

DECRYPTING THE BREEDING BIOLOGY OF THE ELUSIVE AND DECLINING TAHITI PETREL *PSEUDOBULWERIA ROSTRATA*

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ABSTRACT

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Among procellariids, the Tahiti Petrel *Pseudobulweria rostrata* is one of the most endangered and least known species. Its global populations are declining, yet demographic and ecological studies remain scarce. Understanding the breeding cycle and behavior of Tahiti Petrel adults and chicks is essential to develop effective protection measures. To address this knowledge gap, Tahiti Petrel colonies of various sizes were studied at three sites in New Caledonia, with extensive sampling at two main sites and limited sampling at a third. A total of 157 burrows were monitored for up to two years using endoscopic cameras and camera traps. This allowed the depiction of the breeding phenology, reproductive success, frequency of adult nest visits, chick behavior, first emergence, and fledging dates. During the study, 75% of the identified burrows were visited by Tahiti Petrels. Egg-laying peaked in December but occurred year-round, indicating aseasonal breeding by Tahiti Petrels in New Caledonia. The average breeding cycle was 329 ± 11.6 days, including an average incubation period of 55.7 ± 0.9 days and an average chick-rearing period of 110.7 ± 5.6 days. Parents visited nests every 1.3 days on average during chick-rearing. After the chick's first emergence, which typically occurred 31 days before fledging, adult visitation decreased. Chicks did not show defensive behavior against predators, and most chicks fledged after nine days without feeding. Breeding success was 50% at a predator-free site and 32% at a site with invasive predators. These findings suggest high sensitivity to disturbance and depredation, contributing to the species' decline in New Caledonia and elsewhere in the world. Together with previous studies conducted in New Caledonia, these results provide crucial information for the implementation of adapted conservation measures for this declining species.

Key words: Tahiti Petrel, *Pseudobulweria rostrata*, phenology, breeding success, behavior

INTRODUCTION

Procellariidae is one of the most diverse families in the order Procellariiformes, with seven of its 16 genera consisting of shearwaters and petrels. This family has a k-selected life-history strategy, characterized by long lifespan, low reproduction rate (one egg per season), delayed maturity, and long-term mate and site fidelity (Bried & Jouventin, 2002; Warham, 1990). As a result, Procellariidae species are very sensitive to anthropogenic activities and have the highest proportion of threatened species on the International Union for Conservation of Nature (IUCN) Red List (Dias et al., 2019). The main human-related threats include depredation by invasive species (especially feral cats *Felis catus* and rats *Rattus* spp.), light pollution, habitat destruction, bycatch, climate change, human exploitation, and disturbance (Rodríguez et al., 2019). Their sensitivity to these threats makes them excellent indicators of changes in both terrestrial and marine ecosystems (Horn & Whitcombe, 2015), particularly through their demographic parameters, including breeding success, mortality rate, and population size. Procellariidae species are also ecosystem engineers that chemically and physically modify the soil (Bancroft

et al., 2005; Bird et al., 2008; Smith et al., 2011). Despite their importance, efforts to conserve or survey these species in their natural habitat are frequently hampered by a lack of understanding of their breeding biology and ecology, as well as by difficult access to their nesting area. This is particularly true for threatened populations of several petrel species for which very limited data are available (BirdLife International, 2022; Croxall et al., 2012).

Within the Procellariidae family, the Tahiti Petrel *Pseudobulweria rostrata* belongs to the most endangered and least known seabird genus (Gangloff et al., 2012), with three of the four remaining species in the genus classified as Critically Endangered. The Tahiti Petrel is listed as Near Threatened on the IUCN Red List (BirdLife International, 2018), with a global population of 10,000 to 20,000 breeding individuals (BirdLife International 2018; Brooke 2004). However, its population appears to be declining, and much remains unknown about the species' biology, behavior, and ecology. A few studies have explored the vocal repertoire of the Tahiti Petrel (Rauzon & Rudd, 2014), the influence of environmental variables on nest-site selection and breeding success (Pagenaud et al., 2022), and its on-land spatio-temporal distribution (Titmus, 2017; Titmus & Lepczyk, 2025).

Based on preliminary data and a very small sample ($n = 2$ burrows), Villard et al. (2006) attempted to describe the Tahiti Petrel's breeding biology and phenology. Like most petrels, this seabird travels to and from land only at night. It digs burrows under rocks or tree roots in coastal areas or in high-altitude forests (up to ~1,000 m above sea level [asl]), on rocky slopes, and on rocky islands (Pagenaud et al., 2022; Titmus et al., 2017; Villard et al., 2006). Breeding sites are distributed on several Pacific islands: American Samoa, Fiji, French Polynesia, and New Caledonia. In New Caledonia, Tahiti Petrel populations breed mainly on ultramafic mountains (i.e., mountains rich in Mg, Fe, and Ni) on the main island and on some rocky or coral islets in the lagoon (Pagenaud et al., 2022; Villard et al., 2006). Breeding typically occurs in small groups, and burrows are often found in close proximity. Occasionally, isolated pairs are also observed. The species is suspected to be philopatric, showing consistent use of the same burrows over multiple years (Villard et al., 2006; Warham, 1990). Here, we define a colony as a group of burrows delineated by specific geographic or spatial features. For instance, two populations of seabirds residing on separate islands constitute two distinct colonies. Within these colonies, there are smaller, relatively discrete and isolated sub-groups, which we will refer to as sub-colonies (see Pagenaud et al. [2022] for more details about sub-colony determination). Burrows can be very deep (about 2 m) and winding with only one entrance, which makes the survey of their breeding behavior and the content of the nest chamber accessible only with a burrowscope (Pagenaud et al., 2022). Like many other petrels, the Tahiti Petrel faces significant population threats from depredation by invasive species (such as feral cats and rats) and habitat destruction (Croxall et al., 2012; Pagenaud et al., 2021; Palmas et al., 2017), particularly due to mining activities in ultramafic mountain regions (Pagenaud et al., 2021).

Breeding, hatching, and fledging success, as well as breeding phenology and reproductive behavior, are important factors that drive the stability or decline of a population (e.g., Cuthbert & Davis, 2002a; Madeiros et al., 2012; Militão et al., 2017). Long-term monitoring programs are necessary to estimate these key

demographic parameters for long-living seabirds (Buxton et al., 2016; Field et al., 2007). However, long-term data acquisition for petrels is often challenging because most species only visit their colonies at night, nest in underground cavities or burrows on isolated and inaccessible islands or mountains, have long breeding cycles, and are often found in remote locations (Brooke, 2004; Newman et al., 2009; Rodríguez et al., 2019; Warham, 1990). One of the most effective and least disruptive methods for determining demographic and life history parameters is using infrared camera traps and burrowscopes (Bird et al., 2021; Blackmer et al., 2004; Hamilton, 2000).

Because knowledge of biological and ecological parameters are crucial for developing adapted and effective conservation strategies in petrels (e.g., Carlile et al., 2012; Fischer et al., 2021; Jones & Kress, 2012; Miskelly et al., 2009), the specific objectives of this study were to (1) determine the reproductive timing of the Tahiti Petrel and its breeding cycle; (2) evaluate demographic parameters such as breeding, hatching, and fledging success; (3) analyze nest visit frequency and breeding behavior of adults at their burrows; and (4) investigate first emergence of chicks and their behavior outside their burrow. This study was conducted at three breeding sites, two located on rocky islands (Nemou and Mato) and one located on a mining mountain (Tiebaghi mountain).

MATERIALS AND METHODS

Study site and monitoring

This study was conducted in New Caledonia, located in the western South Pacific Ocean, from 2016 to 2020. Research took place at colonies on three islands: the islets of Nemou (20.38°S, 164.04°E) and Mato (22.55°S, 166.80°E), and at Tiebaghi mountain (20.28°S, 164.13°E) on the main island (Grande Terre; Fig. 1). The search for burrows began with a nocturnal visit to potential breeding sites to assess their activity, and was based on vocalizations. In addition, vocalizations from individuals on the ground occasionally helped

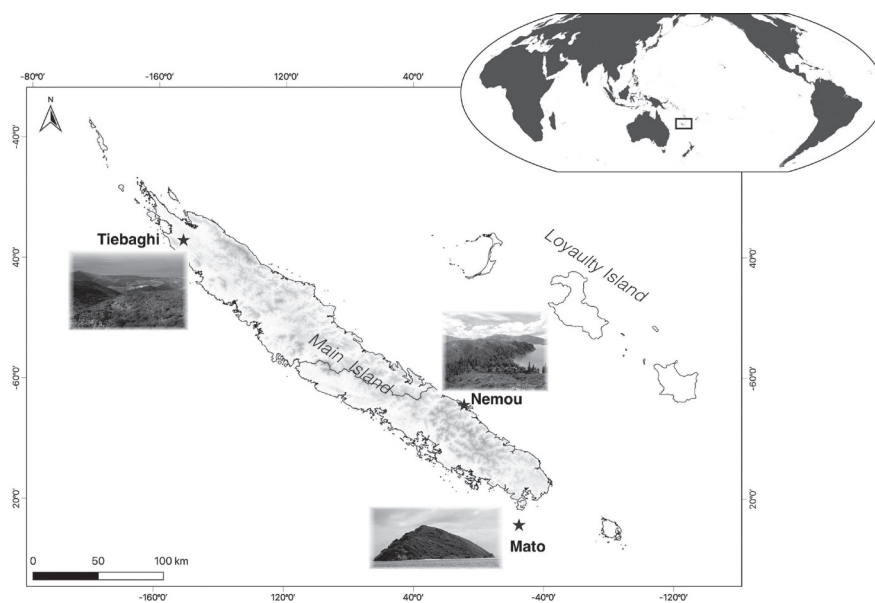


Fig. 1. Location of the New Caledonia archipelago in the western South Pacific region (top left) and the three study sites (main map): Mato in the southern lagoon, Nemou off the east coast, and the Tiebaghi mining mountains.

identify potential breeding pairs. Following the identification of sites with significant vocal activity, burrows in these areas were meticulously searched for breeding pairs, eggs, chicks, or other telltale signs of an active burrow. A burrow was considered recently active based on the presence of adults, feathers, guano, or a sign of reproduction inside the burrow (i.e., egg or chicks). When multiple Procellariid species were present at a site, our prospecting was primarily conducted outside the breeding season of other species.

Nemou, an islet situated 1 km off the east coast of Grande Terre, is 125 ha (1.25 km²) and rises to 168 m asl. The vegetation comprises bare soil, woody-herbaceous maquis, mangrove, and mature forest (Pagenaud et al., 2022). The substrate is mainly composed of ultramafic rocks. The island has two ridges (east and west) and an anthropized area where some of the vegetation has been cut down to allow visitors to come ashore. The islet otherwise is uninhabited and mining-free, but it is occasionally visited by tourists and local people. Three invasive alien species are present: the Rusa Deer *Rusa timorensis*, Pacific Rat *R. exulans*, and Black Rat *R. rattus*. No feral cats have been seen on the island. This site is under the customary authority of the Petit Borendi tribe, and its access is restricted. In this study, the seasons were defined as follows: austral summer (November to April) and austral winter (May to October). Mato, an islet spanning 33 ha (0.33 km²), rises to an elevation of 60 m asl and is characterized by rocky and forest habitats. It is located ~20 km off the southwest coast of Grande Terre. Ninety percent of its vegetation consists of the invasive Mimosoid tree *Leucaena leucocephala*. Although access to this island is not restricted, it is rarely visited due to its distance from Nouméa (~44 km), the main city in the vicinity, and from the nearest mainland port (22 km). In addition to the presence of Tahiti Petrels, Wedge-tailed Shearwaters *Ardena pacifica* and Black-winged Petrels *Pterodroma nigripennis* also breed on this island. The coexistence of multiple species nesting in burrows complicates the identification of Tahiti Petrel burrows at this site. Consequently, the monitored burrows at this site correspond to those where Tahiti Petrels have been directly observed inside or where traces of this species' presence have been detected. Because we continued to identify new burrows during certain visits to the breeding sites, we took care to account for temporal variability in the number of burrows studied in the subsequent analyses.

Tiebaghi is a mountain on the northwest coast of Grande Terre, rising to 600 m asl, and is an active mining site. The vegetation is composed of dry forest and rainforest. Invasive species include feral cats and rats. It is only accessible via the mining access road. The area is highly impacted by mining activities, intense human presence, noise, light, air pollution, and habitat destruction (Pagenaud et al., 2021).

Burrows were monitored for up to two consecutive years using endoscopic cameras (Adult Tortoise Camera System, Burrow Camera Systems) connected to virtual reality glasses (Dominator V3, Fat Shark) and an LCD screen (Fat Screen 7-inch diagonal display LCD color monitor). Due to logistical and access constraints, monitoring methods varied across the study sites. On Nemou, burrow monitoring took place every two months from May 2018 to July 2020. On Mato, monitoring was carried out every four to six weeks from July 2016 to March 2018, depending on weather conditions. On Tiebaghi mountain, burrows were monitored in April, May, and July 2016 only. Camera traps (Moultrie® MCG-12635, 19 × 24.1 × 12.7 cm; Ereagle® E1, 14.5 × 8 cm) were placed in front of 34 active burrows and were set on “motion-activated” with

“high” sensitivity, taking three images per trigger with a 1-s interval and no delay between triggers (Nemou: $n = 15$, Mato: $n = 18$, Tiebaghi: $n = 1$). Camera traps were inspected, and batteries and SD cards replaced, during each burrow monitoring visit.

Breeding phenology

Camera traps and burrowscope were employed to monitor burrows. Due to the suspected asynchronous breeding of Tahiti Petrels in New Caledonia (Brooke, 2004; Pagenaud et al., 2022; Ravache et al., 2020), this study focused solely on the incubation and chick-rearing periods. Previous knowledge of Tahiti Petrel breeding phenology was considered to enhance the precision of estimating these two breeding phases (Villard et al., 2006).

Because the incubation chambers were inaccessible, measuring chicks to determine age was not possible. Therefore, stage of development was estimated based on our knowledge of Tahiti Petrel chick growth from previous monitoring, actual chick observations with the burrowscope, and information from a previous study (Villard et al., 2006). Several chick development stages were estimated from the amount of down lost (Binder et al., 2013), which generally followed a specific sequence. Using camera trap images, we defined six chick development stages: (i) Stage 1: fully downy chicks; (ii) Stage 2: down loss from wings and tail; (iii) Stage 3: down loss from wings, tail, shoulder, and chest; (iv) Stage 4: down loss from wings, tail, shoulder, chest, head, and rump; (v) Stage 5: scattered down remaining on wings, shoulder, chest, head, rump, belly, and nape; (vi) Stage 6: complete loss of down.

Fledging date was identified as the last time we saw the chick in nearly adult plumage (chick development Stage 5 or 6) in the images, with no sign of depredation. Combined with estimated incubation and chick-rearing durations (55 d and 110–120 d, respectively, according to Villard et al., 2006), camera trap images allowed us to estimate egg-laying, hatching, and fledging dates with an accuracy ranging 6–14 d. Hatching dates were estimated by subtracting the average duration of chick-rearing from the fledging date and using the stage of development of the chicks (Binder et al., 2013). Laying dates were estimated by subtracting the average incubation duration from the estimated hatching date. Egg-laying, hatching, and fledging dates were similarly estimated in burrows without camera traps, but with less accuracy, ranging from two to three weeks. For burrows containing a chick during our last visit to Nemou (July 2020), the laying date was estimated by subtracting duration of chick-rearing from the estimated hatching date (Ravache et al., 2020). The mean incubation, chick-rearing, and breeding periods were estimated for successful burrows only using emergence, hatching, and fledging date with an accuracy of two to three weeks.

In order to detect a possible annual peak in egg-laying, we used a Generalized Linear Model (GLM) with a quasibinomial family. The response variable was the ratio between the number of eggs estimated to have been laid on a particular date and the total number of burrows monitored on that day. The explanatory variable was the day of the year as a numeric variable (0–365) transformed into radians in order to treat the variable as circular. This analysis was performed on both sites combined (Nemou and Mato) and on the two sites individually.

The percentage of egg-laying (i.e., the ratio of the number of eggs, hatchlings, or fledglings divided by the total number of burrows

monitored each month), hatching, and fledging were estimated per month for Nemou and Mato only, and visually represented by bar plots. These parameters were also represented using the 1D kernel density estimate with the *stat_density* function implemented in the package “ggplot2” (Wickham, 2016; see Appendix, available online).

Breeding cycle

Breeding cycle duration was calculated as the time elapsed between one egg laying and the next, considering only cases where at least the first reproduction was successful, and using the average duration across study nests. Nesting was considered successful if the egg laid resulted in a fledgling. As petrels are strongly faithful to their nesting sites and breeding partners (Bourgeois et al., 2014; Carlile & O’Dwyer, 2023; Mariné & Cadiou, 2019; Robert et al., 2014), and because banding and identifying the sex of each individual was not possible in this study, we assumed that breeding pairs returned to the same burrow during successive breeding attempts. One burrow was excluded from the analyses because multiple breeding pairs were seen entering the same entrance, suggesting that it either provided access to two different burrows or was used by two pairs sharing the same nest. In addition, we also calculated the time between an unsuccessful breeding attempt and the next breeding attempt.

Breeding productivity

Three indices were used to measure breeding productivity: (1) hatching success, defined as the percentage of eggs laid that successfully hatched, (2) fledging success, defined as the percentage of hatched chicks that fledged, and (3) breeding success, defined as the percentage of eggs laid that produced a fledgling. Burrows found at a late stage of the monitoring period were not included in these calculations to avoid biasing the estimates. To estimate the burrow occupancy, we calculated the proportion of burrows that contained an egg, a chick, or an adult at least once during the survey period.

Burrow activity patterns during chick-rearing

The 10 burrows at which chicks successfully fledged were used to describe the complete pattern of burrow activity during chick-rearing (Nemou: $n = 8$, Mato: $n = 1$, Tiebaghi: $n = 1$). All camera trap images were individually reviewed to determine the presence of adults or chicks. As the age of chicks could not be determined precisely (see above), the number of days before fledging (DBF) served as its proxy. We only used data from the chick-rearing period (i.e., burrows monitored from 44 to 78 DBF) because there were too few data for incubation and early chick-rearing ($n = 1$ burrow). The time of entry and exit from the burrow, time spent inside, and the number of adults present inside or outside the burrow was also determined from camera trap images. Given the imperfect detection of individual entries and exits, we calculated the ratio of the number of entries to exits for each burrow to estimate the percentage of misidentifications. This value ranged 0%–5% among the 10 burrows, with an average entry/exit ratio of 3%.

Chick emergence is considered a key step for burrowing seabirds before fledging and is essential for breeding site imprinting and chick wing exercising (Warham, 1990). Date of chick emergence was the first time a chick appeared outside the burrow in an image. The chick’s time of entry and exit, and time spent outside the burrow, were also calculated. A third-order polynomial regression was used to test

the relationship between the number of days before chick fledging (DBF) and the time spent outside their burrow each night.

It was impossible to weigh the chicks or to observe whether parents fed their chicks without damaging the burrows. It has been shown, though infrequently, that a parental visit to the nest does not necessarily result in feeding the chick (Bester et al., 2002). However, because most visits do result in feeding (Brooke, 2004; Warham, 1996), this metric has been used as a proxy for feeding frequency.

The probability of being fed was calculated for each night as the ratio between the number of burrows visited by parents and the total number of burrows monitored. For most burrow-nesting petrels, chicks are known to lose weight and be fed less frequently towards the end of the chick-rearing period (Gardner, 1999; Priddel & Carlile, 2001; Visser, 2001; Warham, 1990). We hypothesized that this pattern also applies to Tahiti Petrels. To test this hypothesis, the chick-rearing period was divided into two phases to assess any difference in nest visit frequency (i.e., feeding frequency) before and after chick emergence: (i) Feeding 1 (nest visit frequency from the beginning of the camera set up to first emergence), and (ii) Feeding 2 (nest visit frequency from first emergence to fledging). A non-parametric Wilcoxon test with Holm adjustment was used to compare adult nest visit frequency between each breeding phase.

Statistical analyses

All statistical analyses were performed using R software version 4.0.3. Unless stated otherwise, all results are presented as mean \pm standard error (SE).

RESULTS

A total of 116 burrows, spread across 13 sub-colonies, were identified and monitored on Nemou. It is likely that the island hosts more breeding pairs, as some isolated burrows were found after the study finished in 2020. However, these burrows were not included in the current analysis. On Mato, 39 burrows were occupied by Tahiti Petrels within the much larger Wedge-tailed Shearwater colony. Only two burrows were discovered at the Tiebaghi mining site despite intensive searching.

Breeding phenology

On Nemou, 87 of 116 burrows were active at least once, and 108 breeding attempts were recorded (with multiple breeding attempts occurring at some burrows). On Mato, 21 of 39 burrows were considered recently active during the monitoring period, and a total of 18 breeding attempts were recorded. Breeding attempts were recorded in both of the two burrows found in Tiebaghi. In one of the burrows on Tiebaghi, the chick was depredated before fledging, while the second burrow collapsed after the chick fledged in July 2016.

Observation of burrow contents over two years on Nemou indicated that eggs were laid continuously (Fig. 2; Fig. A1 in Appendix). Egg-laying peaks occurred in December in both years (2018: 16%, 2019: 15%). The highest rate of hatching occurred in February 2018 (Fig. 2). Nevertheless, egg-laying and hatching occurred every month, with the lowest occurrence during the austral winter months of June to August (Fig. 3; Fig. A1 in Appendix). Most of the chicks fledged during the austral summer ($n = 35$ fledging from 168 eggs laid), to a maximum of 9% in March 2020 (Fig. 2).

Fledging did not occur every month and was particularly rare during the middle of the austral winter (August to October) (Fig. 3; Fig. A1 in Appendix).

Egg-laying on Mato did not occur every month (Fig. 4), and fewer burrows were found on Mato than on Nemou (four burrows monitored in 2016, 34 in 2017, 38 in 2018). Most egg-laying occurred in late austral summer, with some occurring at the start of the austral winter (June and July), peaking in June 2017 at 29% ($n = 14$). The proportion of chicks fledging reached a maximum at the end of the austral winter in 2016 (October, 25%) and the beginning of the austral summer in 2017 (November, 12%). GLMs did not show a significant peak in the distribution of egg-laying at any particular time of the year when both sites were included in the analyses (cos: $P = .101$; sin: $P = .065$). However, when considered separately, the distribution of egg-laying dates peaked during the second trimester at Mato (cos: est = -0.004 , $P = .02$; sin: est = 0.005 , $P = .02$). No significant pattern was found at Nemou (cos: est = 0.001 , $P = .154$; sin: est = -0.001 , $P = .298$).

Breeding cycle and periods

The average length of the breeding cycle was 329.0 ± 11.6 d (range = 231–374 d; $n = 15$ nests). However, when the first breeding attempt failed, the interval between the first and second egg-laying (i.e., the period used to define the breeding cycle in this study) was shorter, averaging 290.0 ± 19.9 d (range = 136.5–602.0 d, $n = 28$). The average incubation period was 55.7 ± 0.88 d ($n = 68$), while the chick-rearing period was nearly twice as long, at 110.7 ± 5.6 d ($n = 53$). Overall, the average breeding period from egg laying to chick fledging was 166.8 ± 7.2 d ($n = 53$).

Breeding productivity

On Nemou, 75% ($n = 87$) of the 116 burrows were occupied at least once during the two-year monitoring period. A total of 108 breeding attempts were observed within these burrows, with a hatching success rate of 59% and a fledging success rate of 54%. This ultimately led to a breeding success rate of 32%.

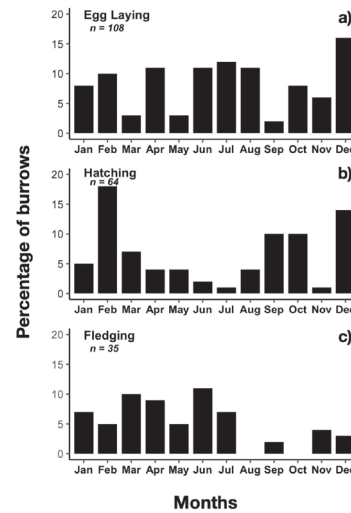


Fig. 3. Monthly breeding cycle of Tahiti Petrels *Pseudobulweria rostrata* on Nemou Island, New Caledonia, from 2018 to 2020, showing the percentage of a) burrows having eggs, b) burrows in which chicks hatched, and c) burrows from which chicks fledged.

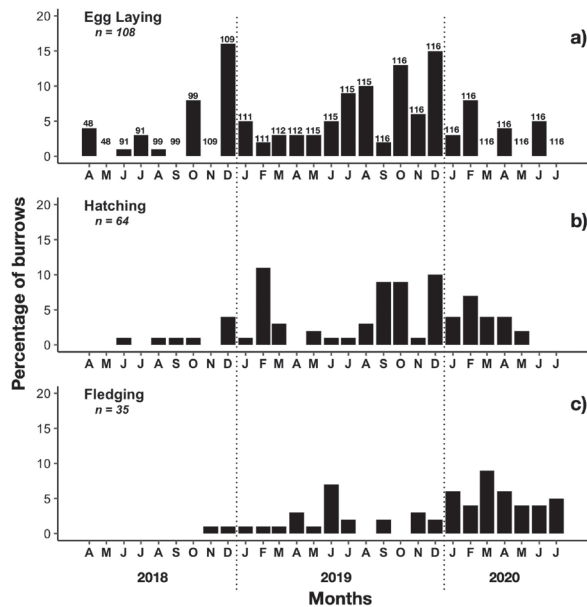


Fig. 2. Annual breeding cycle of Tahiti Petrels *Pseudobulweria rostrata* on Nemou Island, New Caledonia, from April 2018 to July 2020, showing the percentage of a) burrows having eggs ($n = 108$), b) burrows in which chicks hatched ($n = 64$), and c) burrows from which chicks fledged ($n = 35$). The numbers above the bars in a) represent the total number of burrows included when calculating percentages each month (i.e., the study began with 48 burrows found in April 2018 and ended with 116 burrows in September 2019).

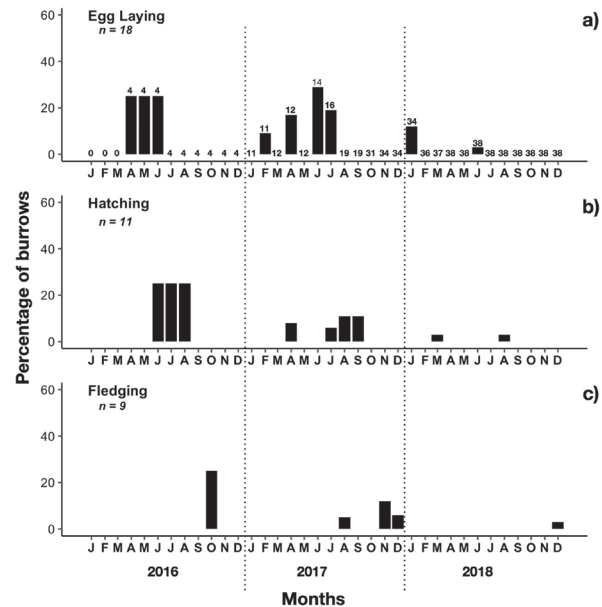


Fig. 4. Annual breeding cycle of Tahiti Petrels *Pseudobulweria rostrata* on Mato Island, New Caledonia, from April 2016 to July 2018, showing the percentage of a) burrows with eggs ($n = 18$), b) burrows in which chicks hatched ($n = 11$), and c) burrows with fledged chicks ($n = 9$). The numbers above the bars in a) represent the total number of burrows included when calculating percentages each month (i.e., the study began with four burrows found in April 2016 and ended with 39 burrows in April 2018).

During the monitoring period (April 2016 to July 2018) on Mato, the occupation rate among the 39 identified Tahiti Petrel burrows reached 75%. Hatching and fledging success rates were higher (61% and 81%, respectively) compared to Nemou, resulting in a breeding success rate of 50%.

Adult burrow activity patterns and nest visit frequency

Among the 161,520 camera images, 9,402 showed evidence of activity for the 10 successful burrows. Analysis of images showed that adult Tahiti Petrels visited their chicks almost every day and a half (1.3 ± 0.03 d on average), spending between 0.4 to 18 h inside the burrow at each visit (Fig. 5). Two peaks of time spent in the burrow were observed at 71 and 10 DBF (7.7 and 18.4 h on average, respectively). Preening behavior and vocalization of parents were observed only at the beginning of incubation at both islets. Thereafter,

adults were mostly silent, entering directly into their burrows upon arrival. The probability of adults visiting the burrow dropped after the emergence of chicks, particularly two weeks before the chick's fledging (Fig. 6). The mean probability of being fed was significantly higher during the "Feeding 1" period than during the "Feeding 2" period (Wilcoxon test, $W = 14,080$, $P = .009$; Fig. 6). On occasion, chicks were fed by both adults on the same night. During the final 9 DBF, most chicks were not fed ($n = 6$).

Chick burrow activity patterns

On average, the first emergence of a chick was 31 DBF (range = 25–65 DBF). Chicks emerged fully downy (Stage 1 of chick development) and went out almost every night until fledging (Fig. 7). Several behaviors at the burrow entrance were observed on images: preening events, sniffing, interactions with the parents,

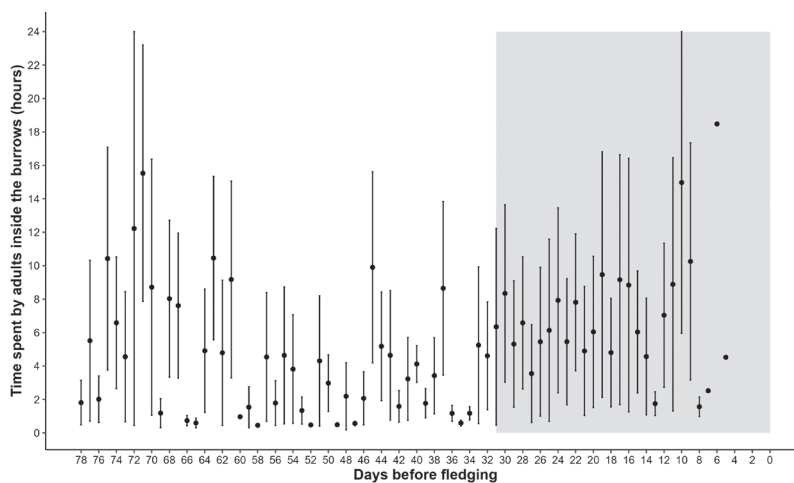


Fig. 5. Average time (points) spent inside the burrow by adult Tahiti Petrels *Pseudobulweria rostrata* as a function of chick age in days before fledging (DBF) on Nemou, Mato, and at Tiebaghi, New Caledonia, and their 95% confidence interval (lines). The shaded grey area indicates the "Feeding 1" and "Feeding 2" periods, which is delimited by the average age of chicks at emergence (i.e., 31 DBF). Numbers of successful burrows monitored by camera traps from chick emergence to age in DBF were as follows: 78–68 DBF ($n = 6$), 68–44 DBF ($n = 7$), 44–0 DBF ($n = 10$).

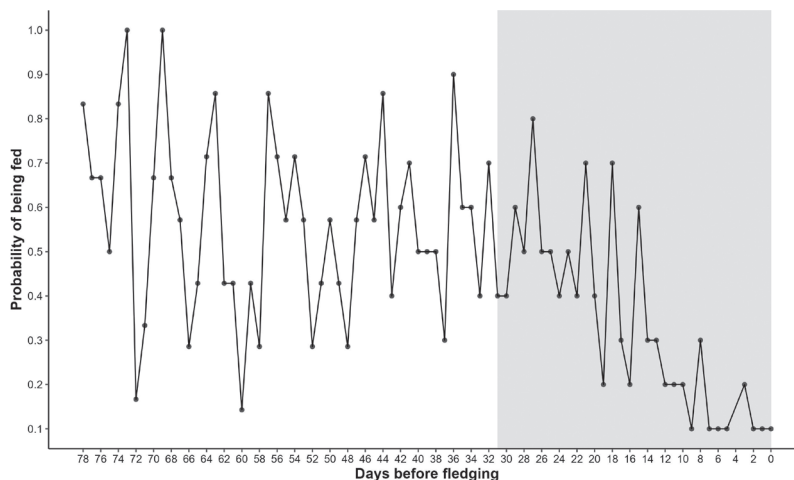


Fig. 6. Daily probability of Tahiti Petrel *Pseudobulweria rostrata* chicks ($n = 10$) being fed as a function of days before fledging (DBF) on Nemou, Mato, and Tiebaghi, New Caledonia. The shaded grey area indicates the "Feeding 1" and "Feeding 2" periods, which is delimited by the average age of chicks at emergence (i.e., 31 DBF). Numbers of successful burrows monitored by camera traps from chick emergence to age in DBF were as follows: 78–68 DBF ($n = 6$), 68–44 DBF ($n = 7$), 44–0 DBF ($n = 10$).

exploration, and wing flapping. In addition, the time chicks spent outside their burrow increased significantly as they approached fledging. They sometimes remained out of their burrows all night, up to 7 or 8 h, re-entering before dawn (Fig. 7, Fig. A2 in Appendix). On one occasion, images captured a rat in proximity to a burrow. Shortly thereafter, the chick was observed outside the burrow for the first time, in the presence of the rat. The chick did not appear in any subsequent images and was not located during later searches. There were no signs of distrust or protection behavior against predation in the photos.

The second-order polynomial regression indicated a significant increase in the time spent outside the burrow by chicks as the fledging date approached ($R^2 = 0.87$, $P < .001$).

DISCUSSION

This study is the first to examine the breeding biology of a *Pseudobulweria* species, incorporating multiple breeding sites, several years of monitoring, and a large sample of monitored pairs. The Tahiti Petrel exhibits breeding biology that is generally similar to other Procellariidae species, except for its breeding phenology.

The colony on Nemou appears to be the largest known for the Tahiti Petrel. In our study, we found 116 burrows, 87 of which were active. However, given that on each visit we discovered new burrows, it is likely that the total population on the island is much larger than the number described here. Only 39 burrows were identified and monitored on Mato (Ravache et al., 2020; Villard et al., 2006; this study). Outside of New Caledonia, colony sizes also appear to be small. In French Polynesia (Raiatea Island), 170 burrows were found, but only 33 were active (Faulquier, 2014); in American Samoa, 25 burrows have been found and monitored (Titmus, 2017). More data are needed to determine whether the Nemou population serves as a source for New Caledonia and/or other parts of the

Pacific. Further studies should focus on population genetics and gene flow to assess the relationships with other populations, as well as on population dynamics to evaluate chick and adult survival.

Breeding phenology and productivity

Populations on both Nemou and Mato showed year-round activity, confirming the asynchronous breeding cycle apparent in other studies (Pagenaud et al., 2021; Ravache et al., 2020; Villard et al., 2006). This behavior might be a mitigation of intra-specific trophic competition (Brooke, 2004). As Tahiti Petrels feed by opportunistic scavenging (Ravache et al., 2020; Spear & Ainley, 1998), their breeding period is probably less dependent on the seasonal presence of particular prey, unlike other season-dependent species, such as Wedge-tailed Shearwaters (Ravache et al., 2020).

On Nemou, a slight but non-significant trend was observed in the egg-laying pattern, with a peak occurring during the austral summer. This trend has also been observed in other petrel species (Brooke, 2004), such as Barau's Petrel *Pterodroma baraui* (Pinet et al., 2009), Soft-plumaged Petrel *P. mollis* (Dilley et al., 2015), and Cook's Petrel *P. cookii* (Imber et al., 2003). On Mato, although the sample was small ($n = 39$), peak egg-laying occurred during the austral winter, probably due to competition for burrows with Wedge-tailed Shearwaters during the austral summer. Additional data and burrow discovery are needed to more precisely estimate the breeding phenology at this site. The breeding cycle lasted ~329 d following a successful breeding event; in cases of breeding failure, the interval between clutches could be shorter. The breeding phenology at Nemou can be characterized as aseasonal, as observed in other tropical environments (Carr et al., 2021). Aseasonal breeding in seabirds is often attributed to the less pronounced seasonal abundance of food resources in tropical oceans (Harrison & Seki, 1987; Weimerskirch, 2007). This year-round reproduction may be facilitated by a stable but consistently low availability of

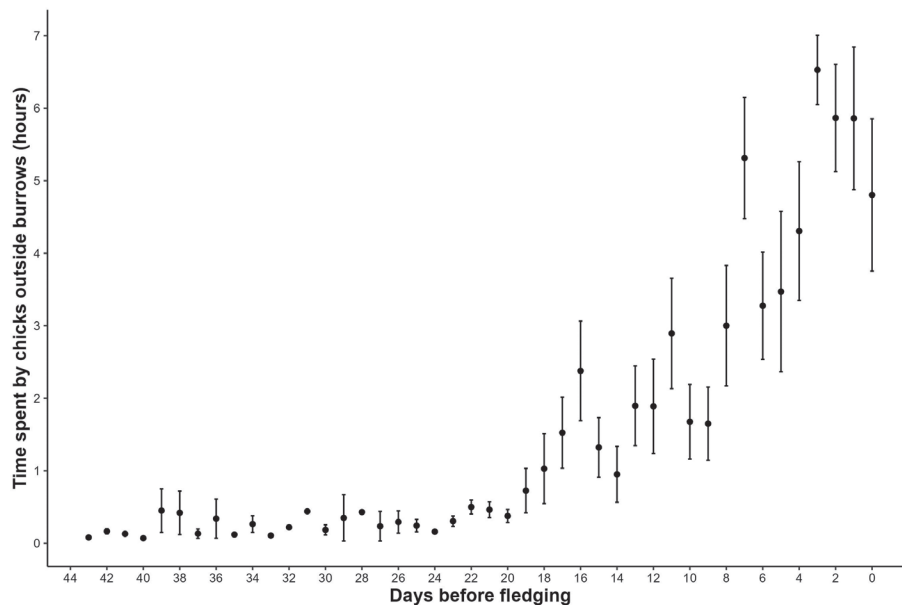


Fig. 7. Average time spent outside the burrow by Tahiti Petrel *Pseudobulweria rostrata* chicks as a function of chick age in days before fledging (DBF) at Tiebaghi, Nemou, and Mato, New Caledonia ($n = 10$). The first point of the x-axis starts at 43 DBF and corresponds to the earliest emergence of Tahiti Petrel chicks. Vertical black lines represent the 95% confidence interval.

food resources, providing opportunities throughout the year for a limited number of breeding pairs (Carr et al., 2021; Tarburton, 2018). Partially synchronized breeding within sub-colonies may be influenced by social attraction during mating.

Tahiti Petrels incubated their eggs for about 56 d, and the average chick-rearing period was 111 d. The estimates for length of incubation and chick-rearing should be interpreted with caution, as they are based on infrequent monitoring, conducted approximately every two months. Additionally, egg neglect can lead to variations in the incubation period, complicating the estimation of lay dates from an average incubation value (Boersma, 1982). These results corroborate those presented by Villard in the early 2000s, which were based on monitoring two breeding pairs, with an incubation period of approximately 55 d and a chick-rearing duration of 110 d. These durations are slightly higher than the Mascarene Petrel *Pseudobulweria aterrima*, which has an incubation period of 49–53 d and a chick-rearing period of 79–90 d (Riethmuller et al., 2012; Virion et al., 2021). The lack of breeding data for other *Pseudobulweria* species precludes any comparison with other closely related species in the same phylogenetic group. However, durations observed for Tahiti Petrel were consistent with those of other tropical and subtropical Procellariidae species (Hamer et al., 2001), which generally have longer incubation and chick-rearing periods than species from temperate zones (Ricklefs, 1966).

Breeding success varied between colonies, with lower hatching and fledging success observed at Nemou, where invasive predator species such as rats have been observed, compared to Mato, which is predator-free. The observed reproductive success of approximately 50% at Mato is consistent with the lower range typically observed in predator-free sites, where breeding success often ranges from 50% to 84% (Cruz & Cruz, 1990; Cuthbert & Davis, 2002b; Virion et al., 2021). For example, the breeding success of managed and predator-free colonies of other burrow-nesting Procellariids was higher for the Bermuda Petrel *P. cahow* (hatching success = 68%) (Madeiros et al., 2012), the Bonin Petrel *P. hypoleuca* (hatching success = 95.5%; fledging success = 93%) (Seto & Conant, 1996), and the Great-winged Petrel *P. macroptera* (hatching success = 59.6%; fledging success = 100%) (Cooper & Fourie, 1991). According to Warham (1990), our estimates of breeding success for Tahiti Petrel would be sustainable for the population. However, due to the varying frequency of monitoring across our study colonies, and the methodological approaches used, our estimates should be interpreted with caution.

The lower breeding success observed at Nemou (32%) is comparable to that of similarly-sized Procellariids breeding in the presence of rats, such as the Providence Petrel *P. solandri* (breeding success of 33.8% or 36% depending on year; Bester et al., 2007). The Nemou rate is at the upper end of what was observed in colonies where predators are present, i.e., varying 12%–30% (Pierce, 2002). Invasive species like rats can deeply affect breeding success, especially a few days before and after hatching (Rodríguez et al., 2019; Tomkins, 1985). The low breeding success observed on Nemou could, therefore, be linked to rodent presence. Although observations of interactions between rats and adults or chicks in our images were infrequent, one probable instance of depredation on a chick was noted. The low breeding success observed could also be partially explained by intraspecific competition for burrows. Intraspecific competition was observed at three of the 34 burrows observed by camera traps, and reproductive failure occurred at two

of these burrows. Reproductive performance could also have been affected by ocean conditions associated with the El Niño–Southern Oscillation (ENSO). A strong El Niño occurred in 2015–2016 and a weak-to-moderate La Niña occurred in 2016–2017, 2017–2018, and 2020–2021, i.e. during our study period. Finally, factors such as breeder fitness, breeding experience, egg neglect, desertion (Bester et al., 2007), nest site characteristics, and the quality of burrows (Pagenaud et al., 2022) may have also influenced our results.

Adult activity pattern and nest visit frequency

Monitoring seabird behavior with camera traps provided complementary information to manual inspections using a burrowscope. Previous studies have demonstrated that this combined approach yields more accurate and reliable data compared to traditional surveys (Bird et al., 2021). Adult Tahiti Petrels were rarely observed vocalizing, except at the beginning of the incubation period. This behavior can make it more difficult to identify the burrows of breeding individuals, especially those with asynchronous breeding (Bretagnolle et al., 2021). In New Caledonia, ground vocalizations of Gould's Petrel *P. leucoptera* are relatively rare, whereas they occur much more frequently in the predator-free population on Cabbage Tree Island. This suggests that the presence of predators may influence the display of vocal activity (N. Carlile, personal communication *in* Portelli, 2016). However, the infrequent vocalizations of Tahiti Petrels at both sites, regardless of the presence or absence of predators, do not support hypotheses about a selection effect induced by depredation pressure.

Adult Tahiti Petrels spent more time with their chick before chick emergence, and adults came back to their burrow regularly to feed their chick (i.e., almost every 1–2 d). Adults returned to their burrow more frequently than other Procellariiform species. For example, the Providence Petrel returns every 2.4 d (Binder et al., 2013), and the Hawaiian Petrel *P. sandwichensis* returns every 2.7 d. In our study, feeding frequency decreased after chick emergence, which is comparable to other Procellariiforms (Binder et al., 2013; Warham, 1990). This behavior may encourage chicks to come out of their burrows to exercise their wings, develop philopatry, and fly away (Binder et al., 2013; Gangloff & Wilson, 2004; Warham, 1990; Warham, 1996).

Chick burrow activity pattern

Generally, for burrow-nesting seabirds, larger species emerge earlier than smaller species (Binder et al., 2013; Miskelly et al., 2009). On average, the first emergence of Tahiti Petrel chicks occurred at 31 DBF, which is much earlier than for other petrels of similar size, regardless of whether there is depredation (e.g., Providence Petrel 19 DBF, Binder et al., 2013; the Pycroft's Petrel *P. pycrofti* eight DBF, Gangloff & Wilson 2004), or there is no depredation (e.g., Bermuda Petrel six DBF, Carlile et al., 2012; the Magenta Petrel *P. magentae* and the Chatham Islands Petrel *P. axillaris* 11 DBF, Miskelly et al., 2009). Reasons for chick emergence are still unclear, but it seems to allow chicks to exercise their wings before departure (Brooke, 2004; Visser, 2001; Warham, 1996). Longer and more frequent excursions from the burrow can lead to faster increases in wing length, greater body mass upon fledging, and earlier fledging (Yoda et al., 2017). However, spending time outside the burrow exposes chicks to depredation, making this behavior maladaptive and detrimental to petrel populations. This is one reason for removing introduced predators from islands.

Conclusions and implications for conservation

The Tahiti Petrel is somewhat atypical, with an aseasonal breeding phenology and asynchronous breeding, although there is partial synchronization between sub-colonies. Long-term research, extensive monitoring, and individual banding are essential to determine if breeding season, breeding success, and breeding cycle length, as reported in this study, accurately represent the entire population. Further, future research should focus on demographic studies at a finer level (i.e., recruitment rate, chick growth and survival, nest survival, banding individuals) to understand the low breeding success of the Nemou population. In New Caledonia, previous studies evaluated the impact of mining activities on Tahiti Petrel populations (Pagenaud et al., 2021), nest-site selection of breeding individuals (Pagenaud et al., 2022), and foraging areas and behavior during the breeding period (Ravache et al., 2022). These recent studies have provided key insights necessary for implementing local conservation measures tailored to the species. Additionally, we recommend further studies on Tahiti Petrel populations elsewhere in the Pacific to determine whether the breeding phenology and biological characteristics are specific to New Caledonia.

Since Tahiti Petrel populations are declining, especially on mountain mining sites (BirdLife International, 2018; Pagenaud et al., 2021), this study provides new data that can be used to restore and protect petrel populations in their natural habitat through the establishment of artificial colonies. These are ecological and predator-free refuges that provide favorable and attractive conditions for breeding (without translocation), such as vocal and olfactory stimulations, combined with artificial burrows (Bolton et al., 2004; Buxton & Jones, 2012; Kildaw et al., 2005; Podolsky, 1990; VanderWerf et al., 2023). Translocation projects involve the displacement of chicks to a safe, artificial site (Buxton & Jones, 2012; Jones & Kress, 2012; Priddel et al., 2006). To this end, knowledge about the timing of emergence and growth of the translocated chicks is crucial for maximizing success. The novel findings of our study provide a foundational basis for conservation planning of the Tahiti Petrel in New Caledonia and across the Pacific Islands.

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