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Breeding biology of Fluttering Shearwaters (*Puffinus gavia*) on Burgess Island in northern New Zealand

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ABSTRACT

The Fluttering Shearwater (*Puffinus gavia*) is an abundant seabird endemic to breeding colonies in northern and central New Zealand. The species remains poorly studied, and here we present the first study to examine its breeding biology in detail. Fluttering Shearwater nests were monitored from laying in September to fledging in January 2016 on Burgess Island in the outer Hauraki Gulf, northern New Zealand. Nine (22%) of forty-one natural nests were located under dense vegetation on the ground. Eggs were laid over a period of 39 days with laying peaking on 12 September. Incubation length was 50.0 ± 3.7 days and chicks fledged after an average of 74.2 ± 4.3 days, from late December to the end of January. Chick growth corresponds to the pattern observed for other Procellariiformes, gaining body mass rapidly to a maximum of 115% of adult mass, and then losing mass until fledging. Chicks were fed most nights throughout chick-rearing. Breeding success was 63.8% and similar to other *Puffinus* species breeding in pest-free colonies. This study provides baseline biological data for a poorly studied, yet common, New Zealand endemic seabird. The obtained new information will allow for further ecological investigations and improved conservation management.

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Breeding success; breeding phenology; chick growth; Procellariiformes; provisioning; seabirds

Introduction

The Fluttering Shearwater (*Puffinus gavia*) is a medium-sized seabird endemic to New Zealand. It is common at sea year-round along the coasts of northern and central New Zealand and frequently forages in large flocks in inshore waters (Gaskin and Rayner 2013). Its main breeding areas are located on islets and islands of the eastern Northland, the Hauraki Gulf, Bay of Plenty and Cook Strait (Taylor 2000; Waugh *et al.* 2013). The total population has been estimated as 100 000 to 1 million (Robertson and Bell 1984); however, no population survey has been undertaken and there are no reliable population estimates or any information on population trends of Fluttering Shearwaters (Taylor 2000; Waugh *et al.* 2013). Introduced mammalian predators are a significant threat to the species, and all known breeding colonies are on mammal-free islands or on islands with Pacific Rats (*Rattus exulans*) present (Taylor 2000). The breeding populations are, however, small on islands with Pacific Rats and eggs and chicks of Fluttering Shearwaters are probably preyed on these islands (Taylor 2000). Introduced predators, including Pacific

Rat, (*Oryctolagus cuniculus*) and cats (*Felis catus*) have been eradicated from at least 14 islands with known Fluttering Shearwater breeding colonies over the past 50 years (Taylor 2000; Towns and Broome 2003). Chicks have been translocated to Long Island in the Marlborough Sounds from 1991 in an attempt to establish a new colony free of introduced predators (Bell 1995). This long-term conservation project has been successful; pairs have since established, and breeding has occurred in consecutive years (Bell *et al.* 2005).

Despite its ubiquitous presence in the waters of northern New Zealand, the breeding biology of the Fluttering Shearwater, surprisingly, remains poorly documented (Brooke 2004; Gaskin and Rayner 2013). Egg laying is reported from late September to the end of October, and chicks are considered to fledge in January in northern New Zealand (Gaskin and Rayner 2013) to February in the Marlborough Sounds in central New Zealand (Bell *et al.* 2005). However, little is known regarding burrow structure, incubation periods, chick growth, provisioning rates, and breeding success of the species. The objectives of this study were to: (1) give information on the body size and mass of breeding birds; (2) characterise breeding habitat and burrow structure; (3) describe the timing of egg laying,

egg size and the duration of incubation; (4) evaluate the timing of hatching and chick growth; (5) analyse food provisioning strategies and calculate meal sizes; and (6) assess breeding success and the effect of investigator disturbance on this parameter. This new information is essential for further ecological investigations and will be an important component for future conservation management of the species, including translocation projects.

Methods

Study site

Burgess Island (Pokohinu) (35°54' S, 175°06' E) is a 56 ha scenic reserve located within the Mokohinau Island group in the outer Hauraki Gulf in northern New Zealand (Figure 1). The island is no longer inhabited, and the only remaining buildings are the lighthouse and the lightkeeper's house. The Pacific Rat (*R. exulans*) was introduced to the Mokohinau Islands prehistorically in 1990 (McFadden and Greene 1994) and the islands are today free of introduced predators. However, the native Swamp Harrier (*Circus approximans*) and Morepork (*Ninox novaeselandiae*) occur on the islands and are active predators of the islands'

seabirds (M. Berg pers. obs.). Burgess Island was inhabited until 1980 at which time the island's lighthouse was automated and the island staff removed. The lighthouse keepers grazed cattle (*Bos taurus*), goats (*Capra aegagrus*), pigs (*Sus scrofa domesticus*) and sheep (*Ovis aries*) resulting in the native vegetation on Burgess Island being heavily depleted and replaced with pasture plants, including buffalo grass (*Bouteloua dactyloides*). Today, previously grazed areas consist of regenerating secondary growth dominated by Large-leaved Muehlenbecia (*Muehlenbeckia australis*), New Zealand Flax (*Phormium tenax*) and Giant Umbrella Sedge (*Carex ustulatus*) (Esler 1978). A total of 46 bird species utilise the island's habitat, including nine species of seabirds (Ismar *et al.* 2014), most notable being large recovering populations of burrowing Procellariiformes including (in order of abundance): Common Diving Petrel (*Pelecanoides urinatrix*), White-faced Storm Petrel (*Pelagodroma marina*), Grey-faced Petrel (*Pterodroma gouldi*), Little Shearwater (*Puffinus assimilis haurakiensis*), Fluttering Shearwater, Black-winged Petrel (*Pterodroma nigripennis*), and Sooty Shearwater (*Ardenna grisea*) (Ismar *et al.* 2012, 2014).

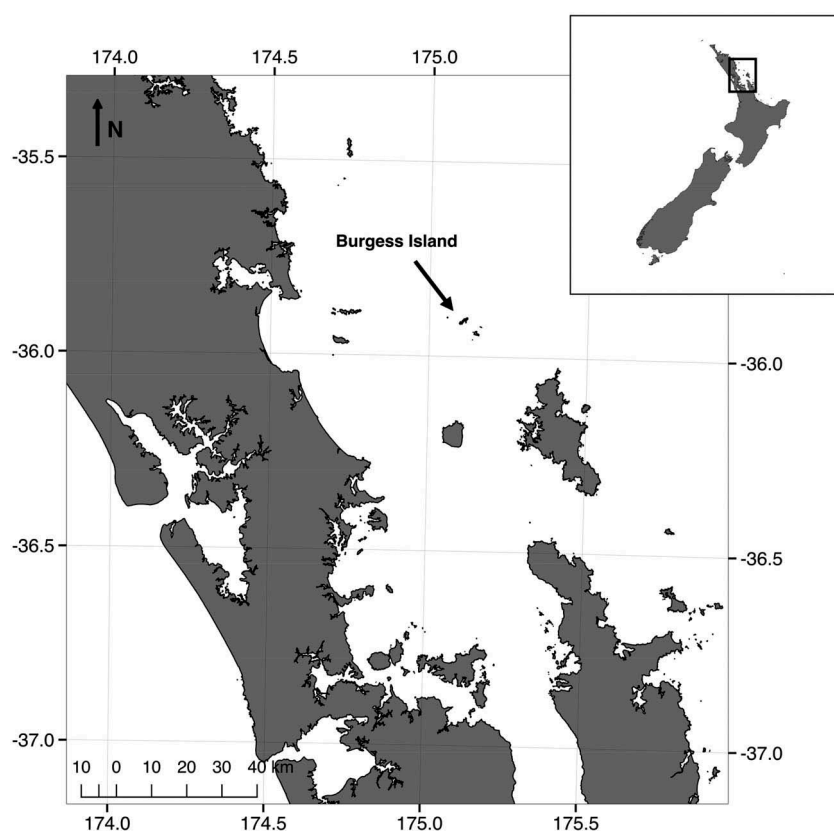


Figure 1. Location of Burgess Island in the outer Hauraki Gulf in northern New Zealand.

Breeding phenology and breeding success

Fieldwork commenced in early September 2015, when Fluttering Shearwaters, based upon previous field observations, were expected to begin breeding activities, until late January 2016, when chicks fledged the island. The study site could not, however, be accessed between 14 November and 7 December when Burgess Island is closed to researchers to allow local iwi Ngāti Rehua to exercise their traditional customary right for the annual harvest of Grey-faced Petrel chicks.

In addition to the small number of pre-installed nest boxes ($n = 2$) being used by Fluttering Shearwater breeding pairs, natural nests were identified through systematic inspection of potential burrows and through response calls from acoustic playback. Once the presence of an incubating Fluttering Shearwater was confirmed, the nest was monitored until the chick fledged or breeding failed. *Puffinus* shearwaters are sensitive to disturbance, especially during incubation (e.g. Harper 1983; Warham 1990; Carey 2009). For this reason, breeding pairs were left undisturbed for 45 days once the laying date was confirmed. This period without nest disturbance was based on the incubation length of the closely related Hutton's (*Puffinus huttoni*) and Manx Shearwater (*Puffinus puffinus*) which lasts 46–55 days and 47–66 days respectively (Cuthbert and Davis 2002a; Brooke 2004). Burrows were then checked with a burrow-scope (Sextant Technology Ltd, Wellington, New Zealand) every day until hatching.

Reproductive parameters were defined following Cuthbert and Davis (2002b). Burrow occupancy was the proportion of burrows that contained a bird incubating an egg. Hatching success was estimated as the proportion of eggs that hatched. Fledging success was calculated as the proportion of chicks that survived in the nest to the late chick-rearing period, and breeding success was the combined product of hatching and fledging success. Reproductive success calculations thus incorporate losses of chicks, nest desertions and unhatched eggs. Nests with only single records of adults present with no confirmation of laying were removed from the analysis as these may have been immature birds prospecting for a burrow (Warham 1990; Bradley *et al.* 1999).

Breeding habitat and burrow structure

All study nests were inspected visually using a burrow-scope either from the burrow entrance or through a manually dug hole over the nest chamber fitted with a

wooden hatch. For each burrow, the number of entrances and nest chambers was recorded. The distance from the nest entrance to the entry of the nest chamber was measured to the nearest 1 cm using a tape measurer. Vegetation within the range of 1 m to the nest entrance was identified to genus level. Habitat type was then determined using a combination of the composition of the surrounding vegetation and classified into: (1) 'Muehlenbeckia', where only Large-leaved Muehlenbeckia was present; (2) 'Mixed', where both Large-leaved Muehlenbeckia and *Carex* spp. were present; (3) 'Grass', where only *Carex* spp. were present; (4) 'Forest', where burrows were on the forest floor without being covered in vegetation; and (5) 'Flax', where burrows were located under New Zealand Flax.

Adult weights and measurements and egg size

We collected measurements of adult Fluttering Shearwaters during the early chick-rearing period from late October to early November. Adults were captured by hand when coming out from the burrow at night and fitted with an individually numbered stainless steel band provided by the Department of Conservation of New Zealand. They were weighed in cotton bags to the nearest 2.5 g with a 600 g Pesola spring balance. Five measurements were also taken: bill length (exposed bill from the bill tip to the start of the feathers on culmen), bill depth (measured at the base of the bill), total bill plus head length, tarsus length and straightened left wing length (measurements as defined by Baldwin *et al.* 1931). The wing was measured to the nearest 1 mm with a stopped rule. All other measurements were made to the nearest 0.1 mm with vernier calliper. The length and breadth of eggs (mm) were measured 45–48 days after laying to the nearest 0.1 mm using a calliper, and egg mass was calculated as mass (g) = $0.00051 \times \text{egg length (mm)} \times \text{egg breadth (mm)}^2$ (Warham 1990). To minimise disturbance we only measured eggs from an opportunistic sample of 13 burrows.

Chick growth and effects of investigator disturbance

During daily checks, if chicks were found damp or had matted down, they were estimated to have hatched within the previous 4 h (Amundsen 1995). Chicks were weighed daily in the same order to the nearest 2.5 g with a 300 g Pesola spring balance and later on with a 600 g Pesola spring balance, and measurements of bill length, tarsus length, and wing length were taken from the first day after hatching until fledging. Since

we were interested in determining both chick growth and the effects of investigator disturbance, we separated our study nests into three groups (Sagar *et al.* 2015): a growth group (intermediate level of investigator disturbance; $n = 21$), a provisioning group (high level of investigator disturbance; $n = 9$, and control group (low level of investigator disturbance; $n = 17$). From the total number of study nests ($n = 47$), burrows were randomly assigned to each group once hatching was confirmed. Chicks in the growth group were weighed and had their wing length, tarsus length, and bill length measured every 3 days until they were presumed to be close to fledging, and after that every 2 days until they fledged. Chicks in the provisioning group were weighed daily and their wing length, tarsus length, and bill length measured every sixth day until their estimated emergence, and subsequently every 2 days until they fledged. Control chicks were weighed and measured immediately after hatching and again as close to fledging as possible.

Meal size and feeding frequency

To measure meal size and feeding frequency, eight chicks in the provisioning group were weighed daily throughout the chick-rearing period. To quantify provisioning frequency, stick palisades were raised at the entrance of the burrows. Displaced sticks indicated either a visit from a parent, emergence of a chick or, potentially, another prospecting seabird. A provisioning event was consequently confirmed by the combination of chicks' overnight mass change or stable mass with recorded entrance activity. To estimate overnight food delivery, we applied the equation described by Hamer *et al.* (1998) for the Manx Shearwater (*P. puffinus*):

$$\text{Overnight food delivery} = 1.32 \times (\text{net mass change}) + 0.086 \times (\text{initial mass}) - 0.47 \times (\text{age in days}) + 21.9.$$

Observations at night were carried out every two or three nights depending on the weather throughout the chick-rearing season to determine the number of times adults visited the burrows, and at which time adults arrived at their burrows. All chicks were weighed and measured in the same order in the morning to standardise for mass loss.

Statistical analysis

Data analysis was performed in R3.2.1 (R Core Team 2016). All data were tested for normality using the Shapiro–Wilk normality test and for equal variance using a Levene's test. We investigated whether burrow length had an impact on breeding success using a Wilcoxon signed-rank test and whether breeding success differed between nest types (e.g. surface nesting or burrow) applying a Pearson's chi-squared test. Chick body mass increase and daily growth rate were based on growth rate data for known-age chicks in the growth and provisioning group and plotted against age and best fitted to a locally weighted scatterplot smoothing where a smooth curve was added to aid visual interpretation. We applied a polynomial regression to examine whether investigator disturbance had affected chick growth by comparing the mass and wing length over time between chicks in the 'growth group' and the 'provisioning group'. All results are presented as the standard deviation of the mean (SD). We consider P -values < 0.05 as significant.

Results

Breeding phenology and breeding success

We confirmed the exact date of laying for 17 Fluttering Shearwater pairs. The mean laying date was estimated at 12 September ± 7.9 days (range = 2 September–10 October). The hatching date was 30 October ± 6.1 days (range = 22 October–5 December; Figure 2). The

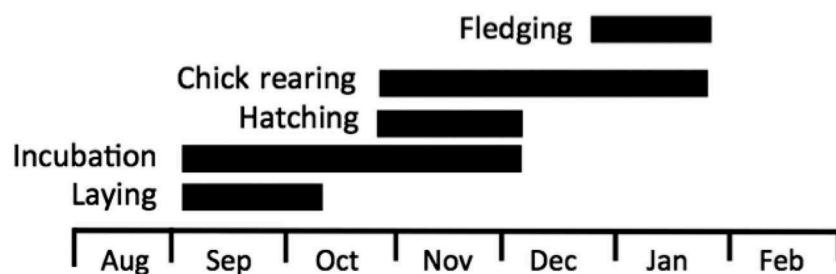


Figure 2. Recorded timing of Fluttering Shearwaters breeding on Burgess Island from September 2015 to January 2016. Mean laying: 12 September ± 7.9 days (range = 2 September–10 October); mean hatching: 30 October ± 6.1 days (range = 22 October–5 December; mean fledging: 9 January ± 3.3 days (range = 28 December–16 January).

incubation period thus lasted 50.0 ± 3.7 days (range = 46–55 days, $n = 11$). Chicks fledged on 9 January ± 3.3 days (range = 28 December–16 January), the chick-rearing period thus lasting 74.2 ± 4.3 days (range = 64–81 days, $n = 20$). The total breeding period (from laying to fledging) was 121.9 ± 4.6 days (range = 114–132 days, $n = 20$).

Overall breeding success was 63.8% ($n = 47$), with hatching success being 73.3%; of the hatched chicks, 88.2% survived. The primary cause of hatching failure was egg loss. Competition with Little Blue Penguins (*Eudyptula minor*) was likely to have been a cause in one case. Thirteen eggs failed to hatch. Of these, one had a crack, seven were infertile or left unattended for too long and five went missing. Of the chicks that hatched but did not survive ($n = 4$), one was flushed out of the burrow during a heavy rainfall event on 3 November, two chicks were found dead in the burrow entrance or just outside the burrow, and one went missing between the last November check and first inspection in December. The growth and mass of these three chicks were not different from other study chicks. There was no apparent difference in hatching success between groups (provisioning group: 89%,

growth group: 74%, control group: 68%) and chick survival (provisioning group: 100%, growth group: 85%, control group: 91%).

Breeding habitat and burrow structure

We identified 52 Fluttering Shearwater nests in mid-September. Of these, 47 were selected as suitable for monitoring (e.g. not too fragile or too close to unsafe cliff edges). Most nests were found close to a suitable take-off place, such as a cliff face or a dense bush. The native shrub *Muehlenbeckia australis* was found within 1 m of 58.5% of Fluttering Shearwater burrows ($n = 41$; Figure 3). Out of the 41 natural burrows examined, two had two nest chambers while all others had a single one. Only one nest chamber was occupied in the two nests with two chambers. All burrows had a single entrance. Nine (22%) of forty-one natural nests were located under dense vegetation on the surface (Figure 3).

Breeding success for birds nesting in vegetation was 59.5% and did not differ significantly from birds breeding in burrows (67.9%) (Pearson's chi-squared test; $\chi^2 = 2.583$, $df = 1$, $P = 0.108$). The average length of Fluttering Shearwater burrows on Burgess Island was

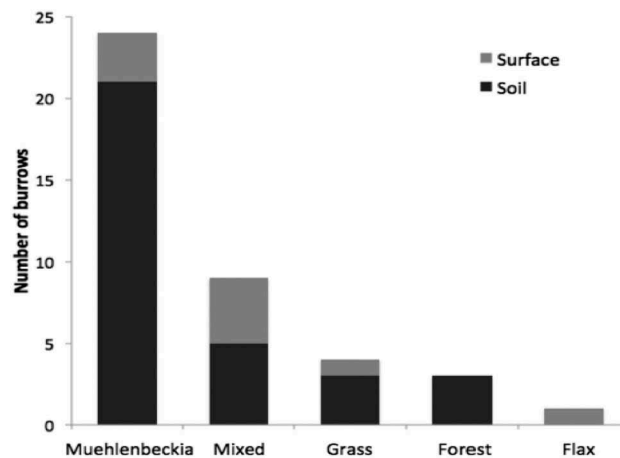


Figure 3. Frequency distribution of habitat types based on assessments of vegetation within 1 m radius around the entrance of active Fluttering Shearwater burrows ($n = 41$) on Burgess Island, 2015–2016. Dark grey represents burrows dug under the soil and light grey represents nests on the ground in dense vegetation.

Table 1. Morphometric measurements and body mass of adult Fluttering Shearwaters and chicks measured during the chick-rearing period on Burgess Island, 2015

Measurements	Adults			Chicks		
	Mean \pm SD	Range	n	Mean \pm SD	Range	n
Body mass (g)	330 \pm 44.0	330 \pm 44.0	35	40.8 \pm 8.9	20–54	12
Bill length (mm)	33.7 \pm 1.4	30.0–36.4	32	14.3 \pm 1.2	12.1–15.6	12
Bill depth at base (mm)	9.8 \pm 2.4	8.0–10.4	32	–	–	12
Total head length (mm)	79.6 \pm 2.8	72.5–87.4	35	–	–	12
Tarsus length (mm)	42.4 \pm 1.7	38.3–45.5	35	18.9 \pm 1.6	18.6–22.1	12
Wing length (mm)	209 \pm 4.0	201–218	35	22.4 \pm 1.9	18–24	12

59 ± 23 cm ($n = 41$). There was a wide range of burrow lengths recorded (22–107 cm), with some birds successfully rearing a chick in burrows that were only 22 cm and 30 cm long. Burrow length was not significantly correlated with breeding success (non-parametric data, Shapiro–Wilk normality test; $W = 0.984$, $P = 0.863$, Wilcoxon signed-rank test; 125.5, $P = 0.160$, $n = 41$).

Adult measurements and egg size

The mean mass of adult Fluttering Shearwaters during the chick-rearing period was 330 ± 44.0 g (range = 225–430 g, $n = 35$). Morphometric measurements of adults are shown in Table 1. The oval, pure white egg had an average mass of 46.0 ± 3.2 g (range = 41.5–46.0 g, $n = 13$).

Chick growth and effects of investigator disturbance

Information on the mass and measurements of 12 newly hatched chicks (<12 h old) is presented in Table 1. Chicks increased in mass by 6.6 ± 1.0 g/

day to reach a peak mass of 378 ± 53 g (range = 258–418 g, $n = 20$ after approximately 59 days). The mass of chicks at fledging was 336.5 ± 43.2 g (range = 255–395 g, $n = 20$ with a total chick-rearing period of 74 ± 4.3 days ($n = 20$; Figure 4(a)). On average, chicks were 15 and 2% heavier than breeding adults at body mass peak and at fledging respectively. Bill and tarsus growth reached asymptotes of 32.7 and 43.2 mm after ~60 and ~45 days of age respectively (Figure 4(b, c)). The average growth rate of the bill and tarsus was 0.3 and 0.6 mm/day respectively. The growth of the wing was largely linear ($R^2 = 0.97$) over the whole chick period and the wing feather growth continued until the time of fledging (Figure 4(d)). Mass and wing length did not differ significantly over time between chicks in the growth and provisioning groups (polynomial regression: mass: $R^2 = 0.92$, $df = 485$, $P = 0.262$; wing length: $R^2 = 0.98$, $df = 222$, $P = 0.229$).

Chick provisioning

Adults generally came ashore around 1 h after complete darkness to feed their chicks. Pairs were

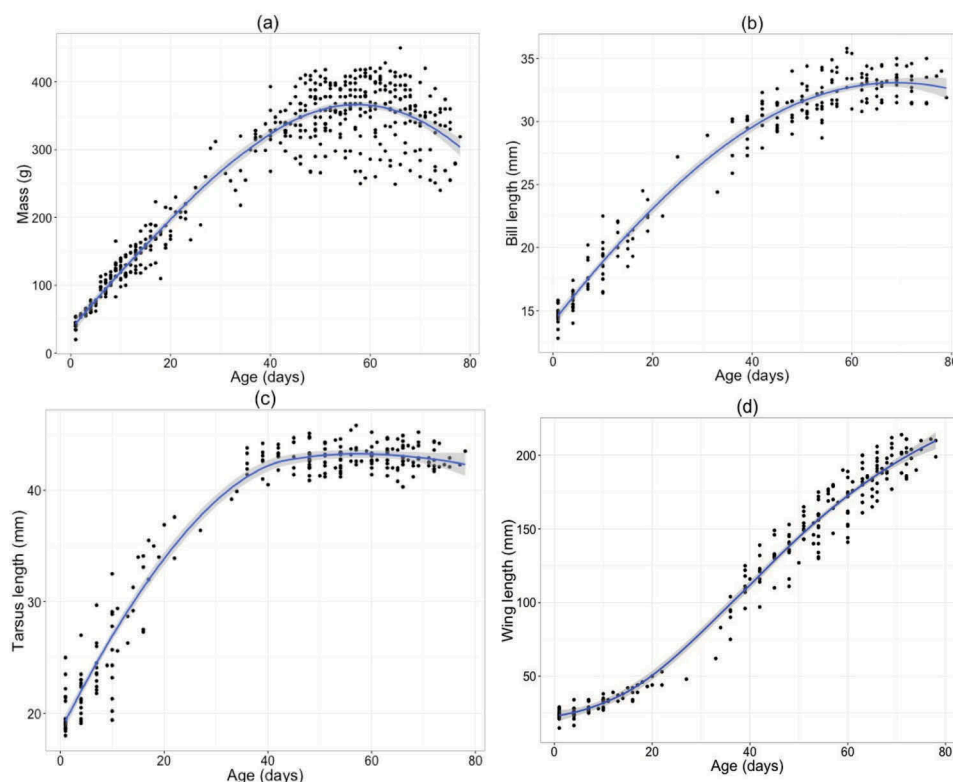


Figure 4. Locally weighted scatterplot smoothing fitted with a smooth curve to aid visual interpretation. Body mass (a), bill length (b), tarsus length (c) and wing length (d) of 20 Fluttering Shearwater chicks from hatching to fledging.

Table 2. Proportion of nights where food was delivered and calculated overnight food delivery mass in relation to chick age in days from hatching ($n = 198$ observations)

Age class (days)	n	Percentages of nights food delivered	Mean amount of food received (g)	SD
1–10	8	96	37.5	23.6
11–20	8	95	35.4	18.2
21–30	2	90	35.2	26.8
31–40	2	95	40.6	33.1
41–50	2	91	48.2	20.5
51–60	8	88	36.4	22.1
61–70	8	67	37.8	22.5
71–78	7	50	34.7	17.4

frequently seen sitting together at the burrow entrance after feeding their chicks through the night, to leave 1–2 h before sunrise. Chicks were fed on 93% of nights during the first 61 days and after that 59% of nights (Table 2). On average, chicks were fed 37.6 ± 22.0 g/night ranging from 15 to 112 g, where the upper end of this range probably indicates double feeds. Provisioning quantity remained constant in size throughout the chick-rearing period (Table 2).

Discussion

Breeding phenology

Our study demonstrates that the population of Fluttering Shearwaters breeding on Burgess Island has a protracted egg-laying period (39 days) similar to what has been described for similar-sized *Puffinus* species, such as Manx Shearwater (37 days; Brooke 1978) and Hutton's Shearwater (28 days; Cuthbert and Davis 2002a). This asynchronous laying contrasts markedly with larger *Puffinus* species that are trans-equatorial migrants, such as Buller's Shearwater (*Ardena bulleri*) and Sooty Shearwater (*A. grisea*), with laying periods of 12 and 7 days respectively (Harper 1983; Warham 1990). Brooke (2004) suggests that large shearwater species, with longer chick-rearing periods, may have difficulty completing the full breeding and migration cycle within 12 months without an extremely coordinated and short egg-laying period. Small- to medium-sized species with shorter chick-rearing periods may, therefore, be under less selection pressure to lay synchronously. The incubation period in Fluttering Shearwater of 50 days is identical, or nearly so, to other related *Puffinus* species: Hutton's Shearwater (*P. huttoni*) 50 days (Cuthbert and Davis 2002a), Audubon's Shearwater (*P. iherminieri*) 49 days (Warham 1990), Black-vented Shearwater (*P. opisthomelas*) 51 days (Keitt *et al.* 2003) and Manx Shearwater 51 days (Brooke 2004).

Breeding success

The breeding success of 63.8% observed for the Fluttering Shearwater population on Burgess Island is comparable to that reported for similar-sized shearwaters not affected by introduced predators (Thompson 1987; Warham 1990). Competition for space is not likely to affect breeding success on Burgess Island. It should, however, be stated that breeding success may vary between years due to other factors such as stochastic events or at-sea food variability (Brooke 2004) and that therefore long-term studies are required to fully understand the breeding success (Warham 1990). For instance, the breeding success of the Hutton's Shearwater varied between 27 and 66% between the years 1990 and 1998 (Cuthbert and Davis 2002b). Our data also support the general pattern that most breeding failures occur during the incubation period (Warham 1990).

Breeding habitat and burrow structure

Fluttering Shearwater nests were found on moderate to steeply angled slopes and often close to cliff edges or rock boulders, which likely facilitates take-off (Brandt *et al.* 1995; Warham 1996), as Fluttering Shearwaters have difficulty taking off from level ground (M. Berg pers. obs.). This is consistent with what has been found for other Procellariiformes, including Yelkouan Shearwater (*Puffinus yelkouan*) and Newell's Shearwater (*P. newelli*) (Warham 1996; Bourgeois *et al.* 2008; Troy *et al.* 2014). Another possible reason to nest on sloping ground is to reduce the risk of flooding following heavy rain (Thompson and Furness 1991). Nine nests were found in dense vegetation on the surface. Surface nesting is exceedingly rare for *Puffinus* species outside of the tropics (Brooke 2004) and, to our knowledge, this is the highest proportion of surface-nesting pairs recorded for any *Puffinus* shearwater, except the Christmas Shearwater (*P. nativitatus*) nesting in the tropical Pacific Ocean (Seto 2001; Mitchell *et al.* 2005). We found no significant difference in breeding success between burrow-nesting and surface-nesting pairs, indicating that the dense vegetation provides sufficient shelter from rain and avian predators. Fluttering Shearwaters have also been found breeding under rock boulders on other offshore islands in the Hauraki Gulf, indicating that this species may be adapted to utilising non-soil habitat (G. Taylor pers. comm.).

The length of Fluttering Shearwater burrows on Burgess Island (59 ± 23 cm) was notably shorter than that reported from the similar-sized Hutton's

Shearwater in the Kaikoura Mountains (87 ± 27 cm; Cuthbert and Davis 2002a) and Sooty Shearwaters on Long Island (84 ± 43 cm; Geary *et al.* 2014). Soil depth and penetrability vary over the colony, but soils are generally shallow and compacted after decades of grazing by livestock (<15 cm) (C. Gaskin unpub. data), and are likely the primary factor influencing burrow structure (Schramm 1986; Cuthbert and Davis 2002a; Troy *et al.* 2016). We found no relationship between burrow length and breeding success, which supports the hypothesis that the species can be highly flexible in its breeding habitat.

Chick growth and provisioning

The growth of Fluttering Shearwater chicks followed the typical pattern reported for most Procellariiformes (Warham 1990; Brooke 2004), with mass being gained to a maximum of 115% of mean adult weight and then steadily being lost until fledging. The observed rate of mass gain was 6.6 g/day. This was higher than that reported from Little Shearwater breeding on the nearby Lady Alice Island (5.8 g/day; Booth *et al.* 2000b), but much lower than reported for Manx Shearwater (15 g/day; Brooke 2004) and Hutton's Shearwater (10–13 g/day; Cuthbert and Davis 2002a). We hypothesise that these inter-species growth rate differences are related to adult mass, where large shearwater species, such as Great Shearwaters (mean adult body mass = 860 g), gain mass more rapidly (19.3 g/day; Cuthbert 2005) than small species such as the Little Shearwater with an average adult mass of 225 g. Skeletal components were similar to other burrow-nesting petrels (Warham 1990), with a rapid growth of bill and tarsus, and slower growth of the wings, which continued growing until fledging. The chick-rearing period of 74 days was similar to that recorded for Audubon's Shearwater (75 days; Warham 1990) and the Manx Shearwater (71 days; Brooke 2004), but considerably shorter than that reported for Hutton's Shearwater (83 days; Cuthbert and Davis 2002a), which nests at high altitude and well inland.

Inter- and intra-specific differences in the duration of the fledging period have been attributed to the provisioning rate of meals to the chick (Warham 1990). As far as our sample of eight to two pairs indicates, on average, chicks were fed 93% of the nights for the first 60 days and on average 59% of the following nights until fledging. Little Shearwaters on the nearby Lady Alice Island in the Hauraki Gulf showed similar feeding frequency (Booth *et al.* 2000a), with an average of 95% of chicks being fed each night. In other similar-sized shearwaters, the intervals between meals

are rarely longer than a few days (Hamer and Hill 1997; Riou and Hamer 2008). On average, meal sizes were 11.4% of total average adult mass, which is similar to the 13% for the Little Shearwater (Hamer 1994), 10% for Cory's Shearwater (*Calonectris diomedea*) (Hamer and Hill 1993) and 12% for the Manx Shearwater (*P. puffinus*) (Hamer *et al.* 1998).

Unlike other shearwater species (Warham 1990; Brooke 2004), but similar to Hutton's Shearwater (Cuthbert and Davis 2002a), Fluttering Shearwater chicks did not leave their burrow and 'wing exercise' in the weeks before fledging. All chicks that were seen outside their burrow left the colony the same night and were not observed in the burrow afterwards. While the reason why Fluttering Shearwaters, at least at our study location, were not observed to exercise their wings is unclear, the presence of Morepork, which has been observed preying on seabirds at night (Anderson 1992; M. Berg pers. obs.), might be a possible explanation. However, smaller petrel species such as diving petrels are often seen to sit in the open at night, which contradicts this hypothesis.

We found no difference in chick survival or chick growth between our growth group, provisioning group and control group. However, although difficult to quantify, our field observations indicate that Fluttering Shearwaters are easily disturbed, especially during pre-laying and early incubation. Therefore, caution should be exercised when surveying nests and investigating hatching date. Many nests were located in soft and friable soil or under vegetation on the ground, and much care must be taken to avoid the risk of collapsing burrows. By following the protocol as described in Sagar *et al.* (2015) we found no statistically significant difference between chick growth and fledgling mass with the degree of investigator disturbance.

Conclusion

The breeding biology of Fluttering Shearwaters on Burgess Island is consistent with what has been reported from other similar-sized *Puffinus* species. However, we found a high proportion of surface-nesting pairs under thick ground cover, possibly due to the effects of long-term grazing modifying soils and habitat types on the island. Chicks were frequently fed daily throughout the chick-rearing period. Major causes of breeding failure are more likely to occur during incubation or due to stochastic events. Although important baseline biological data are provided here, longer-term studies in more than one Fluttering Shearwater colony using standardised methods are required to determine

demographic parameters and help explain variation in breeding success and population resilience.

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