

Flying to the moon: Lunar cycle influences trip duration and nocturnal foraging behavior of the wedge-tailed shearwater *Ardenna pacifica*

Ravache Andreas ^{1, 2, 3, *}, Bourgeois Karen ¹, Thibault Martin ², Dromzée Sylvain ¹, Weimerskirch Henri ⁴, De Grissac Sophie ⁴, Prudor Aurélien ⁴, Lorrain Anne ⁵, Menkes Christophe ², Allain Valerie ⁶, Bustamante Paco ^{7, 8}, Letourneur Yves ³, Vidal Eric ^{1, 2}

¹ IMBE, Aix-Marseille Université, CNRS, IRD, Avignon Université, Centre IRD Nouméa - BP A5, 98848 Nouméa Cedex, New-Caledonia, France

² UMR ENTROPIE (IRD—Université de La Réunion—CNRS), Laboratoire d'Excellence Labex-CORAIL, Institut de Recherche pour le Développement, BP A5, 98848 Nouméa Cedex, New Caledonia, France

³ University of New Caledonia / ISEA, BP R4, 98851 Nouméa Cedex, New-Caledonia, France

⁴ Centres d'Etudes Biologiques de Chizé – CNRS, France

⁵ Univ Brest, CNRS, IRD, Ifremer, LEMAR, F-29280 Plouzane, France

⁶ Secretariat of the Pacific Community, SPC, BP D5, 98848 Nouméa Cedex, New Caledonia, France

⁷ Littoral Environnement et Sociétés (LIENSs), UMR 7266 CNRS - La Rochelle Université, 2 Rue Olympe de Gouges, 17000 La Rochelle, France

⁸ Institut Universitaire de France (IUF), 1 rue Descartes, 75005 Paris, France

* Corresponding author : Andreas Ravache, email address : andreas.ravache@ird.fr

Abstract :

Lunar phase and illumination are known to affect nocturnal behavior of many organisms, particularly through predator-prey interactions. Visual predators can benefit from higher light levels to increase their activity, while prey may decrease their activity to avoid predation. The lower number of nocturnal seabirds observed on colonies during full moon nights has been mostly interpreted as a predation avoidance strategy. However, it is also possible that shearwaters take advantage of the moon's illumination to feed also at night, and stay at sea to forage during full moon nights. We used miniaturized GPS-loggers to obtain 179 tracks from 99 wedge-tailed shearwaters breeding in New Caledonia, to investigate moonlight effects on individual behavior. Lunar phase significantly predicted self-provisioning trip duration, with individuals performing longer trips around the full moon. However, this relationship was not significant during chick-provisioning trips when adults have to frequently return to the colony. Adults mostly returned to the colony during moonlit periods, refuting the predation avoidance theory. Tracked individuals showed an unexpectedly high amount of nocturnal foraging activity (28% of total activity), positively influenced by the presence of the moon. $\delta^{15}\text{N}$ stable isotope values were significantly related to the percentage of nocturnal foraging, but with a weak relationship, impeding our ability to confirm that wedge-tailed shearwaters fed on different prey when foraging at night. This study suggests that reduced colony attendance around the full moon may be linked to greater at-sea foraging opportunities in distant oceanic areas than to increased predation risk on land.

Highlights

► Nocturnal Procellariids decrease their activity on colonies around the full moon. ► It has been previously interpreted as predation avoidance. ► Here, wedge-tailed shearwaters returned to the colony mostly during the moonlit period of the night. ► They foraged more intensively at night under moonlit conditions. ► Decreased activity at the colony may be rather due to higher foraging efficiency of seabirds around the full moon.

Keywords : *Ardenna pacifica*, Foraging, Lunar phase, Moon, GPS-tracking, Stable isotope analyses

40 **1 - Introduction**

41 Lunar cycle is known to influence the behavior and physiology of a wide range of living
42 organisms, as well as predator-prey relationships (Grant et al., 2013; Prugh and Golden, 2014;
43 Zimecki, 2006). Predators relying on visual cues to find their prey can increase their foraging
44 activity at night during higher moonlight intensity, while prey can decrease their activity under
45 such conditions (Martin, 1990; Prugh and Golden, 2014). Of marine taxa, Procellariid seabirds
46 return to their colonies after dark, and adapt at-sea foraging trips to attend the colony under
47 moonless conditions, are most likely to be affected by the lunar cycle. (Brooke, 2004; Mougeot
48 and Bretagnolle, 2000). To date, this avoidance of the colony under moonlight has most
49 commonly been interpreted as an antipredator adaptation. Indeed, moonlight avoidance is
50 related to predation rate in nocturnal Procellariids (Keitt et al., 2004; Watanuki, 1986). Even
51 in predator-free locations, moonlight avoidance has been observed in some populations,
52 allegedly due to an innate and persistent behavior inherited from co-evolution with predators
53 (Bretagnolle et al., 2000).

54 However, reduced activity at the colony during moonlit nights may also be a result of increased
55 activity elsewhere, such as nocturnal at-sea foraging. Procellariiform species, which are visual
56 predators lacking night vision adaptations (Brooke 2004), should, therefore, benefit from
57 moonlight, that would allow improved nocturnal foraging. Several studies have shown that
58 shearwater, petrel and albatross nocturnal at-sea activity was enhanced during full moon
59 nights compared with moonless nights, both during the breeding (Dias et al., 2016; Phalan et
60 al., 2007; Rubolini et al., 2015) and non-breeding periods (Dias et al., 2012; Pinet et al., 2011;
61 Yamamoto et al., 2008). The hypothesis of nocturnal foraging is also supported by increased
62 availability of some seabird prey in subsurface waters during night time thanks to the Diel
63 Vertical Migration (DVM) which is the vertical migration of micronekton, the prey species of

64 many predators, towards the surface at night and in deeper waters during the day (Hays 2003,
65 Brooke 2004). Prey availability at the surface changes along with variations in the DVM, being
66 reduced on full moon nights and higher during new moon nights (Benoit-Bird et al., 2009;
67 Gliwicz, 1986). However, Waap et al. (2017) found no evidence of dietary shift in prey species
68 composition or diversity according to the lunar cycle in nocturnally foraging and shallow-diving
69 Procellariid species, the Bulwer's petrel, which feeds on mesopelagic species brought close to
70 the surface during DVM. Furthermore, research conducted on the same species revealed a
71 relatively weak effect of lunar phase on its activity (10% more time flying during full moon
72 compared to other lunar phase; Dias et al. 2016). Combined, these results suggest that
73 normally deep prey are available at the surface in sufficient amounts to be accessed by
74 seabirds, even during full moon nights.

75 Some Procellariid species, for example wedge-tailed shearwaters (*Ardenna pacifica* Gmelin,
76 1789), are thought to primarily forage during daylight (Catry et al., 2009), and often in
77 association with subsurface predators such as tuna (Au and Pitman, 1986; Hebshi et al., 2008;
78 Miller et al., 2018; Spear et al., 2007). Epipelagic tuna are generally considered to be diurnal
79 foragers (Roger, 1994), although some studies demonstrate occasional nocturnal foraging
80 (Schaefer et al., 2009). These associations, by which surface predators drive prey close to the
81 surface (Ashmole, 1971), facilitate foraging (Hebshi et al., 2008; Miller et al., 2018) for shallow-
82 diving procellariids like wedge-tailed shearwaters (mean maximum diving depth: 5-14 m;
83 Burger 2001; Peck & Congdon 2006). This is particularly true in oligotrophic tropical waters
84 where wedge-tailed shearwaters have been documented foraging in association with
85 yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tuna (Miller et al., 2018).
86 However, wedge-tailed shearwaters have also been documented foraging during full moon
87 nights (Gould, 1967) which suggests that other factors than sub-surface predator associations,

88 for instance the lunar phase or prey migration patterns may influence wedge-tailed
89 shearwaters foraging strategies.

90 If the light of the moon is advantageous to foraging wedge-tailed shearwaters, they may
91 exploit nights around the full moon to extend foraging time and this would be observable as
92 increased foraging activity under moonlit conditions. If nocturnal foraging is linked to the DVM
93 of mesopelagic prey toward the surface at night, we would expect to find an isotopic signature
94 in blood plasma correlated to the proportion of nocturnal foraging, showing a shift in prey
95 between diurnal and nocturnal feeding. Stable isotopes can be used to examine trophic
96 relationships, and they have been used to study niche partitioning that results from different
97 prey or foraging habitats / resource use of consumers (e.g. Navarro et al., 2013; Pontón-
98 Cevallos et al., 2017; Rayner et al., 2016). Finally, if shearwaters avoid returning to the colony
99 in order to reduce predation risk from predators that benefit from brighter moonlight, they
100 should preferentially return to the colony during the moonless part of the night.

101 While the predation avoidance hypothesis in relation to lunar cycle has been extensively
102 tested by analyzing seabird activity patterns at colonies (e.g. Bretagnolle 1990; Mougeot &
103 Bretagnolle 2000; Bourgeois et al. 2008), few studies simultaneously focused on nocturnal
104 foraging activity (but see Rubolini et al. 2015, which found that Scopoli shearwaters
105 *Calonectris domedea* increased their diving activity during full moon nights, but interpreted
106 longer trips around the full moon to be driven by predation avoidance on land rather than
107 higher foraging opportunities at sea). Moreover, most studies on lunar effects on the
108 nocturnal, at-sea activity of seabirds, have been conducted using global location sensor (GLS).
109 These data, only provide information on the time spent on water (e.g. Phalan et al. 2007; Dias
110 et al. 2012; Cruz et al. 2013), but prevent determining what drives that behavior, i.e. whether

111 increased time spent on water during moonlit periods represent foraging activity or loafing.
112 Using high-resolution GPS data, the present study aimed at unravelling the effects of moon
113 illumination and lunar phase on both nocturnal at-colony activity and at-sea foraging in
114 wedge-tailed shearwaters, to understand how they shape their activities. We used
115 miniaturized GPS-loggers to obtain a fine-scale trajectory of foraging trips during breeding
116 season and accurately define resting, commuting and foraging events. We evaluated the
117 proportion of time spent foraging during daytime and night-time and studied lunar phase and
118 moon presence effects upon feeding trip duration, time of return to the colony and at-sea
119 foraging. Finally we performed stable isotope analysis on blood plasma from all individuals, to
120 determine whether we could identify diet differences associated with nocturnal foraging
121 activity established through GPS tracking.

122 **2 - Material and methods**

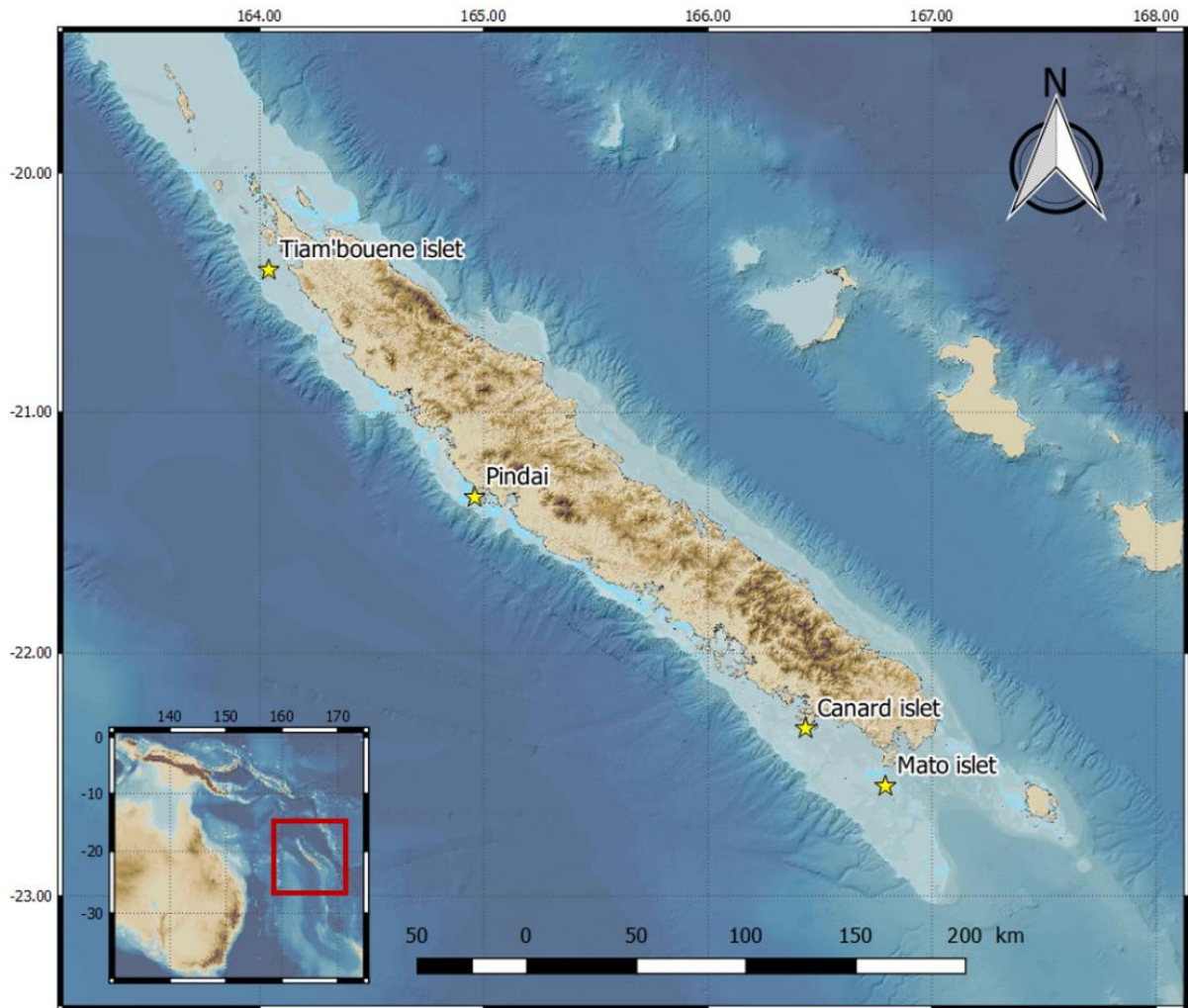
123 **2.1 Ethical statement**

124 All animal experimentation met the Animal Care Committee (ABS) / Association for the Study
125 of Animal Behaviour (ASAB) guidelines for ethical treatment of animals. Permits to handle
126 birds at Mato and Canard fields sites were delivered by New Caledonia's Province Sud (permits
127 nos. 609-2014/ARR/DENV, 2903-2015/ARR/DENV and 2695-2016/ARR/DENV), and at Pindai
128 and Tiambouene fields sites by New Caledonia's Province Nord (permits nos. 161214_AC
129 2303_2016 and 161214_AC2304_2017).

130 **2.2 Field work**

131 Field trips were conducted at four field sites in New Caledonia in the Coral Sea, South-west
132 Pacific, which is home of 500,000 breeding pairs of wedge-tailed shearwaters (Pandolfi and
133 Bretagnolle, 2002). In this geographic area, the wedge-tailed shearwater breeding season

134 begins around the end of October with the return of breeding adults to colonies and is
135 completed at the end of May when chicks fledge (McDuie and Congdon, 2016). GPS-loggers
136 were fitted on breeding adults during the chick-rearing period (from March to April) during
137 two successive years (2017 and 2018) at four breeding sites. One study colony is located on
138 the main island of New-Caledonia (Figure 1): Pindai (21.354°S, 164.954°E) where 37 and 7
139 breeders were equipped in 2017 and 2018, respectively. The three other study sites are
140 located on lagoon islets : Mato (22.55°S, 166.80°E) where 20 and 7 breeders were equipped
141 in 2017 and 2018, respectively, Canard (22.31°S, 166.31°E) where 11 breeders were equipped
142 in 2017, and Tiambouene (20.38°S, 164.04°E) where 17 breeders were equipped in 2018.
143 Breeding adults were fitted with either 4.5 g Ecotone, 6 g Lotek, 5 g Pathtrack or 12.5 g
144 TechnoSmart GPS-loggers, representing 1 to 3 % of wedge-tailed shearwater body weight (413
145 \pm 40 g in the present study), i.e. below the limit commonly accepted to limit behavior
146 modification (Phillips et al., 2003). The lightest GPS-loggers (Ecotone, Lotek and Pathtrack)
147 were attached to three tail feathers using Tesa[®] tape (McDuie et al., 2018), while the heaviest
148 GPS-loggers (Technosmart) were back-mounted to ensure balance during flight would not be
149 affected (Vandenabeele et al., 2014). Locations were recorded every 15 minutes. Birds were
150 captured by hand at their burrow entrance before feeding their chicks. Colonies were
151 monitored every night to recapture birds for logger recovery. A maximum of 0.4 mL of blood
152 was collected on recapture from the tarsal vein using a 0.5 mL 29G syringe. Blood samples
153 were centrifuged within 1 hour from collection to separate plasma and blood cells that were
154 then stored separately in 70% ethanol until stable isotope analyses were run.



155

156 *Figure 1: Map of New Caledonia, showing the location of the four wedge-tailed shearwaters breeding*
 157 *colonies used in this high resolution GPS study of foraging behavior. Inset shows the position of New*
 158 *Caledonia at the eastern edge of the Coral Sea.*

159 **2.3 Definition of nighttime, moonlight intensity and lunar phase**

160 In order to investigate the effect of moonlight on wedge-tailed shearwater foraging behaviour,
 161 the night was defined as the period between astronomical dusk and the beginning of the
 162 astronomical dawn (i.e. when the geometric center of the Sun's disk is 18 degrees below the
 163 horizon). Astronomical dusk and dawn, moon rise and set were computed at each location
 164 recorded by GPS-loggers using the R “suncalc” package (Agafonkin and Thieurmel, 2017),
 165 while moonlight intensity and lunar phase were determined at each location with the R
 166 package “lunar” (Lazaridis, 2014) Moonlight intensity was a value comprised between 0 and 1,

167 0 being the illumination during the new moon or during the moonless part of the night (Before
168 moonrise or after moonset), and 1 the illumination during the brightest full moon. Lunar phase
169 was a value in radians, 0 corresponding to new moon, $\pi/2$ to first quarter (waxing moon), π to
170 full moon and $3\pi/2$ to last quarter (waning moon).

171 **2.4 Foraging trip characteristics**

172 Data from a total of 179 foraging trips were collected during 2017 (n = 126) and 2018 (n = 53)
173 breeding seasons from 99 GPS-tracked individuals. Complete tracks, starting from the
174 departure of the bird and ending at its return to the burrow, represented 85 % of the total
175 number of tracks. Trip duration (days), total distance travelled and maximum distance from
176 the colony (km) were computed using the R package “trip” (Michael et al., 2016). When tracks
177 were incomplete, trip duration was estimated using the individual return date based on
178 observation of birds back at the colony. Durations of nine incomplete tracks were impossible
179 to estimate, and these tracks were removed from the analysis, resulting in a total of 170 trips
180 being considered for trip duration analysis. Trips presenting gaps (n = 20) were removed from
181 total distance travelled analysis, and incomplete trips (i.e. when the battery stopped before
182 the individual began its return to the colony, n = 16) were removed from maximal distance
183 travelled analysis. During the chick-rearing period, pelagic seabirds have to concurrently
184 provide food to their chicks and meet their own needs using zones of high foraging
185 competition near their colony (Furness and Birkhead, 1984; Lewis et al., 2001). In wedge-tailed
186 shearwaters, longer trips are undertaken to ensure self-provisioning whereas shorter trips
187 focus on chick provisioning (Congdon et al., 2005; McDuie et al., 2015, 2018; Weimerskirch et
188 al., *in press*). Thus, we differentiated in this study long trips (> 3 days, n = 50) and short trips
189 (\leq 3 days, n = 119).

190 **2.5 Arrival time at the colony**

191 The time of arrival after a foraging trip was calculated using the first GPS location recorded on
192 land, inside the colony area (i.e the contour of the islet, or within 1 Km around our study).
193 Twenty tracks presenting gaps did not allow us to determine the accurate time and were
194 excluded from this analysis. The arrival time was calculated for the 159 remaining tracks with
195 an estimated accuracy of 15 min. During waxing moon nights, the moon is present in the first
196 part of the night then sets, while during waning moon nights, the moon rises during the night.
197 To investigate the effect of moon presence on wedge-tailed shearwaters arrival time at the
198 colony, we determined whether birds arrived at the colony during the moonless or moonlit
199 part of the night, or even before the astronomical dusk, for each lunar phase.

200 **2.6 Behavioral assessment**

201 Expectation Maximization binary Clustering (EMbC) algorithm (Garriga et al., 2016), a variant
202 of the expectation maximization algorithm in maximum likelihood estimation of Gaussian
203 mixture models, was used to determine wedge-tailed shearwater behavior during their
204 foraging trips using the R package “EMbC” (Garriga et al., 2016). EMbC is a robust multivariate
205 clustering algorithm based on sinuosity and speed of the trajectory calculated using
206 loxodromic distances and bearings of the tracks to determine animal behavior. It requires few
207 prior assumptions, assuming that turn angles between consecutive locations indicate
208 searching or foraging, while straight bouts can be associated with resting (slow) and
209 commuting (fast) (Garriga et al., 2016). This method has been used to assess ecologically
210 meaningful behaviors from geolocation data for a range of seabird species, including
211 Procellariiforms (Bennison et al., 2018; Clay et al., 2019; de Grissac et al., 2017; Mendez et al.,
212 2017). Each GPS location was assigned with one of the four behaviors determined by the
213 algorithm according to speed and turning angle: resting (low speed, low turning angle),

214 commuting (high speed, low turning angle), extensive search (high speed, high turning angle)
215 or intensive foraging (low speed, high turning angle). Resting corresponded to birds sitting on
216 the water, and commuting to birds transiting between the colony and feeding areas, or
217 between feeding areas.

218 In order to estimate individual daily activity patterns, the total number of each of the four
219 behaviors identified by EMbC was summed per hour of the day and divided by the total
220 number of behaviors per hour, thus representing relative proportion of each behavior
221 according to the time of the day. Proportions of each behavior per individual were also
222 computed and compared between the day, the moonlit part of the night and the moonless
223 part of the night in order to determine if behavior varies according to the presence of the
224 moon and if wedge-tailed shearwaters adopted a similar behavior during the moonlit part of
225 the night and during the day. Tracks containing less than 40 GPS locations were excluded from
226 the analysis because they could not effectively represent the activity pattern. Cloud cover was
227 not taken into account in the analysis, due to the poor temporal resolution of the
228 observational data available (minimum 1 observation per day), which does not allow to
229 determine the influence of the cloud cover on light intensity throughout the night.

230 **2.7 Stable isotope analyses**

231 Stable isotopic ratios were used to test for diet or foraging differences between night and day
232 feeding of GPS-tracked wedge-tailed shearwaters. For this purpose, isotopic ratio for stable
233 carbon ($^{13}\text{C}/^{12}\text{C}$, expressed as $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$ expressed as $\delta^{15}\text{N}$) were analyzed in
234 blood plasma of each individuals. $\delta^{15}\text{N}$ values are generally used as a proxy of the trophic level
235 (Minagawa and Wada, 1984), allowing to test whether individuals fed on different prey during
236 the day and at night. Carbon stable isotope values ($\delta^{13}\text{C}$) mainly reflect the foraging habitat /

237 resource use of consumers if significant gradients exist at the base of food webs, which seem
238 less pronounced in the tropics (Jaeger et al., 2010; Newsome et al., 2007). They were used
239 here to test a difference in prey habitat (e.g. offshore vs. onshore, benthic vs. pelagic) between
240 day and night. Plasma isotopic values reflect diet integrated 3 to 4 days prior to sampling,
241 (Hobson and Clark, 1993). Plasma was therefore used to assess recently integrated food items
242 by individuals, most likely during their last recorded trip.

243 Since lipids can affect plasma $\delta^{13}\text{C}$ values, they were removed using 2:1 chloroform: methanol
244 mixture (Hobson and Clark, 1993). Between 0.5 to 5 mg of dried plasma were repeatedly (2–
245 3 treatments) shaken for one hour in 4 ml of the solvent. The sample was then centrifuged at
246 4000g for 5 min and the supernatant containing the lipids was discarded. Lipid-free pellets
247 were dried at 60°C.

248 Sub-samples of plasma and red blood cells were weighed (0.3 mg) with a microbalance and
249 packed into tin cups. Relative abundance of C and N isotopes were determined with a
250 continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an
251 elemental analyzer (Thermo Scientific Flash EA 1112). Results are presented in the δ notation
252 relative to Vienna PeeDee Belemnite and atmospheric N^2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.
253 Replicate measurements of internal laboratory standards (acetanilide) indicated
254 measurement errors <0.10‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

255 **2.8 Statistical analyses**

256 All statistical and spatial analyses were performed using R 3.5.1 (R Core Team, 2018). .
257 Correlation between trip duration and maximum distance from the colony was tested using a
258 Pearson correlation test. In order to test whether birds adjusted their trip duration according
259 to the lunar phase, General Additive Model (GAM) assuming a Poisson error distribution was

260 applied, with trip duration as the dependent variable and lunar phase at the departure of the
 261 colony as fixed factor. Models were applied separately to chick-provisioning and self-
 262 provisioning trips. GAMs were created using the “mgcv” R package (Wood, 2017). Differences
 263 in the proportion of each behavior according to day or night, and moonless or moonlit part of
 264 the night were tested using Wilcoxon-Mann-Whitney rank sum-tests. Generalized Linear
 265 Models (GLMs) with Gaussian family and logit link function were applied on $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values
 266 with proportion of time spent to forage at night, site and year as explanatory variables. All
 267 results are presented as mean \pm standard error.

268 **3 - Results**

269 **3.1 Foraging trip characteristics**

270 The distribution of foraging trip durations suggests a bi-modal distribution with several trips
 271 lasting from 1 to 3 days, and longer trips lasting from 4 to 13 days (Appendix 1). Chick-feeding
 272 trip mean duration was 1.19 days (\pm 0.07, n = 120, Table 1), mean distance travelled 276 km
 273 (\pm 20, n = 100) and mean maximum distance from the colony 102 km (\pm 8, n = 101). Self-
 274 feeding trip mean duration was 7.31 days (\pm 0.37, n = 50), mean distance travelled 1452 km
 275 (\pm 102, n = 30) and mean maximum distance from the colony 401 km (\pm 21, n = 53). Pearson
 276 correlation tests showed that trip duration and maximum distance from the colony were
 277 correlated on average at 88.6 % \pm 3.8 % by site. Thus, we will consider only trip duration in the
 278 following results.

279 *Tableau 1 : Foraging parameters of wedge-tailed shearwaters studied during the 2017-2018 breeding*
 280 *season in New Caledonia*

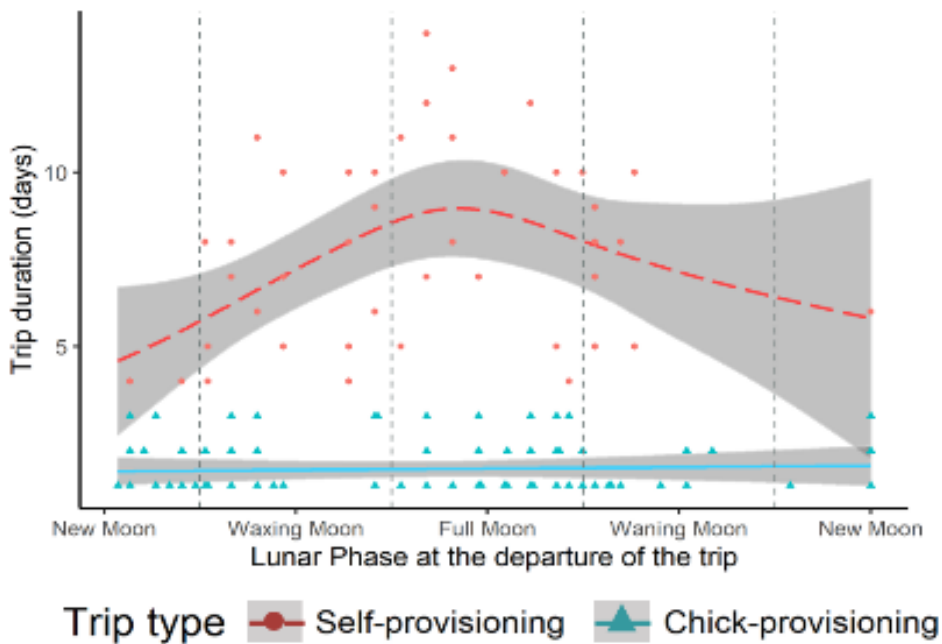
Number of tracked individuals	99
Number of foraging trips	179
Number of GPS-locations	23827
Chick-provisioning - trip duration (days)	1,19 \pm 0,07 (n = 120)
Self-provisioning - trip duration (days)	7,31 \pm 0,37 (n = 50)

Chick-provisioning - distance travelled (km)	276 ± 20 (n = 100)
Self-provisioning - distance travelled (km)	1452 ± 102 (n = 30)
Chick-provisioning - maximal distance from the colony (km)	102 ± 8 (n = 101)
Self-provisioning - maximal distance from the colony (km)	401 ± 21 (n = 53)

281

282 **3.2 Effect of lunar phase on foraging trip duration**

283 GAM did not reveal a significant effect of the lunar phase on chick-provisioning trips (≤ 3 days)
 284 duration (Figure 2; adjusted $R^2 = -0.005$, deviance explained = 0.385%, $n = 120$, $edf = 1$, $p =$
 285 0.521) but duration of self-provisioning trip (> 3 days) was significantly longer when birds
 286 departed around the full moon (Figure 2; adjusted $R^2 = 0.200$, Deviance explained = 25.5 %, $n =$
 287 50 , $edf = 2.702$, $p = 0.038$).

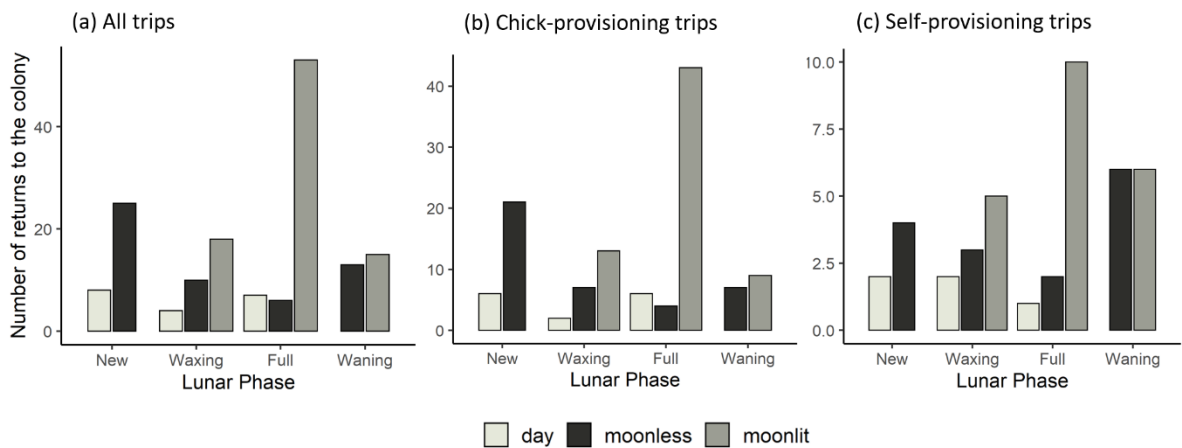


288

289 *Figure 2: Results from generalized additive models that assessed self-provisioning and chick-*
 290 *provisioning foraging trip durations of WTSH from 4 study colonies on New Caledonia, and the*
 291 *relationships with the phase of the moon at the time of departure from the colony. The figure shows a*
 292 *clear relationship with self- provisioning trips (n = 50, dashed line and circles represent individual trips),*
 293 *but no effect of the moon on chick-provisioning trips (n = 120, solid line and triangles)*

294 **3.3 Arrival time at the colony**

295 Among the 160 trips for which arrival time at the colony could be calculated, 19 (12 %) took
296 place during the day, before astronomical dusk or after astronomical dawn. Among the 141
297 arrivals that took place at night, 55 (39 %) occurred during moonless conditions and 86 (61 %) under moonlit conditions (Figure 3). During waxing and waning moons, when the moon is present only during a part of the night, most individuals reached the colony under moonlit conditions (64.3 % during waxing moon, 53.6 % during waning moon). Around the new moon, the moon is absent throughout the night and it is the only case where most of the arrivals took place during moonless conditions (76.5 %), the others occurring before astronomical dusk (23.5 %).



304

305 *Figure 3: Frequency distribution of wedge-tailed shearwaters arrivals to the colony according to the*
306 *presence of the moon for (a) all trips, (b) chick-provisioning trips and (c) self-provisioning trips. Sample*
307 *sizes (number of arrivals to the colony) are as follows: moonless part of nights, n = 55; moonlit part of*
308 *the night, n = 86; outside the complete night, n = 19*

309 **3.4 Activity patterns and lunar cycle**

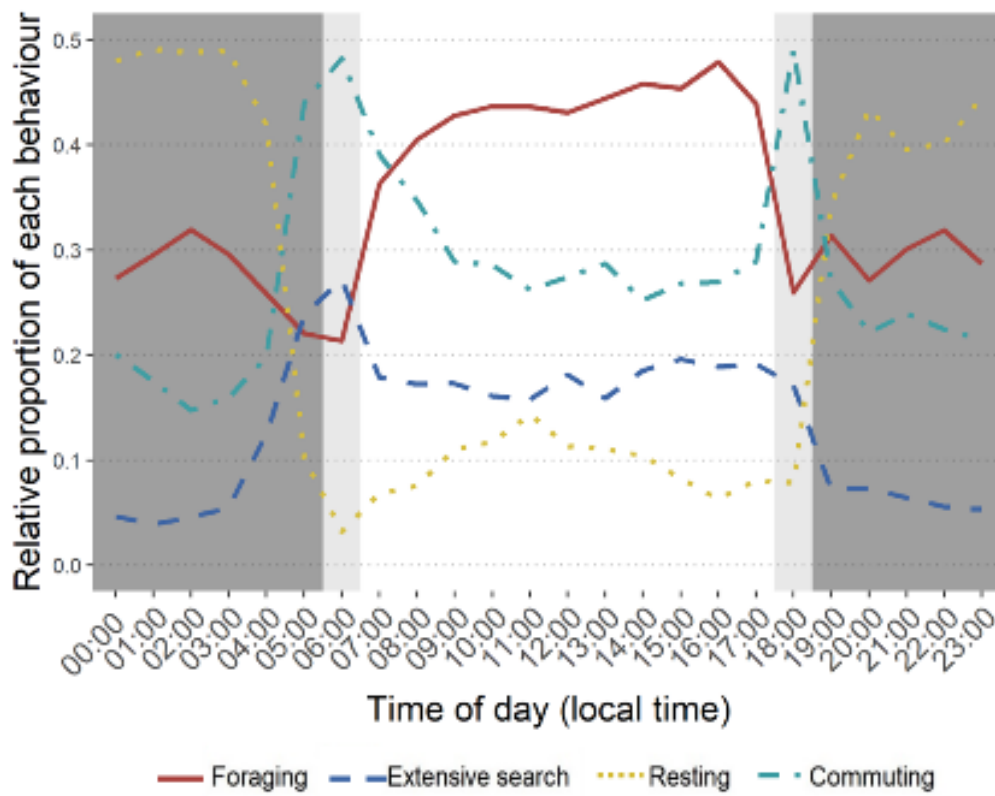
310 When at sea, foraging behavior represented the most important activity during daytime and
311 the second most important during the night (Table 2, Figure 4). Individuals spent most of their
312 time resting on the water during the night, while during the day it was the least represented
313 behavior. Commuting behavior occurred mainly at dusk and dawn. At night, wedge-tailed

314 shearwater behavior was significantly affected by moonlight, with foraging activity occurring
 315 more frequently during moonlit than during moonless periods of the night ($W = 3964.5$, p
 316 < 0.001 ; Figure 5). Furthermore, they foraged more than they rested during moonlit periods
 317 (Wilcoxon-Mann-Whitney $W = 3841.5$, $p = 0.001$) and conversely rested more than foraged
 318 during moonless periods ($W = 779.5$, $p < 0.001$), even though foraging remained lower during
 319 moonlit periods of the night than during daylight ($W = 4695$, $p = 0.008$; Figure 5).

320 On average 72.1 % (± 1.6) of foraging activity occurred during daylight. Daylight foraging
 321 dropped to 68.0 % (± 1.7) when the foraging trips included ≥ 1 night/s away from the colony,
 322 with individual variability ranging between 4 and 94 % of total foraging activity.

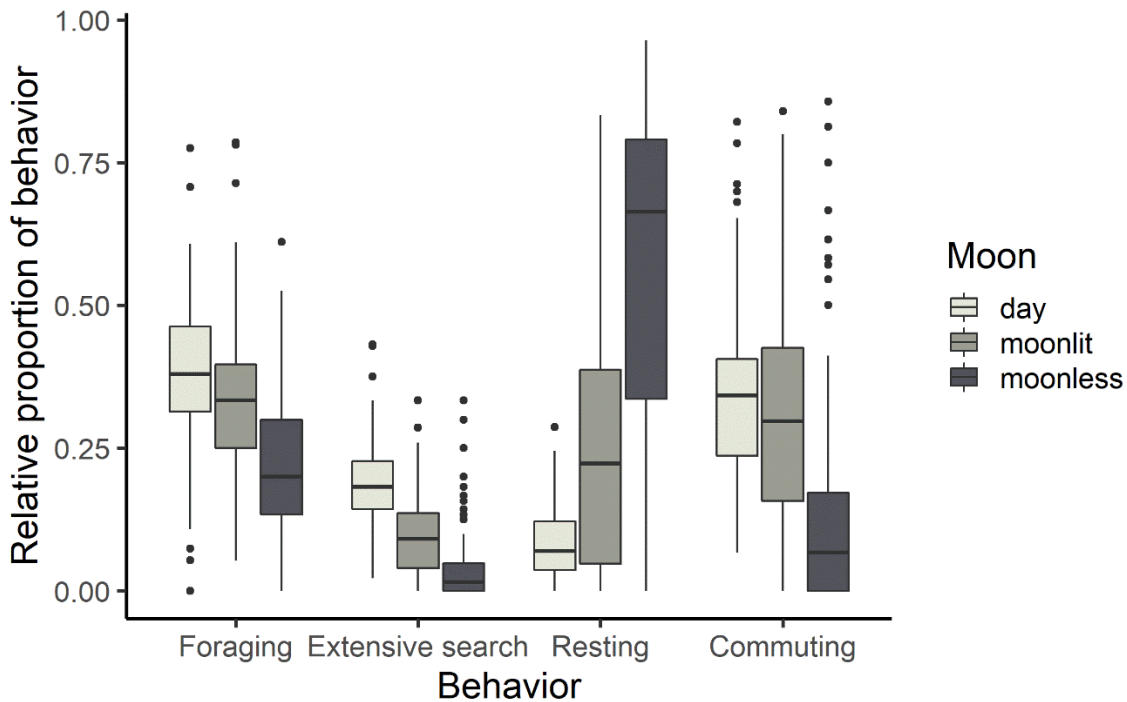
323 *Tableau 2: Proportion (mean \pm SE) of behaviour (foraging, extensive search, resting, commuting)*
 324 *carried out by breeding wedge-tailed shearwaters in New caledonia. Results are presented for night*
 325 *and day confounded (All), during the day (Day), during the night (Night), during the moonless part of*
 326 *the night (Moonless) or during the moonlit part of the night (Moonlit).*

	Foraging	Extensive search	Resting	Commuting
All	0,32 \pm 0,15	0,12 \pm 0,10	0,27 \pm 0,28	0,28 \pm 0,21
Day	0,38 \pm 0,13	0,19 \pm 0,08	0,09 \pm 0,07	0,34 \pm 0,14
Night	0,28 \pm 0,15	0,07 \pm 0,08	0,39 \pm 0,30	0,24 \pm 0,23
Moonlit	0,34 \pm 0,15	0,10 \pm 0,08	0,25 \pm 0,23	0,31 \pm 0,21
Moonless	0,23 \pm 0,13	0,05 \pm 0,08	0,56 \pm 0,29	0,16 \pm 0,22



327

328 *Figure 4: Percentage of time allocated to each behavior (foraging, extensive search, resting or*
 329 *commuting) by New Caledonia breeding wedge-tailed shearwaters, according to the time of day. The*
 330 *dark grey parts represent the night, the light grey parts the dawn and dusk and the white part the day.*



331

332 *Figure 5 : Proportion (mean \pm SE) of behaviors (foraging, extensive search, resting, commuting)*
 333 *assigned along the tracks of New Caledonia breeding wedge-tailed shearwaters according to the*
 334 *presence of the sun and the moon (day, moonlit part of the night or moonless part of the night)*

335 **3.5 Stable isotope analyses**

336 Linear regression models revealed that the $\delta^{15}\text{N}$ values in blood plasma were significantly
 337 affected by the percentage of nocturnal foraging (estimate = -1.98, CI95: [-3.930 : -0.034];
 338 Table 3) indicating a decrease in $\delta^{15}\text{N}$ values along with the time spent foraging at night. The
 339 $\delta^{15}\text{N}$ values were significantly higher during 2018 compare to 2017 (estimate = 1.17, CI95:
 340 [0.752 : 2.906]) and significantly higher in Tiambouene colony compare to Canard (estimate =
 341 -1.15, CI95: [-3.135 : -0.463]). The model also highlighted a significant combined-effect of the
 342 percentage of nocturnal foraging at Pindai (estimate = 2.27, CI95: [0.203 : 4.329]), indicating
 343 that the $\delta^{15}\text{N}$ values were differently affected by the percentage of nocturnal foraging for this
 344 colony.

345 No significant effect of percentage of nocturnal foraging on the blood plasma $\delta^{13}\text{C}$ values was
 346 shown (estimate = 0.25, CI95: [-0.589 : 1.102]).

347 *Tableau 3: Summary tables of linear models explaining trends in nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$)*
 348 *isotopic values from blood plasma of wedge-tailed shearwater as a function of their percentage of*
 349 *nocturnal foraging, colony and year of sampling. Intercept represent the year 2017 and the site Canard*
 350 *islet.*

$\delta^{15}\text{N}$	Estimate	Std.error	t value	P-value
Intercept	9,34	0,38	24,79	***
Percentage of nocturnal foraging	-1,98	0,99	-2,01	*
Site - Mato	-0,37	0,48	-0,77	0,44
Site - Pindai	-0,62	0,40	-1,56	0,12
Site - Tiambouene	-1,14	0,45	-2,53	*
Year - 2018	1,18	0,21	5,58	***
Percentage : Site - Mato	0,10	1,37	0,07	0,94
Percentage : Site - Pindai	2,27	1,04	2,17	*
Percentage : Site - Tiambouene	0,72	1,25	0,58	0,56
$\delta^{13}\text{C}$				
Intercept	-16,99	0,16	-104,29	***
Percentage of nocturnal foraging	0,26	0,43	0,60	0,55
Site - Mato	0,07	0,22	0,32	0,75
Site - Pindai	0,12	0,17	0,67	0,50
Site - Tiambouene	-0,30	0,29	-1,02	0,31
Year 2018	0,32	0,24	1,36	0,18
Percentage : Site - Mato	-0,11	0,67	-0,16	0,87
Percentage : Site - Pindai	1,92	0,45	-0,36	0,72
Percentage : Site - Tiambouene	1,92	1,01	1,90	0,06
Percentage : Year - 2018	-1,82	0,85	-2,13	*

351

352 **4 - Discussion**

353 Wedge-tailed shearwaters performing chick-provisioning trips primarily returned to the
 354 colony under moonlit conditions and lunar phase did not significantly affect chick-provisioning
 355 trip length, indicating that these trips would be conducted regardless of the lunar phase. It is
 356 important for shearwaters to maintain regular chick provisioning and they can achieve this
 357 with short duration trips that are near the colony (McDuie et al., 2018).

358 By contrast, when performing self-provisioning foraging trips, trip lengths were longer around
 359 the full moon than under the new moon. Wedge-tailed shearwaters are known to forage at

360 more distant locations when self-provisioning (Congdon et al., 2005; McDuie et al., 2015)
361 where prey resources may be richer (e.g. Miller et al., 2018; Weimerskirch et al., 1994). We
362 also found that the maximum distance of longer trips was farther from the colony than for
363 shorter trips so WTSH could be taking advantage of increased light available around the full
364 moon to extend foraging time and food assimilation when self-provisioning.

365 This behavior has been previously documented in another shearwater species, the Scopoli's
366 shearwater *Calonectris diomedea*, where (Rubolini et al. (2015) interpreted the longer trips
367 taken by shearwaters under moonlit conditions as a predation avoidance strategy.
368 Furthermore, in that study, the majority of individuals returned to the colony and entered
369 burrows once the night was moonless. Moonlight avoidance when attending colonies has also
370 been documented in other Procellariid species, generally reflected by a lower number of
371 individuals at the colony during the nights around the full moon (Bourgeois et al., 2008;
372 Bretagnolle, 1990; Mougeot and Bretagnolle, 2000; Riou and Hamer, 2008). In contrast, a
373 recent study indicated that streaked shearwaters *Calonectris leucomelas* did not avoid
374 moonlight when arriving at the colony (Tatenhove et al., 2018). In our study, 53 % of wedge-
375 tailed shearwaters returned from chick- and self-provisioning foraging trips during moonlit
376 periods and 12 % of the individuals reached the colony before astronomical dusk. Even when
377 the moon was absent during part of the night, when waxing or waning, only 39 % of wedge-
378 tailed shearwaters returned during moonless periods, which contradicts the predation
379 avoidance hypothesis. Thus, wedge-tailed shearwater trip duration does not seem to be
380 related to the avoidance of predation on land in New Caledonia, despite evidence of predation
381 by feral cats *Felis catus* and peregrine falcons *Falco peregrinus* in at least two colonies (pers.
382 obs.). On the other hand, we cannot exclude that non-breeding individuals may have avoided

383 moonlight, a phenomenon observed in other petrel and shearwater species (Bourgeois et al.
384 2008).

385 During the breeding season, wedge-tailed shearwaters primarily foraged during the day,
386 commuted to and from the colony at dawn and dusk and rested at night. However, the
387 unexpectedly active nocturnal foraging differed from most previous studies that showed little
388 nocturnal foraging in closely related, large shearwaters (600 to 950 g; flesh footed shearwater
389 *Ardenna carneipes*: 2% of dives during night-time, Rayner et al. 2011; sooty shearwater
390 *Ardenna grisea*: <5% of dives, Shaffer et al. 2009; streaked shearwater: 5% of dives,
391 Matsumoto et al. 2012; great shearwater *Ardenna gravis*: <0.5% of dives, Ronconi et al. 2010;
392 short-tailed shearwaters *Ardenna tenuirostris*: lack of dive during the night, Raymond et al.
393 2010). One exception of this contrasted pattern of nocturnal foraging activity between large
394 and small procellariids is the pink-footed shearwater (*Ardenna creatopus*, ~700 g) which
395 performed 22 % of its dives during the night (Adams et al., 2019), which is similar to the 28 %
396 nocturnal foraging by wedge-tailed sheawaters in the present study. Nevertheless, we cannot
397 exclude that our results may be specific to our study populations and/or years as spatial and
398 temporal adjustment of foraging activity has been observed in other seabird populations.
399 Cory's shearwaters *Calonectris diomedea*, for example, become nocturnal foragers when
400 wintering in colder, deeper seas areas of the ocean where the DVM is more prevalent,
401 particularly during moonlit nights (Dias et al., 2012).

402 Interestingly, wedge-tailed shearwaters foraging activity under moonlit conditions became
403 more similar to their diurnal pattern, whereby foraging exceeded resting. Moonlight could
404 provide sufficient light for these predators that, as with many procellariids, rely on visual cues
405 at small spatial scale to hunt for small pelagic prey such as squids and fish (Brooke, 2004;

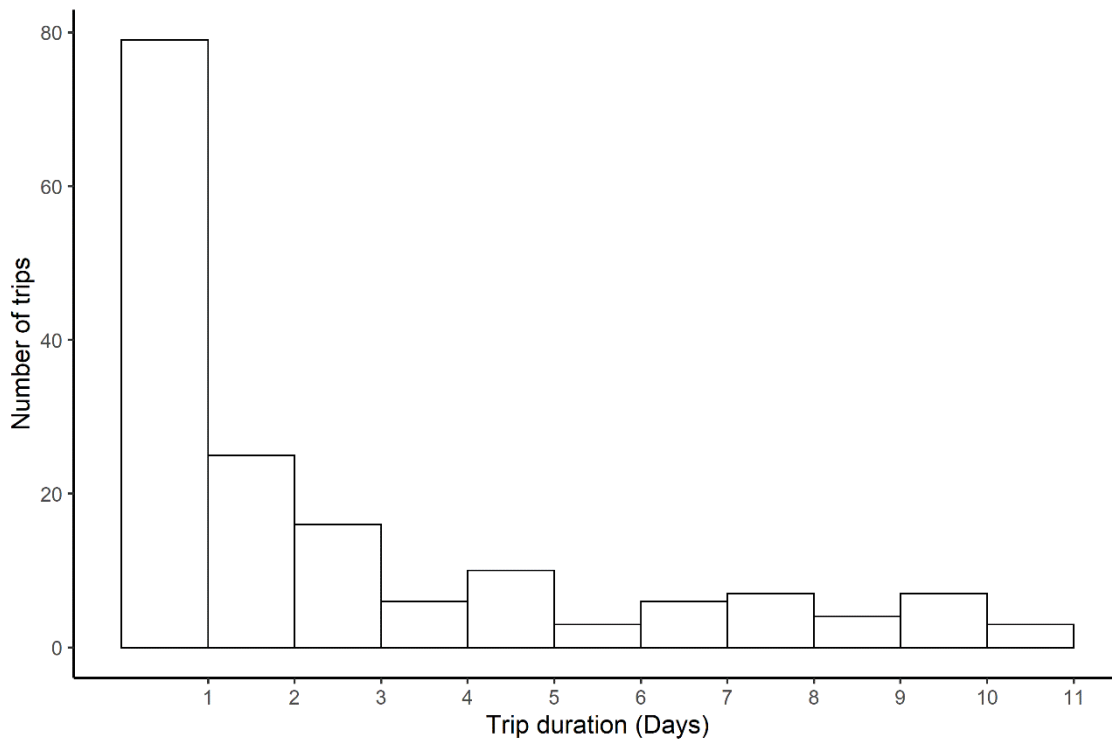
406 Harrison et al., 1983). Remaining at sea for nocturnal foraging consequently delayed these
407 individuals' return to the colony which drove the increase in moonlit commuting behavior.
408 These results are consistent with previous studies conducted on petrels (Dias et al., 2016;
409 Ramos et al., 2016), shearwaters (Dias et al., 2012; Yamamoto et al., 2008) and albatrosses
410 (Phalan et al., 2007), that highlighted a greater movement or foraging activity during moonlit
411 nights. Thus, we think it more likely that longer trips around the full moon are linked to
412 increased foraging opportunities than predation avoidance.

413 Another factor that may cause wedge-tailed shearwaters to remain foraging at-sea
414 nocturnally is the DVM exhibited by mesopelagic fish species (Spear et al., 2007) such as
415 Myctophidae, known to be consumed by wedge-tailed shearwaters (Komura et al., 2018). If
416 DVM makes these species available during the night to shallow divers, such as wedge-tailed
417 shearwaters (Spear et al., 2007), we would expect to see this reflected in divergent values of
418 the stable isotopes $\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$ (Inger and Bearhop, 2008) according to the time spent
419 foraging at night.. The absence of a relationship between $\delta^{13}\text{C}$ values and the proportion of
420 nocturnal foraging may indicate that wedge-tailed shearwaters target similar habitats/species
421 when foraging at night. Alternatively, this could be due to a lack of contrast in $\delta^{13}\text{C}$ values at
422 the base of tropical food webs (Ménard et al., 2007), which prevents differentiation between
423 the foraging habitats used. By contrast, the decrease in $\delta^{15}\text{N}$ values in relation to the
424 percentage of nocturnal foraging supports a possible shift in prey consumption between day
425 and night which is consistent with the assumption that wedge-tailed shearwaters could take
426 advantage of the nocturnal migration of mesopelagic prey to the surface. However, this was
427 a relatively weak relationship compared with the strong differences in $\delta^{15}\text{N}$ values between
428 year and sites and, as such, must be interpreted carefully. Additional diet analyses based on

429 eDNA would be useful to confirm these results, and to better understand the diet of wedge-
430 tailed shearwaters when foraging at night.

431 Based on 179 high resolution WTSH foraging trips, this study strengthens the evidence that
432 the moon strongly affects foraging activity during the breeding season in Procellariids. By
433 tuning self-provisioning foraging trip durations, WTSH were able to extend their foraging time-
434 window and forage day and night by taking advantage of the lengthened light available during
435 the most favorable periods around full moon. This behavioral adjustment could reduce intra-
436 and inter-specific competition for resources with other abundant, and mainly diurnal foraging
437 seabird species that nest in New Caledonia (Spaggiari et al., 2007). This could be of significant
438 importance in an area where very large seabird populations (Pandolfi and Bretagnolle, 2002)
439 rely on poor productivity, oligotrophic waters (Menkes et al., 2015).

440 **Appendixes:**



441

442 *Appendix 1: Histogram of the foraging trip duration of wedge-tailed shearwaters GPS tracked in New*
443 *Caledonia during 2017 and 2018 breeding season.*

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