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

Andreas Ravache[a,b,c,*], Karen Bourgeois[a], Martin Thibault[b], Sylvain Dromzée[a], Henri Weimerskirch[d], Sophie de Grissac[d], Aurélien Prudor[d], Anne Lorrain[e], Christophe Menkes[b], Valérie Allain[f], Paco Bustamante[g,h], Yves Letourneur[c], Éric Vidal[a,b]

[a] *IMBE, Aix-Marseille Université, CNRS, IRD, Avignon Université, Centre IRD Nouméa - BP A5, 98848 NouméaCedex, New-Caledonia, France*

[b] *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*

[c] *University of New Caledonia / ISEA, BP R4, 98851 Nouméa Cedex, New-Caledonia, France*

[d] *Centres d'Etudes Biologiques de Chizé – CNRS, France*

[e] *Univ Brest, CNRS, IRD, Ifremer, LEMAR, F-29280 Plouzane, France*

[f] *Secretariat of the Pacific Community, SPC, BP D5, 98848 Nouméa Cedex, New Caledonia, France*

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

[h] *Institut Universitaire de France (IUF), 1 rue Descartes, 75005 Paris, France*

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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. $\delta^{15}N$ 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.

1. Introduction

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

However, reduced activity at the colony during moonlit nights may

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* Corresponding author at: 101 Promenade Roger Laroque, 98848 Noumea, New-Caledonia, France.
E-mail address: andreas.ravache@ird.fr (A. Ravache).

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also be a result of increased activity elsewhere, such as nocturnal at-sea foraging. Procellariiform species, which are visual predators lacking night vision adaptations (Brooke, 2004), should, therefore, benefit from moonlight, that would allow improved nocturnal foraging. Several studies have shown that shearwater, petrel and albatross nocturnal at-sea activity was enhanced during full moon nights compared with moonless nights, both during the breeding (Dias et al., 2016; Phalan et al., 2007; Rubolini et al., 2015) and non-breeding periods (Dias et al., 2012; Pinet et al., 2011; Yamamoto et al., 2008). The hypothesis of nocturnal foraging is also supported by increased availability of some seabird prey in subsurface waters during night time thanks to the Diel Vertical Migration (DVM) which is the vertical migration of micronekton, the prey species of many predators, toward the surface at night and in deeper waters during the day (Hays, 2003, Brooke, 2004). Prey availability at the surface changes along with variations in the DVM, being reduced on full moon nights and higher during new moon nights (Benoit-Bird et al., 2009; Gliwicz, 1986). However, Waap et al. (2017) found no evidence of dietary shift in prey species composition or diversity according to the lunar cycle in nocturnally foraging and shallow-diving Procellariid species, the Bulwer's petrel, which feeds on mesopelagic species brought close to the surface during DVM. Furthermore, research conducted on the same species revealed a relatively weak effect of lunar phase on its activity (10% more time flying during full moon compared to other lunar phase; Dias et al., 2016). Combined, these results suggest that normally deep prey are available at the surface in sufficient amounts to be accessed by seabirds, even during full moon nights.

Some Procellariid species, for example wedge-tailed shearwaters (*Ardenna pacifca* Gmelin, 1789), are thought to primarily forage during daylight (Catry et al., 2009), and often in association with subsurface predators such as tuna (Au and Pitman, 1986; Hebshi et al., 2008; Miller et al., 2018; Spear et al., 2007). Epipelagic tuna are generally considered to be diurnal foragers (Roger, 1994), although some studies demonstrate occasional nocturnal foraging (Schaefer et al., 2009). These associations, by which surface predators drive prey close to the surface (Ashmole, 1971), facilitate foraging (Hebshi et al., 2008; Miller et al., 2018) for shallow-diving procellariids like wedge-tailed shearwaters (mean maximum diving depth: 5–14 m; Burger, 2001; Peck and Congdon, 2005). This is particularly true in oligotrophic tropical waters where wedge-tailed shearwaters have been documented foraging in association with yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tuna (Miller et al., 2018). However, wedge-tailed shearwaters have also been documented foraging during full moon nights (Gould, 1967) which suggests that other factors than sub-surface predator associations, for instance the lunar phase or prey migration patterns may influence wedge-tailed shearwaters foraging strategies.

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

While the predation avoidance hypothesis in relation to lunar cycle has been extensively tested by analyzing seabird activity patterns at colonies (e.g. Bretagnolle, 1990; Mougeot and Bretagnolle, 2000; Bourgeois et al., 2008), few studies simultaneously focused on nocturnal foraging activity (but see Rubolini et al., 2015, which found that Scopoli shearwaters *Calonectris domedea* increased their diving activity during full moon nights, but interpreted longer trips around the full moon to be driven by predation avoidance on land rather than higher foraging opportunities at sea). Moreover, most studies on lunar effects on the nocturnal, at-sea activity of seabirds, have been conducted using global location sensor (GLS). These data, only provide information on the time spent on water (e.g. Phalan et al., 2007; Dias et al., 2012; Cruz et al., 2013), but prevent determining what drives that behavior, i.e. whether increased time spent on water during moonlit periods represent foraging activity or loafing. Using high-resolution GPS data, the present study aimed at unravelling the effects of moon illumination and lunar phase on both nocturnal at-colony activity and at-sea foraging in wedge-tailed shearwaters, to understand how they shape their activities. We used miniaturized GPS-loggers to obtain a fine-scale trajectory of foraging trips during breeding season and accurately define resting, commuting and foraging events. We evaluated the proportion of time spent foraging during daytime and night-time and studied lunar phase and moon presence effects upon feeding trip duration, time of return to the colony and at-sea foraging. Finally we performed stable isotope analysis on blood plasma from all individuals, to determine whether we could identify diet differences associated with nocturnal foraging activity established through GPS tracking.

2. Material and methods

2.1. Ethical statement

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

2.2. Field work

Field trips were conducted at four field sites in New Caledonia in the Coral Sea, South-west Pacific, which is home of 500,000 breeding pairs of wedge-tailed shearwaters (Pandolfi and Bretagnolle, 2002). In this geographic area, the wedge-tailed shearwater breeding season begins around the end of October with the return of breeding adults to colonies and is completed at the end of May when chicks fledge (McDuie and Congdon, 2016). GPS-loggers were fitted on breeding adults during the chick-rearing period (from March to April) during two successive years (2017 and 2018) at four breeding sites. One study colony is located on the main island of New-Caledonia (Fig. 1): Pindaï (21.354°S, 164.954°E) where 37 and 7 breeders were equipped in 2017 and 2018, respectively. The three other study sites are located on lagoon islets: Mato (22.55°S, 166.80°E) where 20 and 7 breeders were equipped in 2017 and 2018, respectively, Canard (22.31°S, 166.31°E) where 11 breeders were equipped in 2017, and Tiambouene (20.38°S, 164.04°E) where 17 breeders were equipped in 2018. Breeding adults were fitted with either 4.5 g Ecotone, 6 g Lotek, 5 g Pathtrack or 12.5 g TechnoSmart GPS-loggers, representing 1 to 3% of wedge-tailed shearwater body weight (413 ± 40 g in the present study), i.e. below the limit commonly accepted to limit behavior modification (Phillips et al., 2003). The lightest GPS-loggers (Ecotone, Lotek and Pathtrack) were attached to three tail feathers using Tesa® tape (McDuie et al., 2018), while the heaviest GPS-loggers (Technosmart) were back-mounted to ensure balance during flight would not be affected (Vandenabeele et al., 2014). Locations were recorded every 15 min. Birds were captured by hand at their burrow entrance before feeding their chicks. Colonies were monitored every night to recapture birds for logger recovery. A maximum of 0.4 ml of blood was collected on recapture from the tarsal

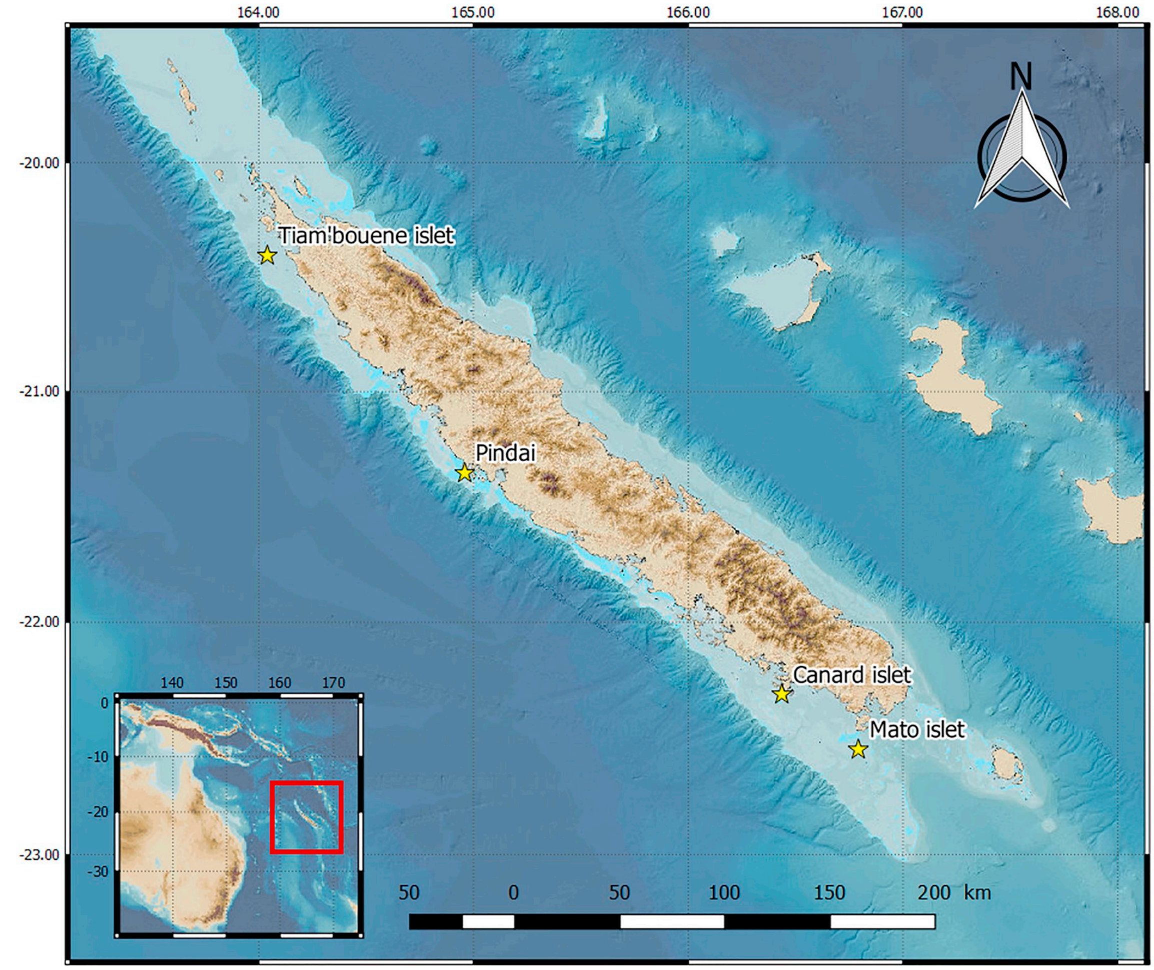

Fig. 1. Map of New Caledonia, showing the location of the four wedge-tailed shearwaters breeding colonies used in this high resolution GPS study of foraging behavior. Inset shows the position of New Caledonia at the eastern edge of the Coral Sea.

vein using a 0.5 ml 29G syringe. Blood samples were centrifuged within 1 h from collection to separate plasma and blood cells that were then stored separately in 70% ethanol until stable isotope analyses were run.

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

In order to investigate the effect of moonlight on wedge-tailed shearwater foraging behaviour, the night was defined as the period between astronomical dusk and the beginning of the astronomical dawn (i.e. when the geometric center of the Sun's disk is 18° below the horizon). Astronomical dusk and dawn, moon rise and set were computed at each location recorded by GPS-loggers using the R “suncalc” package (Agafonkin and Thieurmel, 2017), while moonlight intensity and lunar phase were determined at each location with the R package “lunar” (Lazaridis, 2014). Moonlight intensity was a value comprised between 0 and 1, 0 being the illumination during the new moon or during the moonless part of the night (before moonrise or after moonset), and 1 the illumination during the brightest full moon. Lunar phase was a value in radians, 0 corresponding to new moon, $\pi/2$ to first quarter (waxing moon), π to full moon and $3\pi/2$ to last quarter (waning moon).

2.4. *Foraging trip characteristics*

Data from a total of 179 foraging trips were collected during 2017 ($n = 126$) and 2018 ($n = 53$) breeding seasons from 99 GPS-tracked individuals. Complete tracks, starting from the departure of the bird and ending at its return to the burrow, represented 85% of the total number of tracks. Trip duration (days), total distance travelled and maximum distance from the colony (km) were computed using the R package “trip” (Michael et al., 2016). When tracks were incomplete, trip duration was estimated using the individual return date based on observation of birds back at the colony. Durations of nine incomplete tracks were impossible to estimate, and these tracks were removed from the analysis, resulting in a total of 170 trips being considered for trip duration analysis. Trips presenting gaps ($n = 20$) were removed from total distance travelled analysis, and incomplete trips (i.e. when the battery stopped before the individual began its return to the colony, $n = 16$) were removed from maximal distance travelled analysis. During the chick-rearing period, pelagic seabirds have to concurrently provide food to their chicks and meet their own needs using zones of high foraging competition near their colony (Furness and Birkhead, 1984; Lewis et al., 2001). In wedge-tailed shearwaters, longer trips are undertaken to ensure self-provisioning whereas shorter trips focus on chick provisioning (Congdon et al., 2005; McDuie et al., 2015, 2018; Weimerskirch et al., 2020). Thus, we differentiated in this study long trips ($>$ 3 days, $n = 50$) and short trips ($\leq$ 3 days, $n = 119$).

2.5. *Arrival time at the colony*

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

2.6. Behavioral assessment

Expectation Maximization binary Clustering (EMbC) algorithm (Garriga et al., 2016), a variant of the expectation maximization algorithm in maximum likelihood estimation of Gaussian mixture models, was used to determine wedge-tailed shearwaters behavior during their foraging trips using the R package "EMbC" (Garriga et al., 2016). EMbC is a robust multivariate clustering algorithm based on sinuosity and speed of the trajectory calculated using loxodromic distances and bearings of the tracks to determine animal behavior. It requires few prior assumptions, assuming that turn angles between consecutive locations indicate searching or foraging, while straight bouts can be associated with resting (slow) and commuting (fast) (Garriga et al., 2016). This method has been used to assess ecologically meaningful behaviors from geolocation data for a range of seabird species, including Procellariiforms (Bennison et al., 2018; Clay et al., 2019; de Grissac et al., 2017; Mendez et al., 2017). Each GPS location was assigned with one of the four behaviors determined by the algorithm according to speed and turning angle: resting (low speed, low turning angle), commuting (high speed, low turning angle), extensive search (high speed, high turning angle) or intensive foraging (low speed, high turning angle). Resting corresponded to birds sitting on the water, and commuting to birds transiting between the colony and feeding areas, or between feeding areas.

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

2.7. Stable isotope analyses

Stable isotopic ratios were used to test for diet or foraging differences between night and day feeding of GPS-tracked wedge-tailed shearwaters. For this purpose, isotopic ratio for stable carbon ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$ expressed as $\delta^{15}N$) were analyzed in blood plasma of each individuals. $\delta^{15}N$ values are generally used as a proxy of the trophic level (Minagawa and Wada, 1984), allowing to test whether individuals fed on different prey during the day and at night. Carbon stable isotope values ($\delta^{13}C$) mainly reflect the foraging habitat / resource use of consumers if significant gradients exist at the base of food webs, which seem less pronounced in the tropics (Jaeger et al., 2010; Newsome et al., 2007). They were used here to test a difference in prey habitat (e.g. offshore vs. onshore, benthic vs. pelagic) between day and night. Plasma isotopic values reflect diet integrated 3 to 4 days prior to sampling, (Hobson and Clark, 1993). Plasma was therefore used to assess recently integrated food items by individuals, most likely during their last recorded trip.

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

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

2.8. Statistical analyses

All statistical and spatial analyses were performed using R 3.5.1 (R Core Team, 2018). Correlation between trip duration and maximum distance from the colony was tested using a Pearson correlation test. In order to test whether birds adjusted their trip duration according to the lunar phase, General Additive Model (GAM) assuming a Poisson error distribution was applied, with trip duration as the dependent variable and lunar phase at the departure of the colony as fixed factor. Models were applied separately to chick-provisioning and self-provisioning trips. GAMs were created using the "mgcv" R package (Wood, 2017). Differences in the proportion of each behavior according to day or night, and moonless or moonlit part of the night were tested using Wilcoxon-Mann-Whitney rank sum-tests. Generalized Linear Models (GLMs) with Gaussian family and logit link function were applied on $\delta^{15}N$ or $\delta^{13}C$ values with proportion of time spent to forage at night, site and year as explanatory variables. All results are presented as mean ± standard error.

3. Results

3.1. Foraging trip characteristics

The distribution of foraging trip durations suggests a bi-modal distribution with several trips lasting from 1 to 3 days, and longer trips lasting from 4 to 13 days (Supplementary Fig. S1). Chick-feeding trip mean duration was 1.19 days (± 0.07, *n* = 120, Table 1), mean distance travelled 276 km (± 20, *n* = 100) and mean maximum distance from the colony 102 km (± 8, *n* = 101). Self-feeding trip mean duration was 7.31 days (± 0.37, *n* = 50), mean distance travelled 1452 km (± 102, *n* = 30) and mean maximum distance from the colony 401 km (± 21, *n* = 53). Pearson correlation tests showed that trip duration and maximum distance from the colony were correlated on average at 88.6% ± 3.8% by site. Thus, we will consider only trip

Table 1
Foraging parameters of wedge-tailed shearwaters studied during the 2017–2018 breeding season in New Caledonia.

Number of tracked individuals	99
Number of foraging trips	179
Number of GPS-locations	23,827
Chick-provisioning - trip duration (days)	1,19 ± 0,07 (n = 120)
Self-provisioning - trip duration (days)	7,31 ± 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)

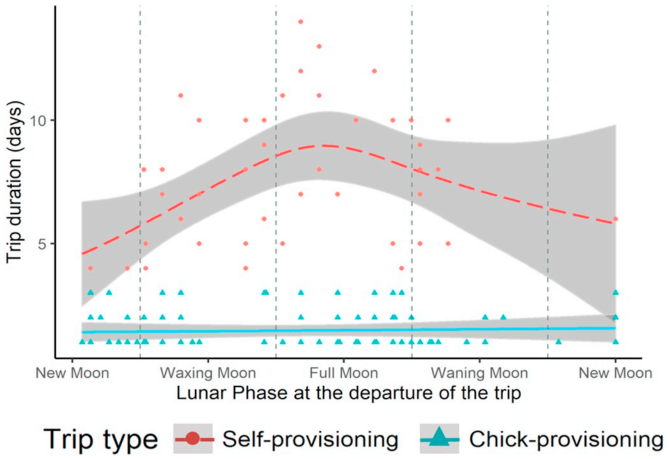

Fig. 2. Results from generalized additive models that assessed self-provisioning and chick-provisioning foraging trip durations of WTSH from 4 study colonies on New Caledonia, and the relationships with the phase of the moon at the time of departure from the colony. The figure shows a clear relationship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

duration in the following results.

3.2. Effect of lunar phase on foraging trip duration

GAM did not reveal a significant effect of the lunar phase on chick-provisioning trips (≤ 3 days) duration (Fig. 2; adjusted $R^2 = -0.005$, deviance explained = 0.385%, n = 120, edf = 1, $p = .521$) but duration of self-provisioning trip (> 3 days) was significantly longer when birds departed around the full moon (Fig. 2; adjusted $R^2 = 0.200$, Deviance explained = 25.5%, n = 50, edf = 2.702, $p = .038$).

3.3. Arrival time at the colony

Among the 160 trips for which arrival time at the colony could be calculated, 19 (12%) took place during the day, before astronomical dusk or after astronomical dawn. Among the 141 arrivals that took place at night, 55 (39%) occurred during moonless conditions and 86 (61%) under moonlit conditions (Fig. 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%).

Table 2

Proportion (mean ± SE) of behaviour (foraging, extensive search, resting, commuting) carried out by breeding wedge-tailed shearwaters in New caledonia. Resulats are presented for night and day confounded (All), during the day (Day), during the night (Night), during the moonless part of the night (Moonless) or during the moonlit part of the night (Moonlit).

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

3.4. Activity patterns and lunar cycle

When at sea, foraging behavior represented the most important activity during daytime and the second most important during the night (Table 2, Fig. 4). Individuals spent most of their time resting on the water during the night, while during the day it was the least represented behavior. Commuting behavior occurred mainly at dusk and dawn. At night, wedge-tailed shearwater behavior was significantly affected by moonlight, with foraging activity occurring more frequently during moonlit than during moonless periods of the night (W = 3964.5, $p < .001$; Fig. 5). Furthermore, they foraged more than they rested during moonlit periods (W = 3841.5, $p = .001$) and conversely rested more than foraged during moonless periods (W = 779.5, $p < .001$), even though foraging remained lower during moonlit periods of the night than during daylight (W = 4695, $p = .008$; Fig. 5).

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

3.5. Stable isotope analyses

Linear regression models revealed that the $\delta^{15}N$ values in blood plasma were significantly affected by the percentage of nocturnal foraging (estimate = −1.98, CI95: [−3.930: −0.034]; Table 3) indicating a decrease in $\delta^{15}N$ values along with the time spent foraging at

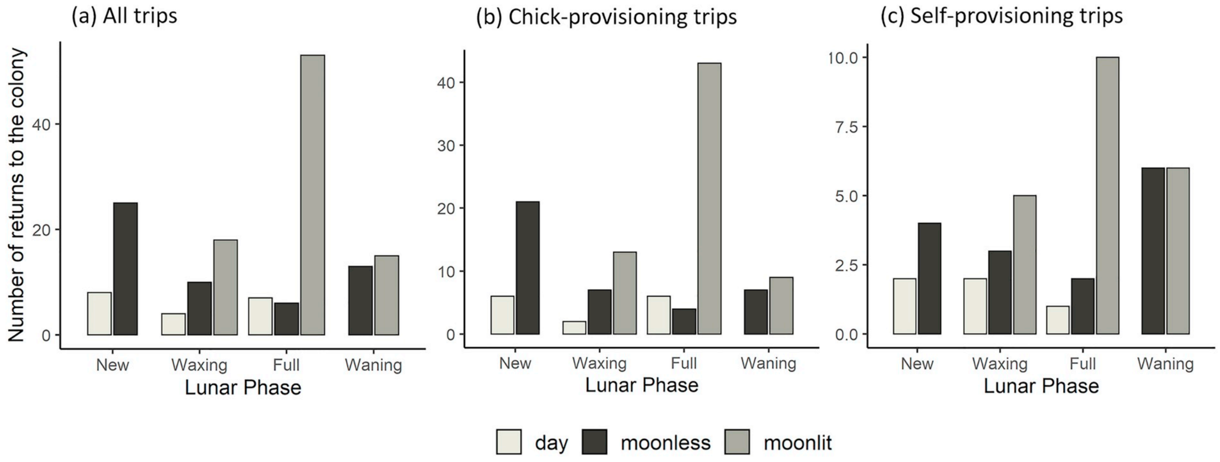

Fig. 3. Frequency distribution of wedge-tailed shearwaters arrivals to the colony according to the presence of the moon for (a) all trips, (b) chick-provisioning trips and (c) self-provisioning trips. Sample sizes (number of arrivals to the colony) are as follows: moonless part of nights, $n = 55$; moonlit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

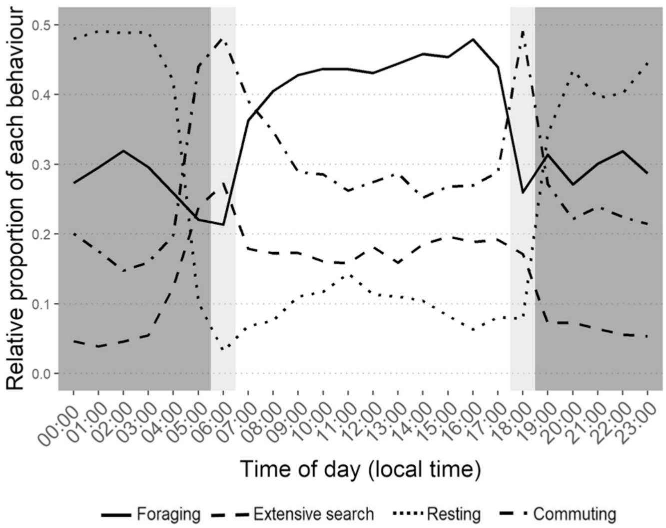

Fig. 4. Percentage of time allocated to each behavior (foraging, extensive search, resting or commuting) by New Caledonia breeding wedge-tailed shearwaters, according to the time of day. The dark grey parts represent the night, the light grey parts the dawn and dusk and the white part the day.

Table 3
Summary tables of linear models explaining trends in nitrogen (δ^{15}N) and carbon (δ^{13}C) isotopic values from blood plasma of wedge-tailed shearwater as a function of their percentage of nocturnal foraging, colony and year of sampling. Intercept represent the year 2017 and the site Canard islet.

δ15N	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
δ13C				
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 - Tiamboune	1,92	1,01	1,90	0,06
Percentage: Year - 2018	−1,82	0,85	−2,13	*

The numbers of * indicates the degree of significance (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

night. The δ^{15}N values were significantly higher during 2018 compare to 2017 (estimate = 1.17, CI95: [0.752: 2.906]) and significantly higher in Tiambouene colony compare to Canard (estimate = −1.15, CI95: [−3.135: −0.463]). The model also highlighted a significant combined-effect of the percentage of nocturnal foraging at Pindai (estimate = 2.27, CI95: [0.203: 4.329]), indicating that the δ^{15}N values were differently affected by the percentage of nocturnal foraging for this colony.

No significant effect of percentage of nocturnal foraging on the blood plasma δ13C values was shown (estimate = 0.25, CI95: [−0.589: 1.102]).

4. Discussion

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

By contrast, when performing self-provisioning foraging trips, trip lengths were longer around the full moon than under the new moon. Wedge-tailed shearwaters are known to forage at more distant locations when self-provisioning (Congdon et al., 2005; McDuie et al., 2015) where prey resources may be richer (e.g. Miller et al., 2018; Weimerskirch et al., 1994). We also found that the maximum distance of longer trips was farther from the colony that for shorter trips so WTSH could be taking advantage of increased light available around the full moon to extend foraging time and food assimilation when self-provisioning.

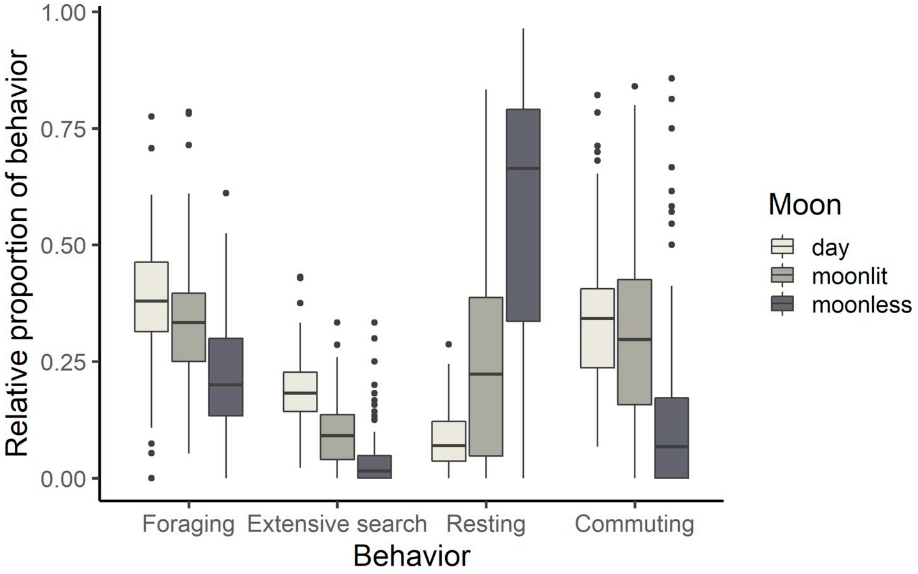

Fig. 5. Proportion (mean ± SE) of behaviors (foraging, extensive search, resting, commuting) assigned along the tracks of New Caledonia breeding wedge-tailed shearwaters according to the presence of the sun and the moon (day, moonlit part of the night or moonless part of the night).

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

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

Interestingly, wedge-tailed shearwaters foraging activity under moonlit conditions became more similar to their diurnal pattern, whereby foraging exceeded resting. Moonlight could provide sufficient light for these predators that, as with many procellariids, rely on visual cues at small spatial scale to hunt for small pelagic prey such as squids and fish (Brooke, 2004; Harrison et al., 1983). Remaining at sea for nocturnal foraging consequently delayed these individuals' return to the colony which drove the increase in moonlit commuting behavior. These results are consistent with previous studies conducted on petrels (Dias et al., 2016; Ramos et al., 2016), shearwaters (Dias et al., 2012; Yamamoto et al., 2008) and albatrosses (Phalan et al., 2007), that highlighted a greater movement or foraging activity during moonlit nights. Thus, we think it more likely that longer trips around the full moon are linked to increased foraging opportunities than predation avoidance.

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

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

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Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any conflict of interest.

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