evant way to extract more out of GLS data further broadly, to provide strong
412 demonstration of animal movement or residency, and to avoid the possible
413 over-interpretation of GLS data.

414 **Compliance with Ethical Standards**

415 *Acknowledgments* Fieldwork activities received the administrative and logisti-
416 cal support from the Fernando de Noronha administration, the Instituto Chico
417 Mendes de Conservação da Biodiversidade (ICMBio, Brazil), the military fire-
418 men from Fernando de Noronha and the TAMAR Project. We also want to
419 express grateful thanks to anonymous reviewers and to colleagues from IFRE-
420 MER and IRD for having helped us significantly on the manuscript.

421 *Funding* This work is a contribution to the TRIATLAS project (funding by
422 the European Union's Horizon 2020 research and innovation program – grant
423 agreement No. 817578). This project has received funding from the Paddle
424 Rise project - European Union's Horizon 2020 research and innovation pro-
425 gram under Grant Agreement No 734271. This study was partially funded
426 by IRD (Mixed International Laboratory Tapioca), CPER Celimer (France),

427 Fundação O Boticário (Brazil), Brazilian National Research Council (CNPq,
428 No. 422759/2016-3). L.B. is research fellow from CNPq (PQ 311409/2018-0).

429 *Conflict of interest* The authors declare that they have no conflict of interest.

430 *Availability of data and material* Data will be added to Movebank.

431 *Code availability* Code is available on our github page: <https://github.com/AmedeeRoy/WaveLightGLS>.

432 *Authors' contributions* A.R., S.B. and K.D. conceived the ideas and A.R. per-
433 formed the analysis; A.R., G.T.N., K.D., C.B., K.D. and S.B. have been on
434 fieldworks for collecting the data; A.R. led the writing of the manuscript. All
435 authors contributed critically to the drafts and gave final approval for publi-
436 cation.

437 **References**

- 438 Antas PTZ (1991) Status and conservation of seabirds breeding in Brazilian
439 waters. ICBP Technical Publication 11:141–158
- 440 Ashmole N (1971) Seabird ecology and the marine environment. *Avian Biology*
441 1:223–286
- 442 Bächler E, Hahn S, Schaub M, Arlettaz R, Jenni L, Fox JW, Afanasyev
443 V, Liechti F (2010) Year-Round Tracking of Small Trans-Saharan Mi-
444 grants Using Light-Level Geolocators. *PLoS ONE* 5(3):e9566, DOI
445 10.1371/journal.pone.0009566
- 446 Ballance LT, Pitman RL, Fiedler PC (2006) Oceanographic influences on
447 seabirds and cetaceans of the eastern tropical Pacific: A review. *Progress*
448 *in Oceanography* 69:360–390, DOI 10.1016/j.pocean.2006.03.013

- 449 Bertrand A, Gerlotto F, Bertrand S, Gutiérrez M, Alza L, Chipollini A, Díaz E,
450 Espinoza P, Ledesma J, Quesquén R, Peraltilla S, Chavez F (2008) Schooling
451 behaviour and environmental forcing in relation to anchoveta distribution:
452 An analysis across multiple spatial scales. *Progress in Oceanography* 79(2-
453 4):264–277, DOI 10.1016/j.pocean.2008.10.018
- 454 Bowler DE, Benton TG (2005) Causes and consequences of animal disper-
455 sal strategies: Relating individual behaviour to spatial dynamics. *Biological*
456 *Reviews* 80(2):205–225, DOI 10.1017/S1464793104006645
- 457 Cazelles B, Stone L (2003) Detection of imperfect population synchrony
458 in an uncertain world. *Journal of Animal Ecology* 72:231–242, DOI
459 10.1046/j.1365-2656.2003.00763.x
- 460 Cazelles B, Chavez M, Berteaux D, Ménard F, Vik JO, Jenouvrier S, Stenseth
461 NC (2008) Wavelet analysis of ecological time series. *Oecologia* 156(2):287–
462 304, DOI 10.1007/s00442-008-0993-2
- 463 Cazelles B, Cazelles K, Chavez M (2014) Wavelet analysis in ecology and epi-
464 demiology: Impact of statistical tests. *Journal of the Royal Society Interface*
465 11:20130585, DOI 10.1098/rsif.2013.0585
- 466 de Santana Campelo RP, Bonou FK, de Melo Júnior M, Diaz XFG, Bez-
467 erra LEA, Neumann-Leitão S (2019) Zooplankton biomass around marine
468 protected islands in the tropical Atlantic Ocean. *Journal of Sea Research*
469 154:101810, DOI 10.1016/j.seares.2019.101810
- 470 Del Hoyo J, Elliott A, Sargatal J (1992) *Handbook of the Birds of the World*,
471 vol 1. Lynx Editions, Barcelona
- 472 Diamond AW (1978) Feeding Strategies and Population Size in Tropical
473 Seabirds. *The American Naturalist* 112(983):215–223
- 474 Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD (2010)
475 Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration.
476 *Proceedings of the National Academy of Sciences* 107(5):2078–2081, DOI

- 477 10.1073/pnas.0909493107
- 478 Ekstrom P (2007) Error measures for template-fit geolocation based on light.
479 Deep Sea Research Part II: Topical Studies in Oceanography 54(3-4):392–
480 403, DOI 10.1016/j.dsr2.2006.12.002
- 481 Fablet R, Chaigneau A, Bertrand S (2013) Multiscale analysis of geomet-
482 ric planar deformations: Application to wild animal electronic tracking and
483 satellite ocean observation data. IEEE Transactions on Geoscience and Re-
484 mote Sensing 52(6):3627–3636, DOI 10.1109/TGRS.2013.2274157
- 485 Friesen VL, Burg TM, McCOY KD (2007) Mechanisms of population differen-
486 tiation in seabirds. Molecular Ecology 16(9):1765–1785, DOI 10.1111/j.1365-
487 294X.2006.03197.x
- 488 Garthe S, Ludynia K, Hüppop O, Kubetzki U, Meraz JF, Furness RW (2012)
489 Energy budgets reveal equal benefits of varied migration strategies in north-
490 ern gannets. Marine Biology 159(9):1907–1915, DOI 10.1007/s00227-012-
491 1978-6
- 492 González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial mi-
493 gration and mixing in the wintering areas of a pelagic seabird. Fron-
494 tiers in Ecology and the Environment 5(6):297–301, DOI 10.1890/1540-
495 9295(2007)5[297:TMAMIT]2.0.CO;2
- 496 Guilford T, Meade J, Willis J, Phillips R, Boyle D, Roberts S, Collett M, Free-
497 man R, Perrins C (2009) Migration and stopover in a small pelagic seabird,
498 the Manx shearwater *Puffinus puffinus* : Insights from machine learning.
499 Proceedings of the Royal Society B: Biological Sciences 276(1660):1215–
500 1223, DOI 10.1098/rspb.2008.1577
- 501 Hill RD (1994) Theory of Geolocation by Light Levels. In: Le Boeuf BJ, Laws
502 RM (eds) Elephant Seals: Population Ecology, and Physiology, University
503 of California Press, Berkeley, USA, pp 227–236

- 504 Jaquetmet S, Le Corre M, Weimerskirch H (2004) Seabird community structure
505 in a coastal tropical environment: Importance of natural factors and fish
506 aggregating devices (FADs). *Marine Ecology Progress Series* 268:281–292
- 507 Jenouvrier S, Weimerskirch H, Barbraud C, Park YH, Cazelles B (2005)
508 Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked
509 to climate. *Proceedings of the Royal Society B: Biological Sciences*
510 272(1566):887–895, DOI 10.1098/rspb.2004.2978
- 511 Kepler CB (1969) The breeding biology of the blue-faced booby (*Sula dacty-*
512 *latra personata*) on Green Island, Kure atoll. *Publications of the Nuttall*
513 *Ornithologists Club* 8
- 514 Leal GR, Furness RW, McGill RAR, Santos RA, Bugoni L (2017) Feeding and
515 foraging ecology of Trindade petrels *Pterodroma arminjoniana* during the
516 breeding period in the South Atlantic Ocean. *Marine Biology* 164(11):211,
517 DOI 10.1007/s00227-017-3240-8
- 518 Lerma M, Serratosa J, Luna-Jorquera G, Garthe S (2020) Foraging ecology
519 of masked boobies (*Sula dactylatra*) in the world’s largest “oceanic desert”.
520 *Marine Biology* 167(6):87, DOI 10.1007/s00227-020-03700-2
- 521 Lewis S, Schreiber EA, Daunt F, Schenk GA, Orr K, Adams A, Wanless S,
522 Hamer’ KC (2005) Sex-specific foraging behaviour in tropical boobies: Does
523 size matter? *Ibis* p 7, DOI 10.1111/j.1474-919x.2005.00428.x
- 524 Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW,
525 Hahn S (2012) Geolocation by light: Accuracy and precision affected by en-
526 vironmental factors. *Methods in Ecology and Evolution* 3(3):603–612, DOI
527 10.1111/j.2041-210X.2012.00185.x
- 528 Lisovski S, Wotherspoon S, Sumner M (2016) TwGeos: Basic data processing
529 for light-level geolocation archival tags R package
- 530 Lisovski S, Schmaljohann H, Bridge ES, Bauer S, Farnsworth A, Gauthreaux
531 SA, Hahn S, Hallworth MT, Hewson CM, Kelly JF, Liechti F, Marra PP,

- 532 Rakhimberdiev E, Ross JD, Seavy NE, Sumner MD, Taylor CM, Winkler
533 DW, Wotherspoon SJ, Wunder MB (2018) Inherent limits of light-level ge-
534 olocation may lead to over-interpretation. *Current Biology* 28(3):R99–R100,
535 DOI 10.1016/j.cub.2017.11.072
- 536 Lisovski S, Bauer S, Briedis M, Davidson SC, Dhanjal-Adams KL, Hallworth
537 MT, Karagicheva J, Meier CM, Merkel B, Ouwehand J, Pedersen L, Rakhim-
538 berdiev E, Roberto-Charron A, Seavy NE, Sumner MD, Taylor CM, Wother-
539 spoon SJ, Bridge ES (2019) Light-level geolocator analyses: A user’s guide.
540 *Journal of Animal Ecology* 89(1):221–236, DOI 10.1111/1365-2656.13036
- 541 Longhurst AR, Pauly D (1987) *Ecology of Tropical Oceans*. 574.52636 L6,
542 Academic Press, San Diego
- 543 Mancini PL, Bond AL, Hobson KA, Duarte LS, Bugoni L (2013) Foraging
544 segregation in tropical and polar seabirds: Testing the Intersexual Com-
545 petition Hypothesis. *Journal of experimental marine biology and ecology*
546 449:186–193, DOI 10.1016/j.jembe.2013.09.011
- 547 Mancini PL, Hobson KA, Bugoni L (2014) Role of body size in shaping the
548 trophic structure of tropical seabird communities. *Marine Ecology Progress*
549 *Series* 497:243–257, DOI 10.3354/meps10589
- 550 Mancini PL, Serafini PP, Bugoni L (2016) Breeding seabird popula-
551 tions in Brazilian oceanic islands: Historical review, update and a call
552 for census standardization. *Ornithology Research* 24(2):94–115, DOI
553 10.1007/BF03544338
- 554 Merkel B, Phillips RA, Descamps S, Yoccoz NG, Moe B, Strøm H (2016)
555 A probabilistic algorithm to process geolocation data. *Movement Ecology*
556 4(1):26, DOI 10.1186/s40462-016-0091-8
- 557 Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE
558 (2008) A movement ecology paradigm for unifying organismal movement
559 research. *Proceedings of the National Academy of Sciences* 105(49):19052–

- 560 19059, DOI 10.1073/pnas.0800375105
- 561 Nelson B (2005) *Pelicans, Cormorants, and Their Relatives*. Oxford University
562 Press
- 563 Newton I (2008) *The Migration Ecology of Birds*. Academic Press, London
- 564 Nunes GT, Bertrand S, Bugoni L (2018) Seabirds fighting for land: Phenotypic
565 consequences of breeding area constraints at a small remote archipelago.
566 *Scientific Reports* 8:665, DOI 10.1038/s41598-017-18808-7
- 567 Olson PA, Ballance LT, Hough KR, Dutton PH, Reilly SB (2001) Summary
568 of seabird, marine turtle, and surface fauna data collected during a survey
569 in the eastern tropical pacific ocean July 8 - December 9, 2000. NOAA
570 Technical Memorandum NMFS p 67
- 571 Phillips R, Silk J, Croxall J, Afanasyev V, Briggs D (2004) Accuracy of geolo-
572 cation estimates for flying seabirds. *Marine Ecology Progress Series* 266:265–
573 272, DOI 10.3354/meps266265
- 574 Poli CL, Harrison AL, Vallarino A, Gerard PD, Jodice PGR (2017) Dy-
575 namic oceanography determines fine scale foraging behavior of Masked
576 Boobies in the Gulf of Mexico. *PLOS ONE* 12(6):e0178318, DOI
577 10.1371/journal.pone.0178318
- 578 Pollet IL, Hedd A, Taylor PD, Montevecchi WA, Shutler D (2014) Migratory
579 movements and wintering areas of Leachs StormPetrels tracked using geolo-
580 cators. *Journal of Field Ornithology* 85(3):321–328, DOI 10.1111/jfo.12071
- 581 Ropert-Coudert Y, Wilson RP, Daunt F, Kato A (2004) Patterns of energy ac-
582 quisition by a central place forager: Benefits of alternating short and long for-
583 aging trips. *Behavioral Ecology* 15(5):824–830, DOI 10.1093/beheco/arh086
- 584 Rosch A, Schmidbauer H (2018) WaveletComp R package
- 585 Rouyer T, Fromentin JM, Stenseth NC, Cazelles B (2008) Analysing multiple
586 time series and extending significance testing in wavelet analysis. *Marine
587 Ecology Progress Series* 359:11–23, DOI 10.3354/meps07330

- 588 Sazima I, de Almeida LB (2008) The bird kraken: Octopus preys on a sea
589 bird at an oceanic island in the tropical West Atlantic. *Marine Biodiversity*
590 *Records* 1:e47, DOI 10.101/S1552a20a005458
- 591 Schacter CR, Jones IL (2018) Confirmed year-round residence and land roost-
592 ing of Whiskered Auklets (*Aethia pygmaea*) at Buldir Island, Alaska. *The*
593 *Auk* 135(3):706–715, DOI 10.1642/AUK-17-235.1
- 594 Serrano-Meneses MA, Székely T (2006) Sexual size dimorphism in seabirds:
595 Sexual selection, fecundity selection and differential niche-utilisation. *Oikos*
596 113(3):385–394, DOI 10.1111/j.0030-1299.2006.14246.x
- 597 Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar
598 PM, Moller H, Taylor GA, Foley DG, Block BA, Costa DP (2006) Mi-
599 gratory shearwaters integrate oceanic resources across the Pacific Ocean
600 in an endless summer. *Proceedings of the National Academy of Sciences*
601 103(34):12799–12802, DOI 10.1073/pnas.0603715103
- 602 Sommerfeld J, Kato A, Ropert-Coudert Y, Garthe S, Hindell MA (2013)
603 Foraging Parameters Influencing the Detection and Interpretation of Area-
604 Restricted Search Behaviour in Marine Predators: A Case Study with the
605 Masked Booby. *PLoS ONE* 8(5):e63742, DOI 10.1371/journal.pone.0063742
- 606 Stenhouse IJ, Egevang C, Phillips RA (2012) Trans-equatorial migration, stag-
607 ing sites and wintering area of Sabine’s Gulls *Larus sabini* in the Atlantic
608 Ocean: *Sabine’s Gull migration*. *Ibis* 154(1):42–51, DOI 10.1111/j.1474-
609 919X.2011.01180.x
- 610 Torrence C, Compo GP (1998) A practical guide to wavelet analysis. *Bulletin*
611 *of the American Meteorological society* 79(1):61–78
- 612 Wakefield E, Phillips R, Matthiopoulos J (2009) Quantifying habitat use and
613 preferences of pelagic seabirds using individual movement data: A review.
614 *Marine Ecology Progress Series* 391:165–182, DOI 10.3354/meps08203

- 615 Weimerskirch H, Wilson RP (2000) Oceanic respite for wandering albatrosses.
616 Nature 406(6799):955–956, DOI 10.1038/35023068
- 617 Weimerskirch H, Le Corre M, Gadenne H, Pinaud D, Kato A, Ropert-Coudert
618 Y, Bost CA (2009) Relationship between reversed sexual dimorphism, breed-
619 ing investment and foraging ecology in a pelagic seabird, the masked booby.
620 Oecologia 161(3):637–649, DOI 10.1007/s00442-009-1397-7
- 621 Wilkinson BP, Haynes-Sutton AM, Meggs L, Jodice PGR (2020) High spatial
622 fidelity among foraging trips of Masked Boobies from Pedro Cays, Jamaica.
623 PLOS ONE 15(4):e0231654, DOI 10.1371/journal.pone.0231654
- 624 Wilson R, Grémillet D, Syder J, Kierspel M, Garthe S, Weimerskirch H,
625 Schäfer-Neth C, Scolaro J, Bost C, Plötz J, Nel D (2002) Remote-sensing
626 systems and seabirds: Their use, abuse and potential for measuring ma-
627 rine environmental variables. Marine Ecology Progress Series 228:241–261,
628 DOI 10.3354/meps228241
- 629 Wilson RP, Culik BM, Kosiorek P, Adelung D (1998) The over-winter
630 movements of a chinstrap penguin (*Pygoscelis antarctica*). Polar Record
631 34(189):107–112, DOI 10.1017/S0032247400015242
- 632 Wotherspoon SJ, Sumner MD, Lisovski S (2016) SGAT: Solar/Satellite geolo-
633 cation for animal tracking R package
- 634 Young H, Shaffer S, McCauley D, Foley D, Dirzo R, Block B (2010) Re-
635 source partitioning by species but not sex in sympatric boobies in the
636 central Pacific Ocean. Marine Ecology Progress Series 403:291–301, DOI
637 10.3354/meps08478

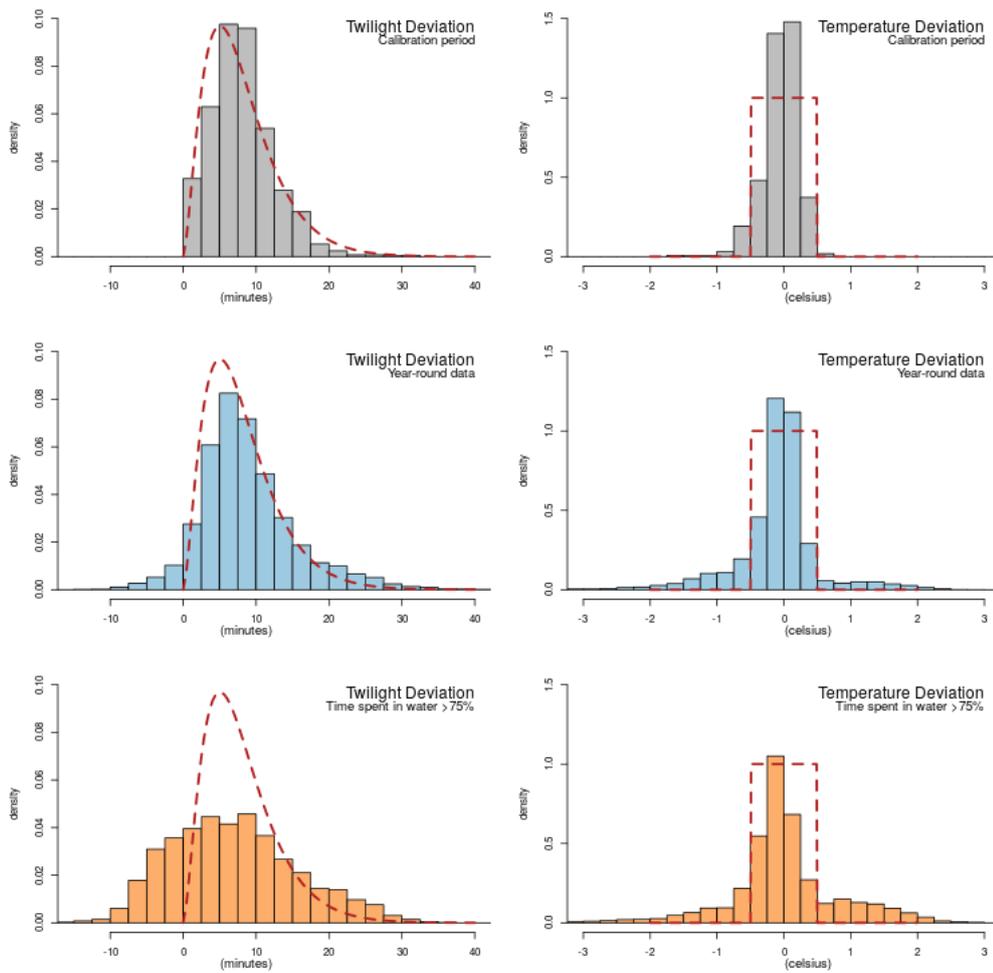


Fig. 1 Twilight times and temperature deviation at Fernando de Noronha. Grey histograms consider the calibration period only (10 May 2017 to 15 June 2017). Blue histograms consider all deployment period (05 May 2017 to 24 April 2018). Orange histograms consider periods where the mean saltwater immersion time is above 75%. Red-dotted curves correspond to the error structure used in Fig. 2

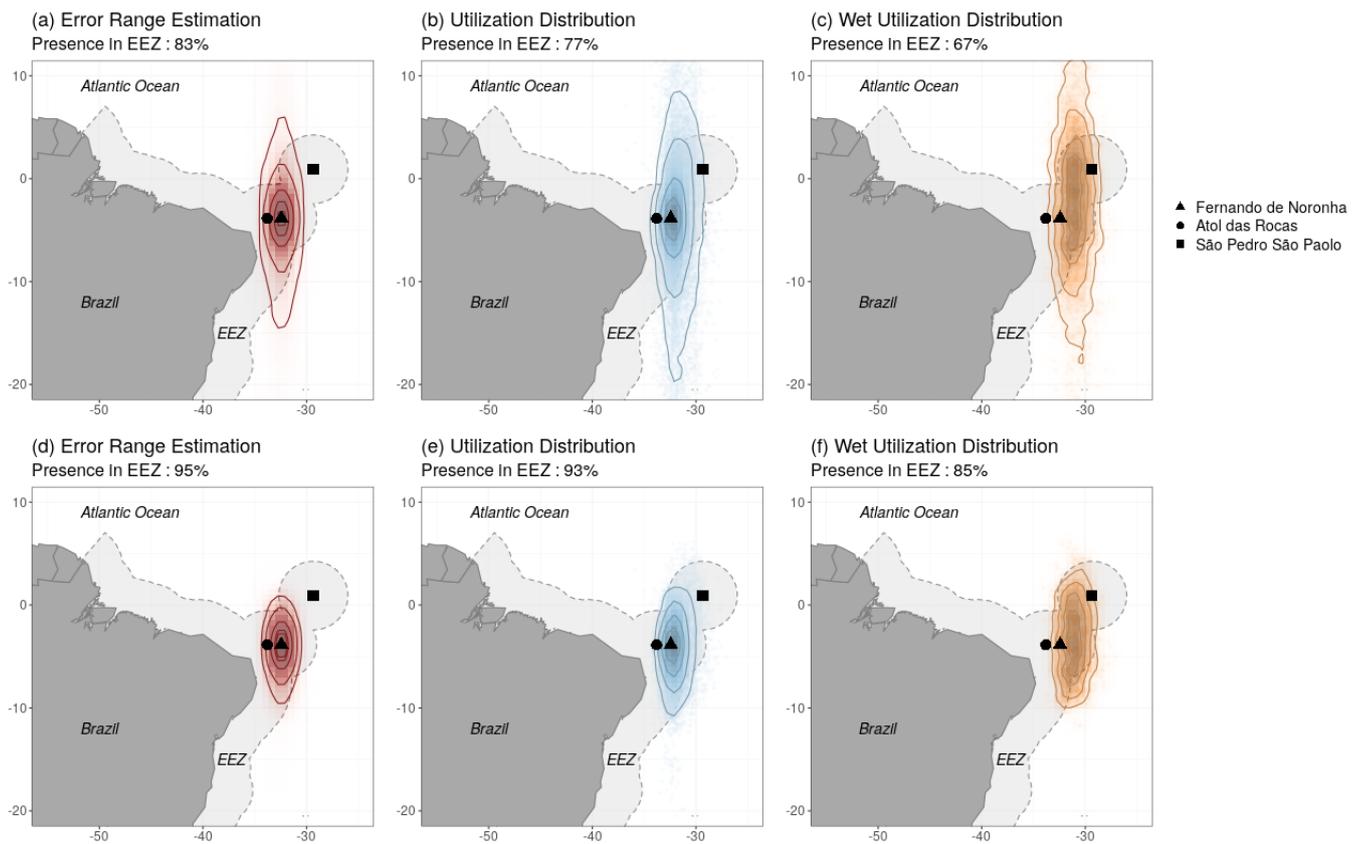


Fig. 2 Maps of geolocation error (a and d) correspond to the geographical error range estimation of a GLS fixed at Fernando de Noronha, Brazil, based on the error structure presented in Fig. 1. Maps of utilization distributions (b and e) have been estimated using observed data from all GLSs. Maps of wet utilization distribution (c and f) correspond to positions where the mean proportion of time spent on water is above 75%. In (a, b and c) all coordinates have been used, in (d, e and f) positions with temperature deviation over 0.5°C were removed. Contours correspond to confidence intervals of 10, 25, 50, 75, and 90%. Black points refer to main islands around FdN. EEZ stands for the Exclusive Economic Zone

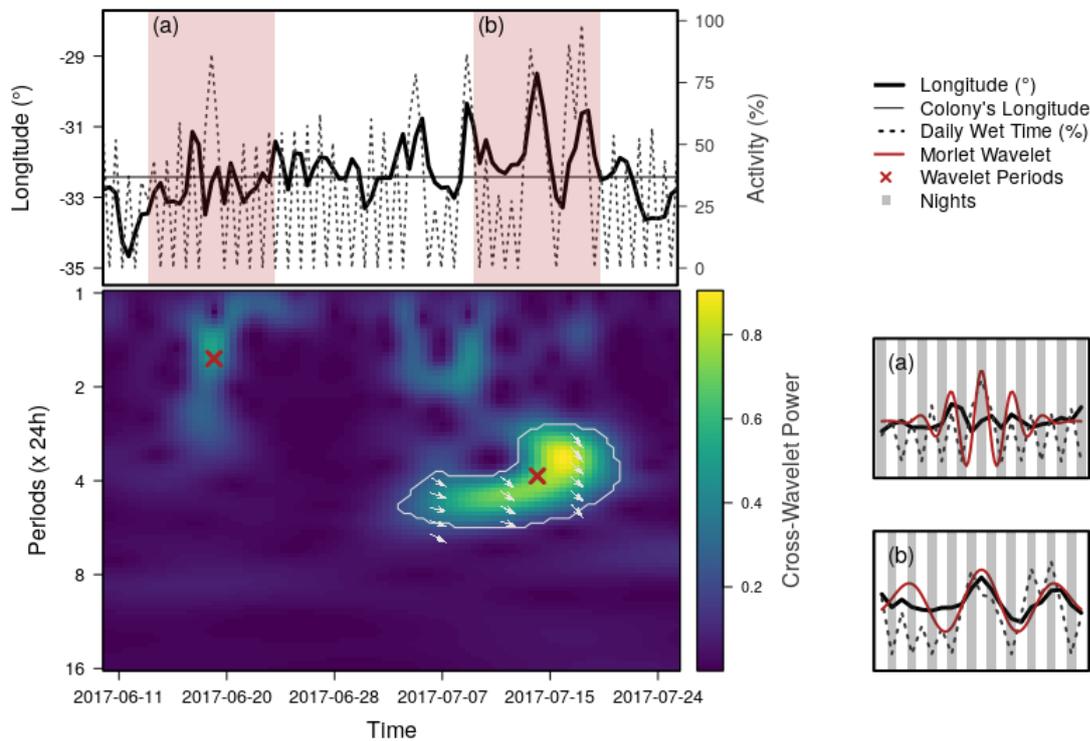


Fig. 3 Illustration of the cross-wavelet theory based on GLS time-series derived from one individual and the associated cross-wavelet power matrix. The upper plot is longitude and saltwater immersion time-series. The bottom plot is the cross-wavelet power coefficient matrix. In such matrix, each power coefficient depends on one specific pair time/scale. The two plots on the right (a) and (b), illustrate how to compute such coefficients for the time/scale pairs marked with red crosses. In both cases, black lines consist in raw time-series for distinct time-windows, red lines show the Morlet wavelet with associated period, and grey rectangles show nights. Finally, coefficient matrix with significant synchronicity ($p < 0.01$; lower left panel) are contoured with white lines, and white arrows illustrate the difference of phases between these synchronized time-series. Arrows pointing to the right (respectively left) indicate that the two series are in phase (respectively anti-phase)

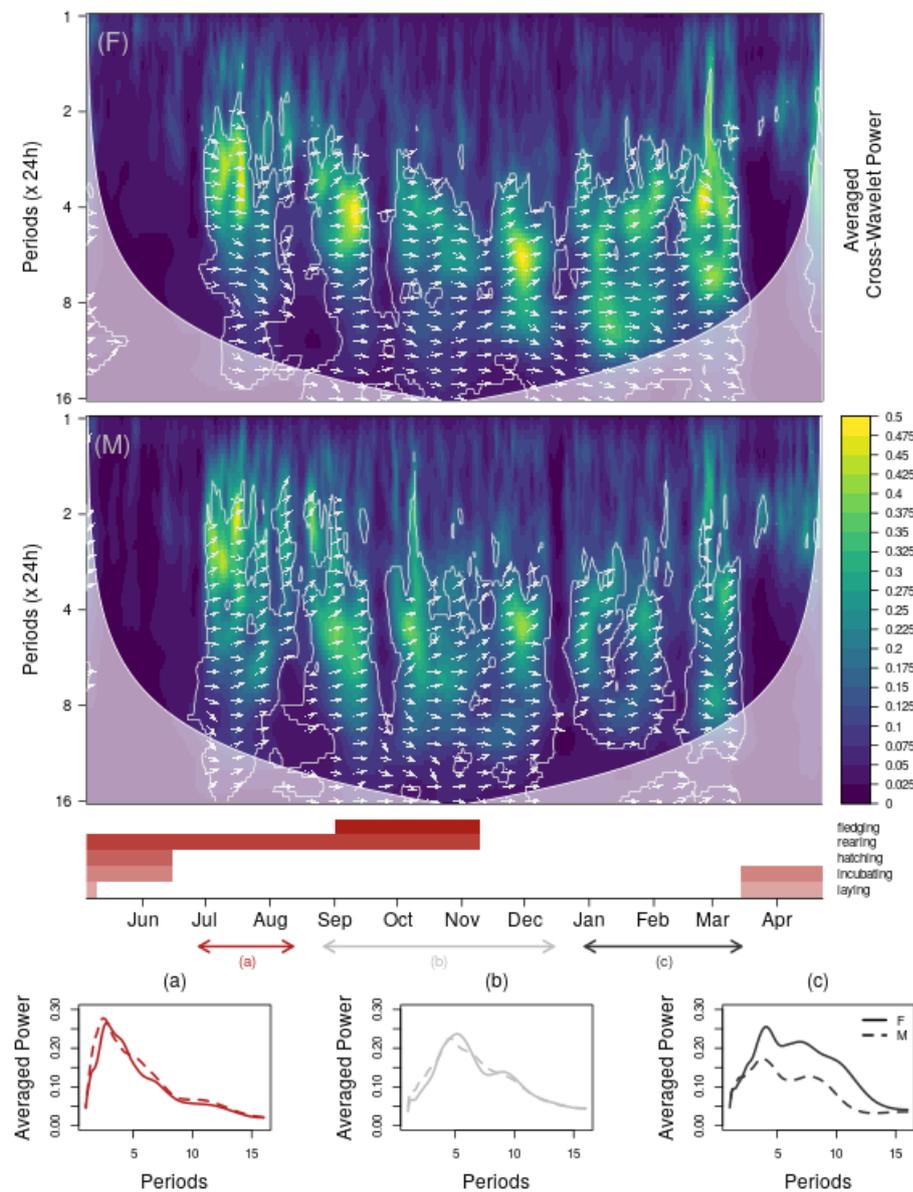


Fig. 4 Averaged cross-wavelet matrixes of longitude and activity time-series based on the analysis of all GLSs over the whole deployment for females ($n = 14$; (F)) and males ($n = 17$; (M)). White lines contour the time/period pairs where at least one individual has shown significant joint-periodicity between the two time-series. White arrows illustrate the difference of phases between the two time-series (see Fig. 3 for further explanations). The white area corresponds to the cone of influence (sensu Cazelles et al., 2008). The different stages of the phenology of masked boobies are indicated for Fernando de Noronha (center panel), Brazil, based on in situ observations. Lower panel show the averaged power over the three respective time-windows: (a) early chick-rearing, (b) late chick-rearing to post-breeding and (c) pre-breeding periods. Individual analysis are available on a GitHub repository (AmedeeRoy/WaveLightGLS)

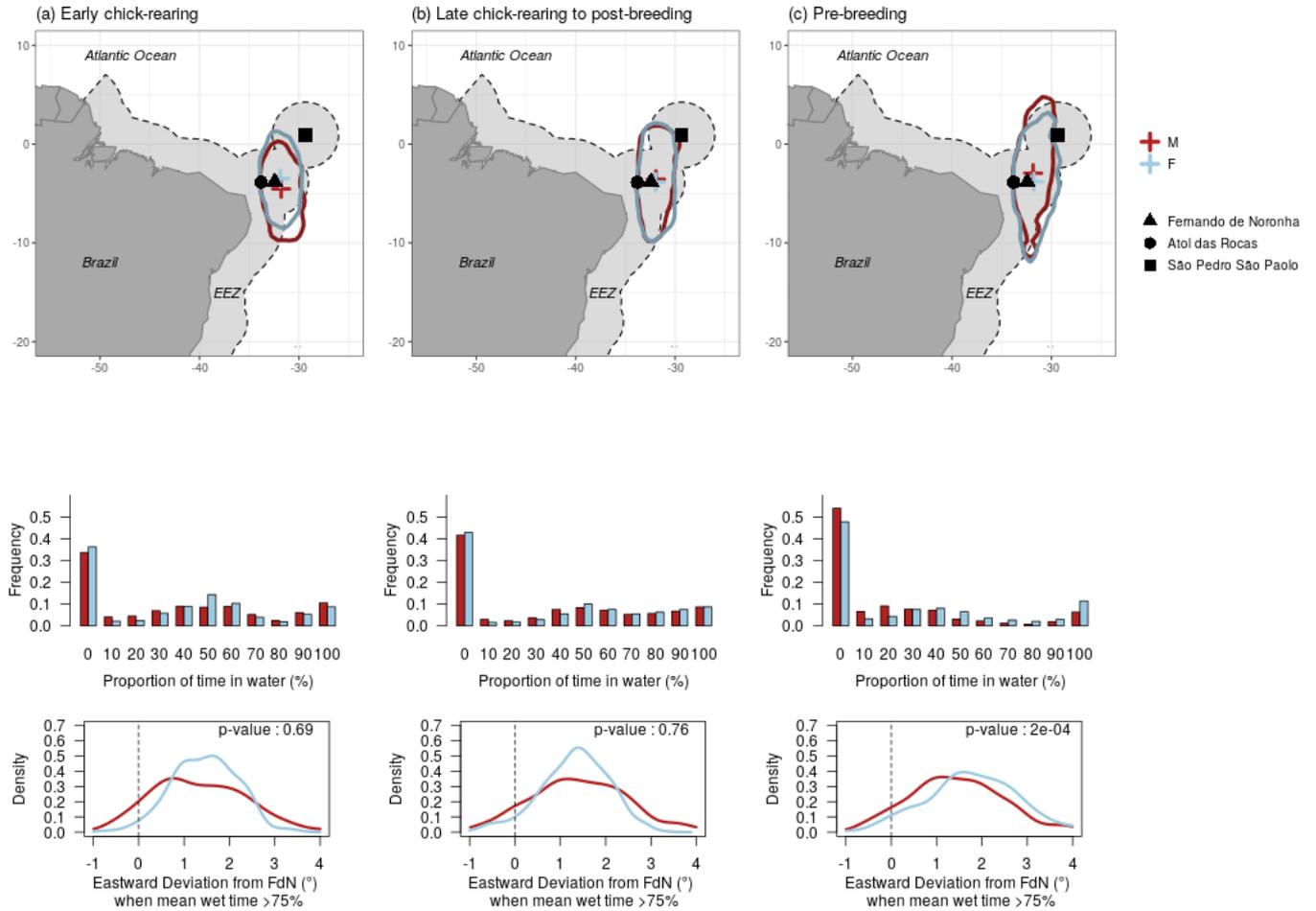


Fig. 5 Sex-specific utilization distributions for specific time-windows, where columns correspond to time-windows described in Fig. 4. (a) early chick-rearing, (b) late chick-rearing to post-breeding and (c) pre-breeding periods. Maps illustrate the utilization distribution by sex (F: females-light blue, M: males-red) for the associated periods. Contours represent utilization distribution of 90%, and crosses the mean positions. Black points refer to main islands around FdN. Histograms (center panels) show at which frequency birds spent proportion of time rather in wet or dry environment during the associated period. Density plots (lower panels) illustrate the eastward deviations of positions with activity higher to 75% for the associated periods. p-values specify the significance of difference in mean between the two distributions derived from Welch Two Sample t-test