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**Patterns of nest attendance during the
breeding season of the Little Penguin
(*Eudyptula minor*)**

A thesis presented in partial fulfilment of
the requirements for the degree of

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in
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Kororā. Emily Yap, 2022. Watercolour on fine art paper.

Abstract

Understanding the breeding behaviour of Little Penguins is essential to gauge reproductive success. This study is the first to examine Little Penguins from Port Tarakohe in the Tasman District of New Zealand, focusing on colony attendance during the 2022 breeding season.

Daily nestbox monitoring was utilised for the first time in New Zealand to investigate nest attendance and breeding stages of the Little Penguin. The first analytical chapter is a colony-level investigation, identifying patterns and cycles of nestbox attendance in various categories, including males and females, breeding pairs, and breeding and non-breeding birds. The lunar cycle is also examined as a potential influence on attendance behaviour. The second analytical chapter assesses the nestbox attendance of individual breeding pairs within the Port Tarakohe colony, as the breeding season progresses through its stages.

Observations from the first chapter include that pairs of Little Penguins synchronised their colony attendance over multiple months of the breeding season, corresponding to the stages of courtship, incubation and guard. Courtship and egg-laying were found to occur approximately four weeks apart, in multiple distinct waves. Male and female members of separate breeding pairs were found to synchronise their nestbox attendance during the incubation and guard phases. The nestbox attendance of non-breeding birds was found to vary cyclically over a four-week period, and appeared to increase close to the time of the full moon although this was not significant.

The second chapter reveals that average incubation period and guard period lengths are consistent with those reported from other colonies. Mean nestbox attendance during the incubation periods of breeding pairs was observed to be equal between different sexes. Incubation spell length was observed to rise and fall predictably over the incubation periods of different breeding pairs. One-chick clutches were observed to be guarded for longer than two-chick clutches.

These findings complement, contrast with, and extend previous observations on colony attendance made at other Little Penguin colonies, and serve as a base for future research on the Port Tarakohe colony.

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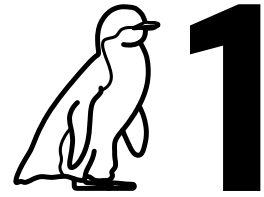
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Introduction

1.1 The Little Penguin (*kororā*)

1.1.1 Taxonomy

There are 18 recognised extant species of penguins in the family *Spheniscidae*, ranging from the largest, the Emperor Penguin (*Aptenodytes forsteri*), to the smallest, the Little Penguin (*Eudyptula minor*). The Little Penguin, also known as the *kororā* in Māori, is considered the smallest penguin species, with a height around 30 to 35 cm. These penguins typically weigh around 1 kg, though this varies depending on the time of year and food availability (Marchant & Higgins, 1990). They are easily recognized by their distinctive slate-blue plumage with a white underside (Marchant & Higgins, 1990). In Australia, Little Penguins are also referred to as Blue Penguins or Fairy Penguins.

The overall morphology of male and female Little Penguins is similar, although the species does exhibit sexual dimorphism. Male Little Penguins tend to be larger than females and have larger bills (Arnould et al., 2004; Hocken & Russell, 2002). Additionally, the beaks of female Little Penguins are more slender, while males have a more prominent upper mandible (Kinsky, 1960).

In New Zealand, most Little Penguins belong to the *Eudyptula minor* species, except for those in the Otago region. Populations in Otago and Australia share the same species, *Eudyptula novaehollandiae*. Previously, it was thought that these two species were subspecies. However, research in 2017 revealed osteological differences between them, supporting the classification of two separate species (Grosser et al., 2017). This finding was further corroborated by a genetic analysis published in 2019 (Cole et al., 2019).

The white-flipped penguin, *Eudyptula albosignata* (Allen et al.), is recognised either as a subspecies or a morph of the Little Penguin (O'Brien, 1940). To date, *E. albosignata* breeds mainly in Canterbury, New Zealand, with larger populations at Banks Peninsula and Motunau Island (Challies & Burleigh, 2004).

1.1.2 Distribution

Little Penguins are found primarily around coastal regions in southern Australia and in New Zealand (Grosser et al., 2015). Little Penguins in Australia are distributed along the southern coastline, as well as Tasmania and Phillip Island. Little Penguins are present in both the North and South Islands of New Zealand, and surrounding islands such as the Chatham Islands, Stewart Island, and Tiritiri Matangi Island (Grosser et al., 2015; Miyazaki & Nakagawa, 2015). In the North Island, the main locations of Little Penguins include Auckland, Hawke's Bay, Taranaki, Napier, and Wellington. In the South Island they are mainly observed at Golden Bay (in the Tasman District), Oamaru (in Otago), Otago Peninsula, Kaikoura, and Banks Peninsula (in Christchurch). Little Penguins are found in a range of habitats. They nest underneath vegetation, inside rock crevices, in caves, and occasionally below houses and construction (Braidwood et al., 2011).

1.1.3 Conservation status and threats

The New Zealand Department of Conservation has classified the conservation status of *Eudyptula minor* as "At Risk — Declining" (Robertson et al., 2021). Little Penguins face various natural and human-induced threats. They are particularly susceptible to bacterial and fungal infections, as well as parasites (Harrigan, 1992; Hocken, 2000; Rensburg, 2010). Human-related threats include habitat loss, vehicular danger (from both terrestrial and aquatic vehicles), reduced food availability due to

fishing activities, and entanglement in bycatch (Hocken, 2000). Oil spills represent another significant threat, with devastating impacts on penguin populations. In 1995, for instance, 1,894 Little Penguins were found covered in oil after a spill in Tasmania, Australia (Goldsworthy et al., 2000). Similarly, the 2011 Rena oil spill in Tauranga, New Zealand resulted in the deaths of 2,030 seabirds, including many Little Penguins, with 383 out of 420 rescued birds identified as Little Penguins (Sievwright, 2014).

Natural predators include marine animals such as fur seals, leopard seals, and killer whales. In Australia, land predators of Little Penguins include iguanas, rats, cats, and foxes (Colombelli-Négrel & Tomo, 2017; Kirkwood et al., 2014). In New Zealand, introduced mammalian predators pose a significant threat to Little Penguins, as they do to other many native birds. Ferrets, stoats, and rats are known to prey on eggs, chicks, and even adult penguins (Hocken, 2000; Perriman & Steen, 2000). These predators raid nests, hunting for eggs and chicks, and additional threats come from domestic and wild cats and dogs (Hocken, 2000).

After egg-laying, the incubation period begins, with male and female penguins alternating shifts at the nest (Kato et al., 2008). While one parent incubates the eggs, the other forages at sea. The incubation period lasts 30 to 40 days, after which the eggs hatch (see Table 1.2). The newly hatched chicks enter a phase known as the guard period, during which one parent stays in the nest to guard the chicks while the other forages for food. Parents alternate these roles every day, and the guard period typically lasts about two to three weeks (Numata et al., 2004).

During the post-guard stage, both parents depart the nest to forage simultaneously, leaving chicks alone (Saraux et al., 2011b). Parents will continue to bring back food for the chicks, supporting their growth and the development of waterproof feathers necessary for independence. After two to four weeks, the fully-grown chicks fledge and leave the nest to forage independently at sea (Saraux et al., 2011b).

1.2.3 Moulting

After the breeding season, adult Little Penguins spend some time feeding before returning to the colony to moult (Reilly & Cullen, 1983). The moulting process entails birds shedding their old feathers and growing new ones. In the case of Little Penguins, moulting is crucial to maintain a waterproof layer for swimming, and to provide insulation for warmth (Reilly & Cullen, 1983). Little Penguins moult once a year, typically from January to March/April. While moulting, they stay in their nest and fast for two to three weeks as the new feathers grow (Reilly & Cullen, 1983).

Table 1.2: Mean lengths (days) of Little Penguin incubation periods recorded in previous papers.

Mean	Incubation period				Nest check frequency	Number of birds	Number of nests	Location	Year	Reference
	SE	<i>n</i>	Min	Max						
35.50	0.25	48	31	40	Daily	106	53	Phillip Island, AUS	1995	Chiaradia & Kerry (1999)
35.40		142	33	44	Daily		105	Phillip Island, AUS	1998	Kemp & Dann (2001)
35.10	0.32	10			Every 2 days	20	10	Phillip Island, AUS	2004	Kato et al. (2008)

1.3 Penguin Colonies

Nest monitoring is a method often used to observe seabird behaviour (Braidwood, 2009; Chiaradia & Kerry, 1999; Numata et al., 2000). Seabirds nest on land and leave their nest to forage in the ocean for food, spending several days or weeks offshore before returning to their nest sites. The nest attendance pattern of seabirds may be influenced by a range of environmental factors, such as prey availability, season/time of year, sea surface temperature, and the phase of annual cycles such as breeding or moult (Berlincourt & Arnould, 2015).

Penguins are Southern hemisphere seabirds native to South Africa, New Zealand, Australia, Antarctica, and various Pacific islands. Penguins mostly breed in colonies — for example, the Emperor Penguin and King Penguin incubate in densely-packed huddles (Nesterova et al., 2010). The Yellow-eyed Penguin, *Megadyptes antipodes*, is a notable exception to this norm (Darby et al., 1990). Synchronisation in individual behaviour and nest attendance can be observed both between individual birds and at a colony level. Little Penguins will arrive onshore together in small groups called ‘rafts’ to finish the journey to their colony, and will also depart their nests to forage in the ocean at similar times (Reilly & Cullen, 1981; Stahel & Gales, 1987).

The following pages will further discuss the nest attendance of penguins and other seabirds, focusing predominantly on the behaviour of the Little Penguin during the breeding season. The primary driver for leaving the colony is the need to forage, which directly influences penguin presence or absence within the colony. Examining the colony attendance of birds therefore necessitates an analysis of their foraging patterns. This chapter will also review potential factors influencing the foraging trip choices of penguins.

1.4 Little Penguin colony attendance

1.4.1 Colony arrival and departure

As previously stated, Little Penguins typically go out to sea at dawn and return at dusk. Klomp & Wooller (1991) observe that the Little Penguin colony on Phillip Island, Australia, demonstrated a distinctive attendance pattern in which most birds arrived at the colony approximately 1 to 2 hours after sunset (see Figure 1.1). Penguins may time these movements to occur around dawn and dusk to reduce the risk of predation, aiming to limit visibility for potential predators while still being able to navigate between their nesting sites and the open sea (Rodriguez et al., 2016). The hypothesis surrounding this behaviour will be discussed further in the section on attendance in relation to moonlight.

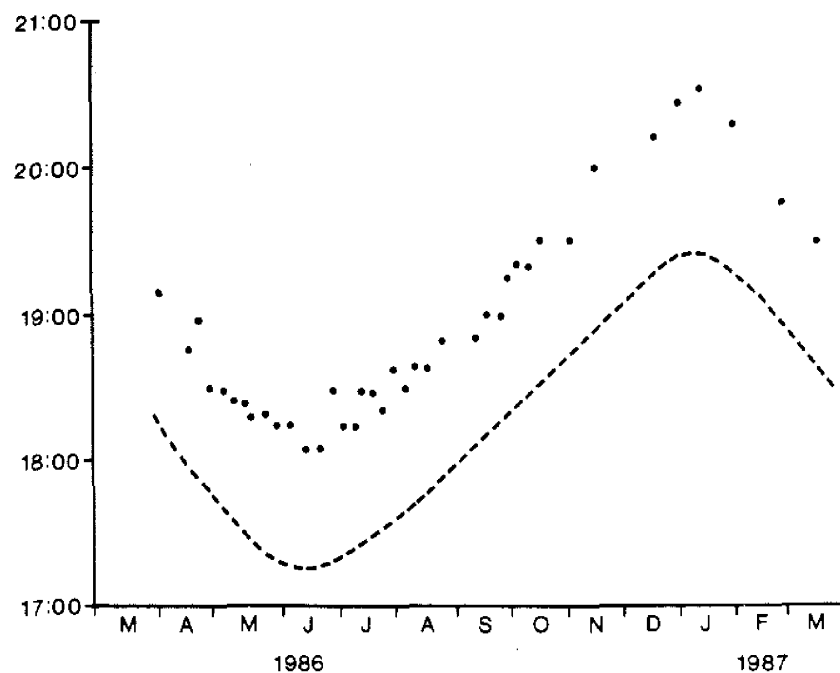


Figure 1.1: The times at which the first group of Little Penguins came ashore on Penguin Island, Western Australia, during 1986/87 (•), in relation to the time of sunset (broken line). Adapted from Klomp & Wooller (1991).

1.4.2 Annual attendance

Little Penguins are usually either out at sea foraging or present at their nest sites. In comparison to other penguin species, Little Penguins are generally considered sedentary (Ainley & Wilson, 2023). These inshore seabirds remain close to their nest sites all year round, diving relatively close to the coast in comparison to penguin species that engage in trips further out at sea (Hoskins et al., 2008). Annually, colony attendance peaks during the moult and breeding seasons, when Little Penguins may often be found in their nests. Outside of those seasons, Little Penguins often undertake longer and more frequent foraging trips out to sea.

During the moulting period, Little Penguins remain in their nest, fasting while their old feathers moult into a new set. Moulting usually extends until March (Reilly & Cullen, 1983), after which, penguins head off to sea to feed and gain back lost body weight. From April to June, Little Penguins are usually found engaged in long foraging periods that can go on for multiple weeks. Reilly & Cullen (1981) examined Little Penguin attendance at the Summerland colony on Phillip Island. They observe a three-weekly cycle in the number of Little Penguins present from April to September (see Figure 1.2). The peaks and troughs reveal that the colony arrivals and departures of individual birds tend to fall on similar days. As winter approaches, attendance shows an upward trend, while the three-week cycle remains consistent (Reilly & Cullen, 1981). Two times as many males than females were recorded present in nests in the months closer to breeding. This pattern of attendance shows a significant level of synchronisation between the penguins and demonstrates a potential rhythmic behavioural pattern in these birds.

Reilly & Cullen (1981) also note a consistent low probability of finding birds in their nests for the three to four months following moult. Figure 1.2 shows the number of birds present increasing significantly in the two to three months leading up to egg-laying. This increase in attendance is likely mainly due to birds returning to the colony for courtship.

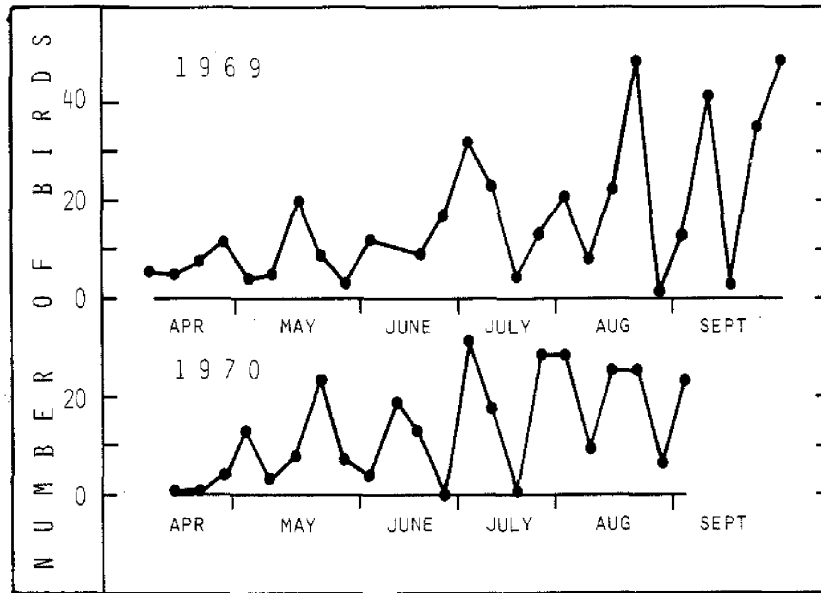


Figure 1.2: Number of Little Penguins in the Summerland colony at weekly checks in 1969 and 1970. Adapted from Reilly & Cullen (1981).

A similar pattern is observed by Agnew (2007) in the number of Little Penguins that returned to the colony at Oamaru, New Zealand in winter. From the end of May to August in 2006, there was a regular cycle in the number of penguins seen arriving during evening viewings (see Figure 1.3). Large peaks of 90 to 100 birds occur every three weeks, with a smaller peak of approximately 60 to 70 birds occurring in-between. These results coincide with Reilly and Cullen (1981)'s 1969 result in Fig 1.3. Taken together, these observations demonstrate that Little Penguins in colonies from different countries exhibit similar trends in annual colony attendance.

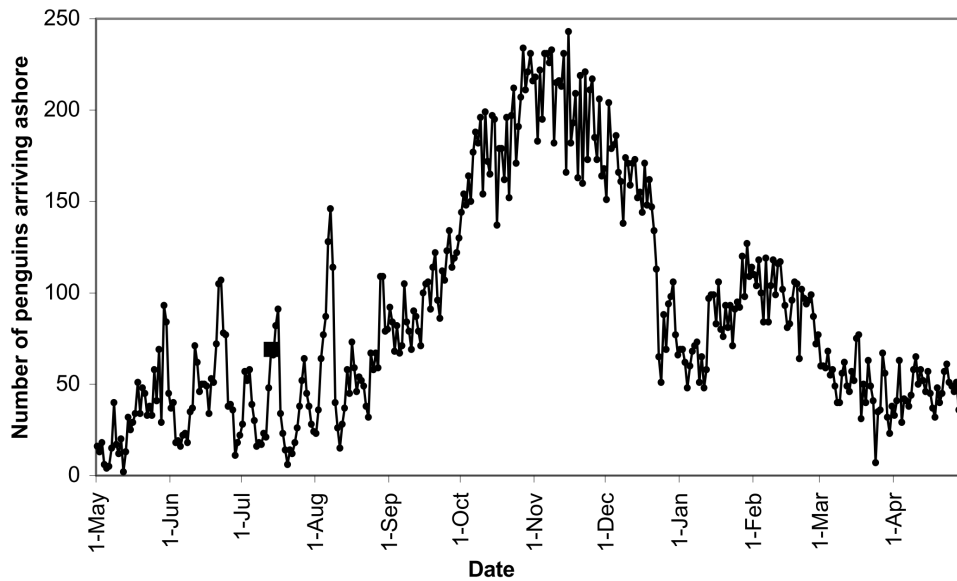


Figure 1.3: Number of penguins that arrived during evening viewings during the 2006 breeding season, counted for one hour after first arrivals. Solid square shows first day eggs were laid. Adapted from Agnew (2007).

1.4.3 Breeding season attendance

1.4.3.1 Pre-breeding

Males and female Little Penguins begin the breeding season by returning to their colony to meet at potential nest sites. This event, known as courtship, happens approximately one month before the onset of egg-laying (Chiaradia & Kerry, 1999). Chiaradia & Kerry (1999) observed male Little Penguins arriving at the nest site earlier than their female counterparts 60% of the time. 25% of the time, both the male and female arrived together, with the remaining 15% being instances where the female penguin arrived before the male. This behaviour supports the idea that male Little Penguins are primarily responsible for claiming a nest site and guarding it until the female mate arrives (Reilly & Cullen, 1981).

Additionally, both males and females generally remain in their nest for about 5 days after courtship before returning to feed (Chiaradia & Kerry, 1999). Right before egg-laying, male penguins again tend to return to the nest before the females, and stay longer than they do (Chiaradia & Nisbet, 2006). It is hypothesised that female birds spend extended periods foraging in the ocean right before egg-laying in order to accumulate sufficient mass necessary for egg production (Chiaradia & Kerry, 1999).

1.4.3.2 Egg-laying

During the egg-laying period, female Little Penguins remain in the nest for a few days to lay the clutch. Chiaradia & Kerry (1999) found that among observed females, most laid clutches of two eggs, remaining in their nestboxes for a mean of 5.6 ± 3.1 days. The first eggs of clutches were laid 4.9 ± 2.8 days on average after the female's arrival at the nest. Male birds stayed for a similar number of days to their female counterparts, and were typically absent the morning the first egg is laid (Chiaradia & Kerry, 1999).

1.4.3.3 Incubation

Little Penguins require large amounts of energy during the breeding season, particularly in the stages after egg-laying (Gales & Green, 1990). The incubation period of Little Penguins lasts for approximately 35 days, but can range from 31 to 40 days (Chiaradia & Kerry, 1999; Kato et al., 2008; Kemp & Dann, 2001). This stage of breeding consists of one parent incubating eggs — that is; undertaking an incubation spell — while the other is out foraging. These roles are alternated throughout the incubation period.

The length of incubation periods has been found not to vary significantly between successful and unsuccessful breeding attempts (Chiaradia & Kerry, 1999). However, the length of incubation spells does seem to have a significant effect on whether incubation is successful.

While Little Penguins are able to embark upon long foraging trips during the non-breeding winter season (McCutcheon et al., 2011), foraging trips are generally shortened during breeding due to additional parental responsibility. Incubation foraging trips generally vary from 1 to 9 days (Kato et al., 2008). Shorter trips by one bird result in shorter fasting periods for the partner at the nest, making it more likely for them to remain in the nest and reducing the likelihood of egg abandonment. Continuous incubation by parents ensures that the eggs receive consistent warmth and better temperature regulation as parents replenish their energy more frequently. However, extended foraging trips may be more advantageous, as they allow the birds to spend more time feeding and accumulating necessary weight, which may have prolonged benefits throughout the rest of the breeding season (Numata et al., 2000).

The sections below further discuss the foraging patterns observed during the incubation period and the factors influencing the duration of these trips, all of which impact the colony and nest attendance of Little Penguins during the breeding season.

The incubation spells exhibited by Little Penguins demonstrate a temporal pattern. According to Kato et al. (2008), incubation starts with relatively shorter trips at the beginning after egg laying, with foraging trips becoming longer during the middle of the incubation period, and then shortening to single-day or overnight trips towards the end. As egg hatch approaches, there is an increase in single-day foraging trips made by the parents (see Figure 1.4). Findings from Phillip Island observations in the 1992/1993 breeding season further support the presence of single-day spells towards the end of incubation (Collins et al., 1999). This behavioural shift could be caused by parents increasing their vigilance as egg hatch approaches, enabling them to provide immediate food to newly hatched chicks. The detection of egg movement or signs such as pipping may be useful tells in this regard.

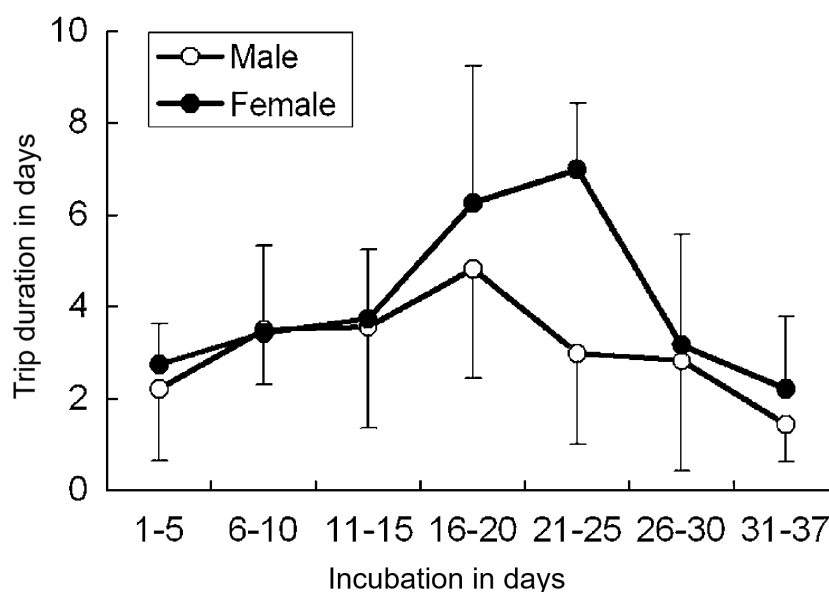


Figure 1.4: Change of trip duration in relation to timing of departure within the incubation stage of male and female Little Penguins. Vertical bars indicate standard deviation (SD). Adapted from Kato et al. (2008).

1.4.3.4 Chick rear

The chick-rearing stage in seabirds is known to be a high-energy demand period within their annual cycle (Bethge et al., 1997; Gales & Green, 1990; Weimerskirch et al., 2003). Adult birds spend as much of their energy as possible on finding food to sustain themselves, and on providing food, warmth and

protection for their chicks. High foraging efficiency is most important for seabirds during this period. Various factors, such as food density, specifically affect the attendance patterns of birds rearing chicks (as opposed to incubating birds) (Harding et al., 2007). During times of food scarcity, parents with chicks spend less time in the colony, indicating a larger requirement for foraging during the chick stage. Other factors, such as the parent's overall body condition, foraging ability, and age may also contribute to the length of their foraging trips during chick rearing.

Some seabird species alternate short and long foraging trips during the guard period. For example, the Wandering albatross (*Diomedea exulans*) alternate between short and long trips during chick rearing (Weimerskirch et al., 1997). The mean length of short trips by male Wandering albatross was 2.12 ± 1.32 days and for females it was 2.75 ± 1.49 days. The mean length of long trips by males was 9.49 ± 2.44 days and for females it was 11.39 ± 4.33 days.

During the start of chick rearing for the Northern gannet (*Morus bassanus*), adults exhibit shorter foraging trips while their young chicks are alone (Lewis et al., 2004). The length of foraging trips increases when chicks are older, particularly after four weeks when they are no longer guarded by the parents. During this phase, parents make longer foraging trips corresponding to the increasing age of the chicks.

As with most penguin species, Little Penguin chick-rearing involves two distinct stages. The first, known as the guard stage, continues the structure that started during incubation — one parent remains in the nest with the young chicks while the other parent forages for food (Numata et al., 2004). This period is essential for the initial weeks after egg-hatch, as chicks must receive thermoregulation from the parent while their insulative layer of down is not yet fully formed. Parental presence also provides protection against predators that might harm the young chicks, and ensures the chicks do not prematurely leave the nest. Foraging trips during the guard period usually span only a single day, as parents are limited by the need to return promptly to their chicks (Collins et al., 1999). The guard period of Little Penguins typically ranges between 15 to 20 days (Table 1.3), but has been observed to last as short as 8 days (Chiaradia & Kerry, 1999) and as long as 39 days (Braidwood, 2009).

During the second stage, known as post-guard, both parents leave the chicks unattended in the nest and go out to sea to forage, securing sufficient nourishment for the older chicks. As chicks increase

in age and body mass, more effort is required from parents to retrieve enough food. Breeding female Little Penguins are found to extend the duration of their bottom dives as their offspring age (Zimmer et al., 2011). The primary challenge for breeding birds during post-guard is to balance the demands of their growing offspring with the required maintenance of their own body condition. In the event of a failed breeding attempt (where all eggs or chicks are lost), parents may initiate a replacement clutch (Reilly & Cullen, 1981).

Table 1.3: Mean lengths (days) of Little Penguin guard periods recorded in previous papers.

Mean (days)	SE	<i>n</i>	Minimum	Maximum	Nest check frequency	Location	Year	Reference
15.1	1.00	12	10	22		Motuara Island, NZ	1998	Numata et al. (2004)
20.0	1.00	14	16	28		Oamaru, NZ	1998	Numata et al. (2004)
21.3	1.60	23	14	39		South Westland, NZ	2008	Braidwood (2009)
14.5	3.6		8	25		Phillip Island, AUS	1995	Chiaradia & Kerry (1999)
15.0	0.54	54			Daily	Phillip Island, AUS	1995	Chiaradia & Nisbet (2006)
19.0	0.54	54			Daily	Phillip Island, AUS	1996	Chiaradia & Nisbet (2006)
20.0	0.75	44			3 times a week	Phillip Island, AUS	2000	Chiaradia & Nisbet (2006)
16.0	0.69	52			3 times a week	Phillip Island, AUS	2001	Chiaradia & Nisbet (2006)
20.0	0.57	50			3 times a week	Phillip Island, AUS	2002	Chiaradia & Nisbet (2006)

Occasionally, Little Penguins may lay one-egg clutches, or may lose an egg or chick later in the breeding season, leaving the parents to guard a single chick. Parent birds may adapt their guarding and foraging behaviour depending on the size of their clutch. Breeding Chinstrap penguins (*Pygoscelis antarcticus*) guarding two chicks were found to spend a longer daily time at sea than those with a single chick clutch (Meyer et al., 1997). As the food requirement for two chicks is significantly more than that of a single chick, single chicks tend to exhibit faster growth and achieve greater overall body mass compared to those from two-chick clutches (Ainley & Schlatter, 1972).

The guard period length of one-chick and two-chick clutches were recorded to vary significantly in a study by Braidwood (2009) on the Little Penguin colony in South Westland, New Zealand. One-chick clutches were found to be guarded for 10 days longer on average than two-chick clutches (see Figure 1.5). This suggests that the parents of single chicks likely experience reduced pressure to provide food. Extended guard periods may then result from adults experiencing less pressure to forage for extended periods at sea, allowing more time for chick protection (Braidwood, 2009). Results from the Oamaru and Motuara Island colonies further support this idea (Numata et al., 2004) (see Table 1.3).

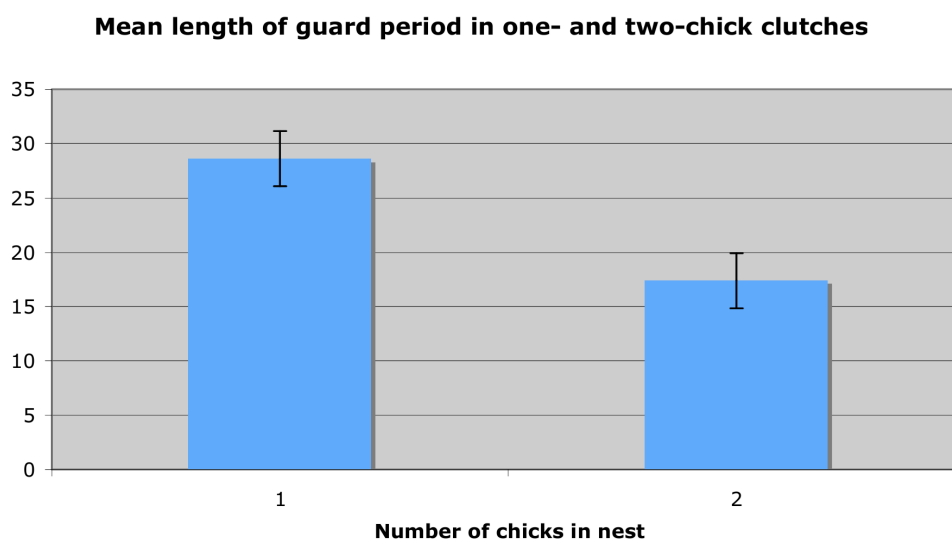


Figure 1.5: Mean (SE) Length in days of guard period in one-egg and two-egg clutches Adapted from Braidwood (2009).

Table 1.4: Mean lengths of guard periods for one-egg and two-egg Little Penguin clutches recorded in previous papers.

Guard period (1 chick)			Guard period (2 chicks)			Location	Year	Reference
Mean	SE	<i>n</i>	Mean	SE	<i>n</i>			
18.8	1.50	4	13.3	0.70	8	Motuara Island, NZ	1998	Numata et al. (2004)
26.0	0.70	3	18.4	0.50	11	Oamaru, NZ	1998	Numata et al. (2004)
28.6	2.60	8	17.4	1.00	15	South Westland, NZ	2008	Braidwood (2009)

1.4.4 Colony attendance in relation to light

1.4.4.1 Seabird behaviour in relation to light levels

Light levels influence nearly all biological activities in birds, including foraging, predator avoidance, migration, and mate selection. Some species of birds, when active after dusk, depend primarily upon moonlight for these activities. The lunar cycle, also known as the moon cycle, is a recurring pattern of changing moonlight intensity over approximately 29.5 days, influenced by the moon's position relative to the Earth and Sun. The cycle encompasses various phases of the moon, ranging from the new moon, which does not reflect any light from the Sun towards Earth, to the full moon, which reflects light maximally.

Seabird behaviour can vary significantly under different moonlight levels. Some species of seabirds have been discovered to exhibit patterns of behaviour in relation to the lunar cycle. For example, the frequency of night-time flights is high during full moons for certain seabird species (Bonnet-Lebrun et al., 2021; Dias et al., 2012). Foraging trips undertaken by Scopoli's Shearwaters (*Calonectris diomedea*) were found to be significantly longer over brightly-moonlit nights than over dark nights during the non-breeding season (Rubolini et al., 2015).

During the breeding season, the colony attendance patterns of penguins and other seabirds are different due to the specific demands of breeding. The importance of caring for eggs and chicks strongly influences both attendance and foraging behaviour, and thus they may be less influenced by lunar phases. For example, the foraging trips undertaken by Scopoli's Shearwaters during chick

rear trips were found to be of similar length — between 1 to 2 days — irrespective of different lunar phases during the period of observation. Self-feeding trips, however, were much longer in general, and significantly longer near the time of full moon than the time of new moon (see Figure 1.6) (Rubolini et al., 2015).

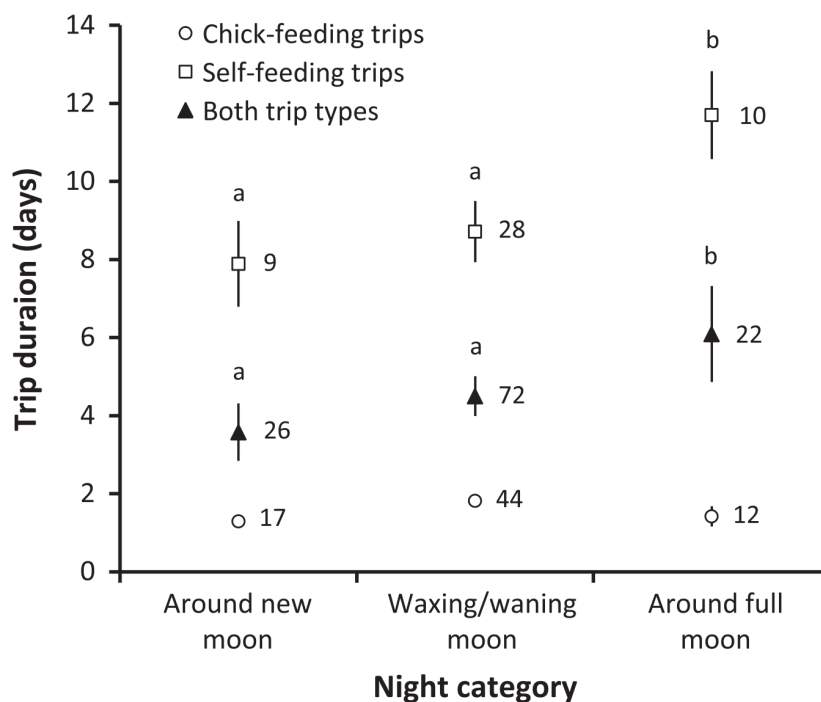


Figure 1.6: Mean (SE) trip duration of Scopoli's Shearwater chick-feeding and self-feeding trips in relation to night category at trip departure. Numbers denote number of trips, while different letters denote categories that differed statistically ($p \leq 0.05$) at post hoc tests carried out within each trip type level. Adapted from Rubolini et al. (2015).

1.4.4.2 Little Penguin behaviour in relation to light levels

Penguins rely on visual cues to forage for food (Howland & Sivak, 1984). Little Penguins are acknowledged to be diurnal hunters (Cannell & Cullen, 1998; Klomp & Wooller, 1991), but can be active at night inside their colonies. Although penguins in general are able to dive during the night, they typically prefer to hunt during hours of daylight, and are less likely to pursue fish under darker conditions. This has been observed with Adelie Penguins, *Pygoscelis adeliae* (Naito et al., 1990) and Gentoo Penguins, *Pygoscelis papua* (Williams, 1991)). Little Penguins dive to depths anywhere between 5 and 50 meters when foraging (Gales et al., 1990). Cannell & Cullen (1998) studied Little Penguin diving in an indoor pool at Phillip Island, demonstrating a positive correlation between light

levels and the probability of Little Penguins pursuing fish (see Figure 1.7). Their results show that Little Penguins catch no fish during light levels below 0.01 $\mu\text{Einstein}/\text{m}^2/\text{s}$, equivalent to the light level observed 10 to 25 minutes before dawn and after dusk.

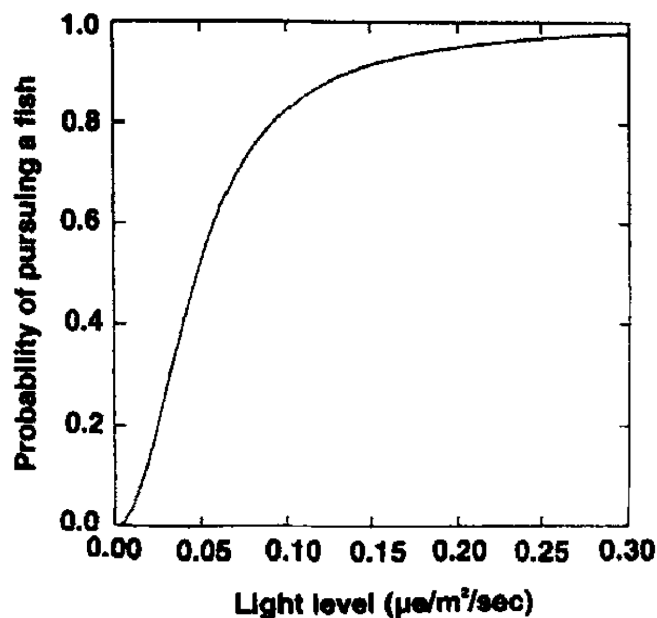


Figure 1.7: Probability of a Little Penguin chasing a fish at different light levels. Adapted from Cannell & Cullen (1998).

1.4.4.3 Little Penguin colony attendance in relation to lunar phases

Another factor that might affect the colony attendance behaviour of seabirds is the potential risk of being exposed to predators. The ‘predation avoidance’/‘moonlight avoidance’ hypothesis described by Rubolini et al. (2015) theorises that brightly moonlit nights increase overall visibility, enabling the predators of seabirds to hunt more effectively. Compounding this, Cruz et al. (2013) posits that the prey of seabirds may also exhibit more cautious behaviour under strong moonlight, potentially reducing foraging efficiency.

To date, there has only been cursory observation of the colony and nest attendance behaviours of Little Penguins in relation to lunar phases. Rodriguez et al. (2016)’s study found that fewer Little Penguins arrived ashore when the moon was full. Additionally, Little Penguins were observed to exhibit earlier arrivals and later departures close to and during the full moon. However, in a different

study, the number of Little Penguins observed in Lipson Cove, South Australia was not affected by differing intensities of moonlight (Iasiello & Colombelli-Négrel, 2025).

Little Penguins were observed under varying light levels in the Penguin Parade on Phillip Island, Australia. Rodriguez et al. (2018) found that Little Penguins consistently preferred to travel on well-lit paths over unlit paths when returning to their nest site. However, the role of moonlight in their decision to return to the colony from the ocean remains under-explored.

1.5 Factors influencing foraging trips

1.5.1 Body condition

The body condition of seabirds is often suggested to be the most important determining factor affecting the length of foraging trips. Seabirds require optimal body condition and stamina to effectively navigate the environmental challenges of both oceanic and coastal habitats. Body weight and overall physical health are critical factors that influence their travel efficiency, predator avoidance capabilities, and ability to capture prey. Seabirds with better body condition are more able to withstand environmental stressors, optimise foraging efficiency, and thereby improve their reproductive success and survival rates. Body mass is used as a strong indicator of body condition in seabirds and has been shown to affect foraging trip behaviour. For example, Sooty Shearwaters that have lower body mass before a trip — especially those with a body mass under 750 g — tend to take longer foraging trips (Weimerskirch, 1998).

During reproduction, a time of high energy cost, individuals with a higher initial body mass face less personal risk. This phenomenon is demonstrated clearly by Numata et al. (2000) in a study on the body condition of Little Penguins at the Motuara Island and Oamaru colonies. Little Penguins in Oamaru exhibited shorter and much more frequent foraging trips than those in Motuara Island. The average length of incubation spells seen in Motuara Island was 6.2 ± 0.6 days ($n = 23$) for males and 5.2 ± 0.5 days ($n = 15$) for females. These spells were longer than ones taken by individuals in Oamaru, with an average length of 2.9 ± 0.3 days ($n = 18$) for males and an average length of 3.2 ± 0.4 days ($n = 20$) for females.

Numata et al. (2000) observed higher average mass gains per foraging trip for individuals at Motuara Island than at Oamaru, due to the longer trip length. However, Little Penguins in Oamaru were found to maintain a better body condition on average when examining average daily body mass loss over the incubation period. At Motuara Island, the mean body mass of male Little Penguins was 1070 ± 17.0 grams ($n = 36$) and the females were 971 ± 13.8 grams ($n = 38$) — a significantly lower average body mass than at Oamaru, where males were recorded to weigh 1200 ± 15.5 grams ($n = 35$) on average; females 1076 ± 19.4 grams ($n = 35$) on average.

Though it is a small sample size, the average mass gain observed by Numata et al. (2000) through the entire incubation period for both male and female individuals at the Oamaru colony (Males 12.6 ± 1.8 grams ($n = 4$), Females 12.8 ± 0.5 grams ($n = 3$)) is significantly higher than that for individuals at the Motuara colony (Males 3.0 ± 0.3 grams ($n = 2$), Females 1.3 ± 0.1 grams ($n = 5$)).

Mean body mass and mean condition index figures were found by Numata et al. (2000) to be significantly lower during incubation ($F_{1,140} = 50.42, p < 0.001$ and $F_{1,140} = 56.77, p < 0.001$ respectively) for penguins at Motuara Island than for penguins at Oamaru. Locations with greater food availability create more opportunity for birds to gain weight and therefore have a better overall body condition. This enables them to provide sufficient energy during incubation and into the chick care stage.

1.5.2 Food availability

The body condition of seabirds is significantly affected by the availability of food (Harding et al., 2011). When prey is scarce, seabirds are forced to take longer or more frequent foraging trips, which puts additional strain on their energy and fat reserves (Fayet et al., 2021). Previous research has shown that food availability influences both breeding success (Chivers et al., 2012) and population growth (Barbraud et al., 2018) in seabirds. Low prey numbers may drive seabirds further and further away from their nests in search of food, reducing colony attendance. During the breeding season, this may especially contribute to starvation for both chicks and adults (Chivers et al., 2012).

While low food availability has a pronounced effect on the frequency and duration of foraging trips, high food availability does not necessitate the same relationship. Findings from Harding et al. (2007), depicted in Figure 1.8, demonstrate that the colony attendance of breeding birds increases as food density rises from 0.01 gm^{-3} to 0.058 gm^{-3} (see Figure 1.8). However, increases in prey availability past that level do not strongly correlate with colony attendance. This may suggest that when food availability is not limited for breeding seabirds, the choice of when to leave the nest to forage may be more strongly dependent on individuals' current body conditions or other environmental factors.

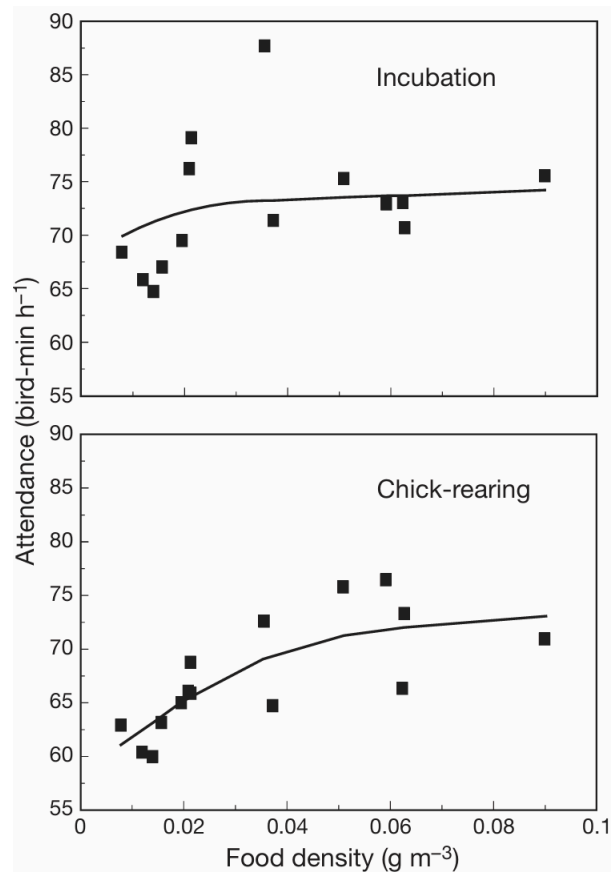


Figure 1.8: Model-averaged fit of the non-linear relationship between attendance during incubation and chick-rearing versus local prey density for *Uria aalge*. Fitted curve based on Akaike information criterion weights. Adapted from Harding et al. (2007).

1.5.3 Environmental conditions

Seabird colony attendance is found to be influenced by various environmental conditions, such as sea surface temperature, weather patterns, windspeed, and tidal or wave heights (Henson et al., 2007). Strong wind events are found to negatively impact the length of foraging trips for breeding Little Penguins (Saraux et al., 2016). Little Penguins were found to take longer foraging trips when wind conditions were extreme, an observation particularly evident during the post-guard period. However, during the incubation and guard phases, intense wind was found not to have a significant effect on the duration or nature of foraging trips. This may be due to parents prioritising returning to their chicks regardless of wind conditions, as eggs and chicks are in a more vulnerable state during these stages.

Sea surface temperature, referred to here as SST, is the temperature at the surface of the ocean. Lower SSTs have been shown to result in higher prey capture success by Little Penguins (Carroll et al., 2016). As SSTs elevate, prey capture success begins to positively correlate with longer foraging trips, and negatively with prey capture success — this is due to SSTs affecting prey populations (Carroll et al., 2016). Furthermore, a paper looking at timing of breeding in South-East Australia Little Penguin colonies has found peak egg-laying to occur when SSTs around the breeding colony are low, and when chlorophyll levels are high (Berlincourt & Arnould, 2014). Lower SSTs may serve as a signal of high prey availability, potentially triggering the onset of breeding.

1.5.4 Breeding pair behaviours and responsibilities

Paired female and male Little Penguins contribute relatively equally to parenting, sharing responsibilities such as incubation and chick rearing. However, males and females typically possess slightly different body condition due to variations in body size and weight (Arnould et al., 2004). As noted above, body condition is a factor that influences foraging behaviour. During the winter/non-breeding season, foraging trip lengths between sexes were found not to differ significantly even though females tended to forage over significantly larger areas (mean = 1983 km²) than males (mean = 841 km²) across the observation period (McCutcheon et al., 2011). However, findings from Saraux et al. (2016) show that the average amount of food provided to chicks by female Little Penguins during post-guard (249 ± 2 g) is less than by males (276 ± 2 g). Conversely, Bethge et al. (1997) reports male Little Penguins travelling longer distances when foraging than the female birds. However, the sample size in this study is small, and there may be inaccuracies in sex identification.

Differences in the length of foraging trips were observed between sexes during incubation, but not during the guard period (Saraux et al., 2016). In contrast to the findings in the preceding paragraph, Saraux et al. (2016) observed females taking longer foraging trips (4.03 ± 0.01 days) on average in comparison to males (3.18 ± 0.01 days) during incubation. Kato et al. (2008) found that male Little Penguins at Phillip Island performed twice as many one-day trips as their female counterparts during the incubation period (see Fig. 1.8). Notably, longer trip durations observed during the study were overwhelmingly undertaken by females.

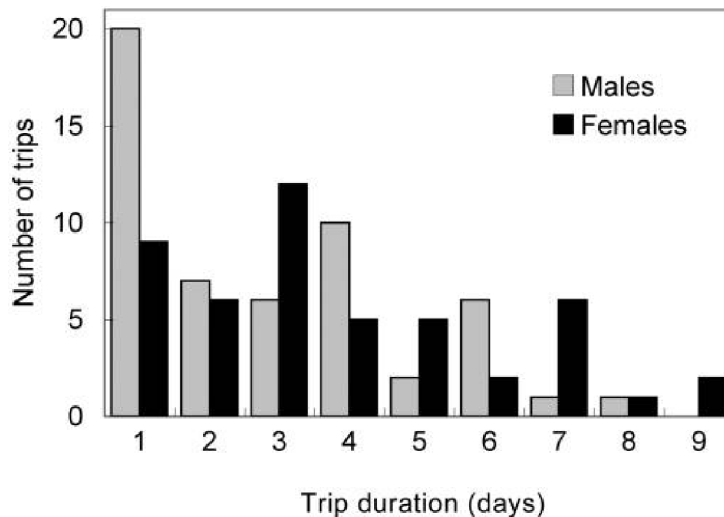


Figure 1.9: Foraging-trip duration of male and female Little Penguins during the incubation stage. Adapted from Kato et al. (2008).

1.5.5 Ages of breeding pairs

The breeding performance of Little Penguins increases with age until individuals reach approximately eight years old. Past this age, breeding performance generally starts to decline (Nisbet & Dann, 2009). The success of the breeding season, as discussed above, is largely influenced by foraging trips to sustain both members of the breeding pair as well as any offspring. Female Little Penguins between the ages of 5 to 10 years are observed to have high diving competency, requiring fewer diving attempts and exhibiting better foraging performance overall. This age group likely consists of individuals that have sufficient foraging experience from past years while still being in prime body condition (Zimmer et al., 2011). This age group also has been observed to produce a higher number of fledgling chicks compared to younger and older individuals (Nisbet & Dann, 2009). A separate paper found that Little Penguins of both sexes increase in foraging ability until individuals are 10 years old (Saraux & Chiaradia, 2022). Overall, Little Penguins between 5 and 10 years old are expected to undertake more efficient foraging trips during the breeding season, which allows them to attend to their chicks more frequently and effectively (see Figure 1.10) (Nisbet & Dann, 2009).

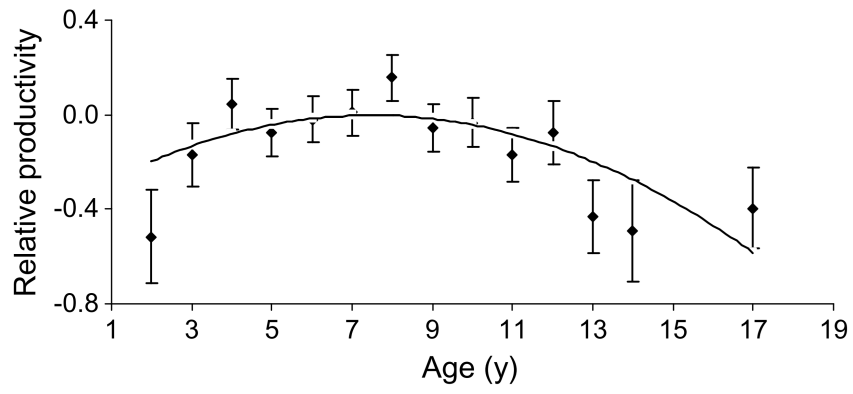


Figure 1.10: Dependence of relative productivity in Little Penguins on age. Data plotted are mean \pm 1 SE. Adapted from Nisbet & Dann (2009).

1.6 Port Tarakohe nestbox colony

Port Tarakohe, depicted in Figure 1.11, is situated on Ligar Bay in the Golden Bay/Mohua area, located in the Tasman District of the South Island in New Zealand. In 2019, the Mohua Penguin Trust was established to protect and improve the existing Little Penguin population in Golden Bay. Their initiatives have included the building, placement, and replacement of nestboxes, as well as auxiliary shelters and rat traps. Notably, new wooden nestboxes were built and placed around the port by volunteers in May 2020, adding to and replacing the existing nesting options for resident Little Penguins. The result of this work is 150 total nestboxes situated around Port Tarakohe.

This site was selected due to the work of Mohua Penguin trust in securing and maintaining the colony, providing a substantial foundation for research. The colony has been subject to long-term nestbox monitoring, meaning that individual birds are likely more habituated to the contact of researchers and volunteers, reducing behavioural disruption. The relative inaccessibility of the site also limits interference from the public. This site does not contain artificial lighting, however, its location within a port means that some illumination may be present from the dock or from nearby boats.



Figure 1.11: Photograph of Port Tarakohe, looking southeast towards the hills.
Captured in October 2022.

1.7 Outline of thesis

This thesis examines the colony attendance of Little Penguins, observing patterns both at an overall colony level and within individual breeding pairs. Daily and weekly nestbox checks were conducted from late winter in 2022 to the end of summer in 2023 to determine trends in overall colony attendance as well as during various breeding stages, particularly incubation and guard. This thesis aims to provide new insight into the Little Penguin's breeding behaviour through their comings and goings from their nestboxes. Observations and data analysis on the length of incubation periods, incubation spells and guard periods from this study will be compared with findings from previous studies. Furthermore, the attendance of non-breeding birds will be analysed in relation to the lunar cycle to uncover any patterns.

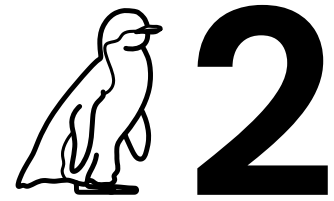
Chapters 2 and 3 of this thesis will be treated as separate individual papers, each with their own body of results and separate discussions. Chapter 4 concludes with an integrated, high-level overview of the study's findings and proposes suggestions for further research.

Questions this thesis aims to answer:

- Chapter 2 What patterns can be found from observing the weekly and daily colony attendance of Little Penguins at Port Tarakohe from late winter to early summer?
- Does the colony attendance of non-breeding Little Penguins confirm the three-week cycle demonstrated by Reilly & Cullen (1981)?
- Upon investigation of the data from daily monitoring, is there any relation between the attendance of non-breeding Little Penguins and lunar phases?
- Chapter 3 What patterns or observations can be extracted from the daily nestbox attendance data for breeding pairs and between breeding pairs, particularly during incubation?
- How does the statistical analysis of incubation periods, incubation spells, and guard periods from this study differ from that of previous findings?

How do the incubation spells exhibited by male and female individuals within breeding pairs compare to each other, and are these similar to previously reported results?

Does the length of the guard period for single-chick clutches differ from that for clutches of multiple chicks? How does this compare to previously reported results?



Colony Attendance of the Little Penguin

2.1 Introduction

2.1.1 The Little Penguin

Little Penguins (*Eudyptula minor*) are the smallest extant penguin species, standing approximately 30 cm high and weighing about one kilogram when fully grown. The Little Penguin is known as the *kororā* in Māori – in Australia it is called the *fairy penguin*. This species is found along the west coast of Australia, as well as the coasts of mainland New Zealand and surrounding islands. They have a slate-blue plumage with a white underside (Marchant & Higgins, 1990).

The breeding season of Little Penguins usually runs through winter and into summer. Egg-laying occurs as early as May until December (Reilly & Cullen, 1981). Breeding begins with courtship, with Little Penguins returning to the colony approximately a month before egg-laying begins (Chiaradia & Kerry, 1999). Male Little Penguins tend to arrive back before the females. Little Penguins typically lay two eggs in a clutch, but occasionally just a single egg (Reilly & Cullen, 1981).

Once eggs are laid, males and females take turns to incubate them. One member will stay in the nest while the other is out feeding in the ocean. This incubation stage takes approximately 35 days (see Table 1.2) (Kato et al., 2008; Kemp & Dann, 2001). Once the eggs hatch, the parents guard the chicks in shifts, with one bird staying in the nest while the other forages for food. The period over which Little Penguins guard their chicks typically ranges from 15 to 21 days (see Table 1.3). As the chicks grow and require more food, both parents eventually leave the nest to forage. This is often referred to as the post-guard period.

2.1.2 Colony attendance during non-breeding seasons

Little Penguins, like most other penguins, return to their colonies one to two hours after sunset and depart one to two hours before sunrise. Many penguin species spend some months at sea away from their colony during the autumn/winter months post-moult (Gales & Green, 1990). Little Penguins, however, are considered inshore foragers that stay relatively close to their colonies year-round. The non-breeding season occurs sometime between late January to approximately May depending on the colony and location. Little Penguins return to their colonies typically between February and March to moult (Reilly & Cullen, 1983). During moult, birds will stay in their nest for two to three weeks as they shed their old feathers and grow new ones, during which time overall colony attendance is high. After the moulting process is complete, Little Penguins spend most of their time at sea foraging during autumn to early winter. The length of foraging trips during this time may extend up to 49 days, but the vast majority of trips observed are completed in a single day (McCutcheon et al., 2011).

Reilly & Cullen (1981) conducted research on the Little Penguin colony at Phillip Island, Australia, utilising weekly nest checks to record that individuals congregated at the colony site on a three-week cycle (Figure 2.1).

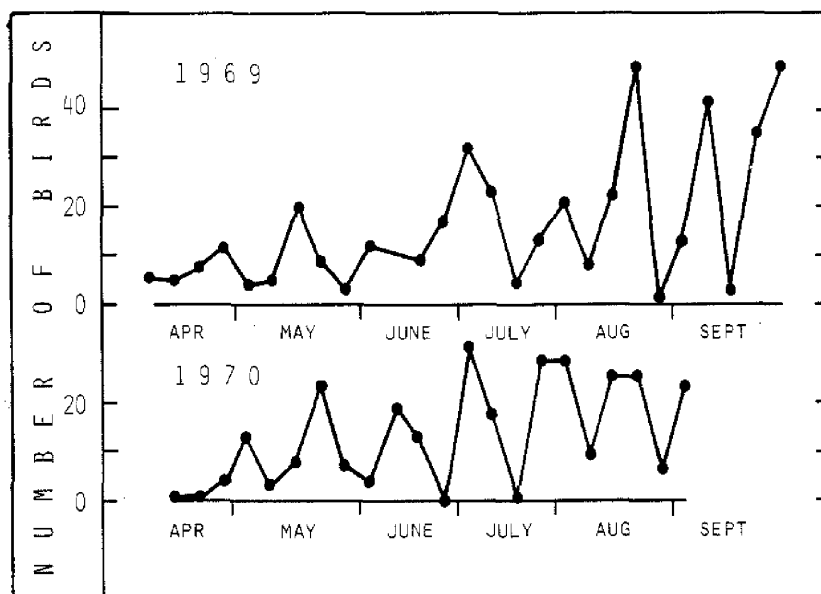


Figure 2.1: Number of Little Penguins in the Summerland colony at weekly checks in 1969 and 1970. Adapted from Reilly & Cullen (1981).

2.1.3 Colony attendance during the breeding season

Breeding adult penguins arrive at the colony to initiate courtship about four weeks before egg-laying (Chiaradia & Kerry, 1999). Males usually return to the colony before females (Chiaradia & Kerry, 1999), and remain at the nest site longer than females during this initial period. The supposed reason for males typically arriving first is so they can establish a territory and secure a site for the female partner to lay eggs.

Male and female Little Penguins share the parental role relatively equally, with both participating in egg incubation, chick care and feeding the young (Dann & Cullen, 1990). Incubation spells are the periods between foraging trips in which parents take turns to incubate. Table 2.1, which depicts data on the lengths of male and female incubation spells, does not reveal any significant differences between the sexes.

Table 2.1: Mean lengths (days) of incubation spells for sexes individually and cumulatively recorded in previous papers.

Incubation spell (Both sexes)			Male incubation spell			Female incubation spell			Nest check frequency	N° of birds	N° of nests	Location	Year	Reference
Mean (days)	SE	<i>n</i>	Mean (days)	SE	<i>n</i>	Mean (days)	SE	<i>n</i>						
4.8	1.20	17									Phillip Island, AUS	1992	Collins et al. (1999)	
3.9	0.60	16									Phillip Island, AUS	1993	Collins et al. (1999)	
3.4			3.5	0.17	54	3.4	0.32	49	Daily	106	53	Phillip Island, AUS	1995	Chiaradia & Kerry (1999)
			3.0	0.22	10	4.1	0.38	10	Every 2 days	20	10	Phillip Island, AUS	2004	Kato et al. (2008)
			3.2	0.01		4.0	0.01		Daily	222		Phillip Island, AUS	2001- 2011	Saraux et al. (2016)
			2.9	0.30	18	3.2	0.40	20	Daily	64	34	Oamaru, NZ	1998	Numata et al. (2000)
			6.2	0.60	23	5.2	0.50	15	Daily	74	39	Motuara Island, NZ	1998	Numata et al. (2000)

However, in a study observing the Little Penguin colony at Phillip Island by Kato et al. (2008), females were found to take foraging trips averaging one day longer than males, perhaps due to requiring additional resources to replenish their body condition after egg-bearing. Conversely, Saraux et al. (2011a) found that sex does not significantly influence foraging trip length during the breeding season. In another study, the level of overall parental care between sexes did not differ significantly despite females providing slightly less food to their chicks (Saraux et al., 2011b). Individual variability in foraging trips may depend more upon location, environmental conditions, or differences in body condition than upon sex. During the stage of chick guard, both parents take turns going on single-day foraging trips while the other is present with the chicks. The nature of these trips does not differ significantly between male and females (Chiaradia & Kerry, 1999).

2.1.4 Colony attendance in relation to lunar phases

Little Penguins are known to be diurnal hunters, relying mainly on visual cues when diving for food. Like other species of penguins, such as the Galapagos (*Spheniscus mendiculus*), Yellow-eyed (*Megadyptes antipodes*), and African (*Spheniscus demersus*) penguins, Little Penguins leave and return to their colony during the dark hours close to dawn and dusk (Boersma, 1974; Darby et al., 1990; Petersen et al., 2006).

A research paper by Rodriguez et al. (2016) examining the arrivals and departures of Little Penguins at the Summerland Peninsula, Australia in relation to the lunar cycle revealed that the Little Penguins were less likely to make a return to the colony during full-moon nights. However, the smaller Little Penguin population at Lipson Island Conservation Park did not exhibit the same phenomenon (Iasiello & Colombelli-Négrel, 2025). Looking at seabird behaviour more generally, Bastos et al. (2022) in a recent study on Cory's shearwaters found that individuals adapted their nest arrivals to align with the onset of a waning moon and exhibited significantly later arrivals during waxing moons.

2.1.5 Aims of Chapter 2

This chapter aims to uncover and analyse trends in the colony attendance of Little Penguins nesting at Port Tarakohe, addressing gaps in existing attendance research by examining the patterns of both breeding and non-breeding birds with daily and weekly nestbox monitoring. Multiple categories

of nestbox-related data have been recorded for examination, including the number of nestboxes containing both eggs and chicks, as well as the numbers of male and female Little Penguins present in singles and pairs.

The data to be presented reveals various patterns of attendance in relation to breeding season stages, which supplement or contextualise results from previous papers. Newly-observed patterns of breeding season colony attendance in relation to lunar phases will also be presented and discussed.

2.2 Materials and methods

2.2.1 Study site and physical monitoring

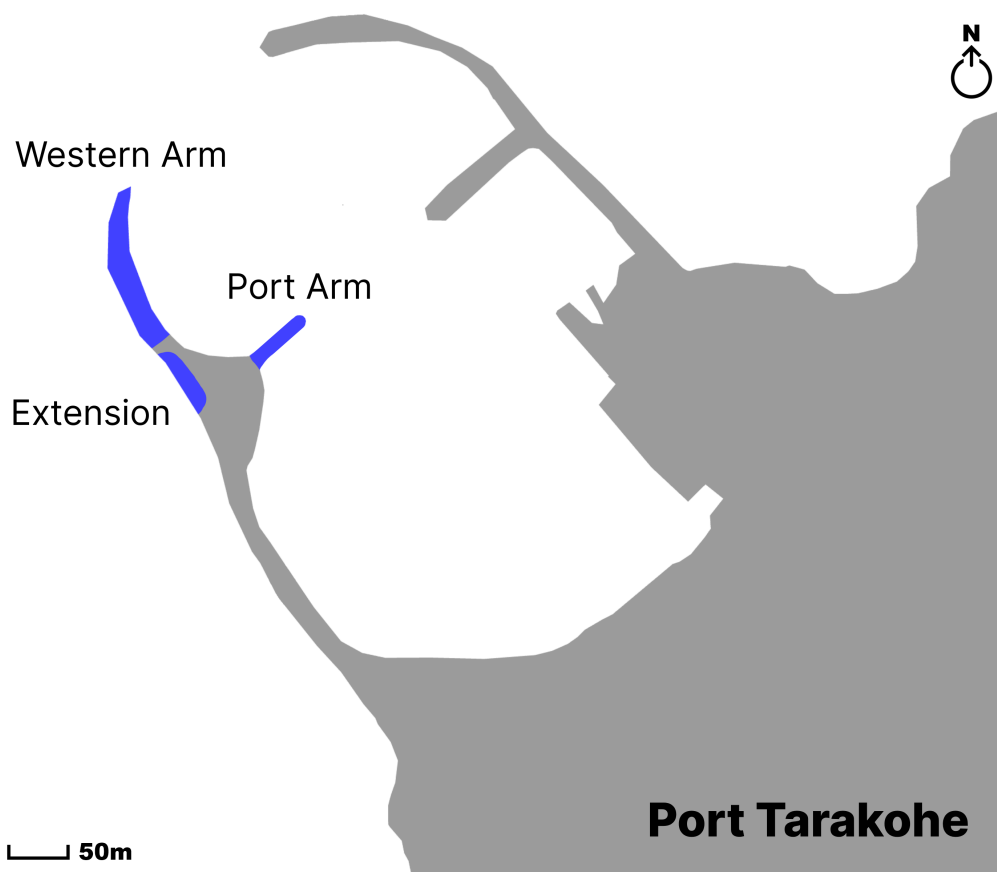


Figure 2.2: Map of Port Tarakohe, Golden Bay, New Zealand. The three coloured and labelled segments indicate areas of nestbox placement.

This study was conducted from July 2022 to January 2023 at Port Tarakohe, Golden Bay in New Zealand, under a protocol approved by the Massey University Animal Ethics Committee (09/76) and the Department of Conservation (Permit ECHB-23237-RES). The Little Penguin colony present there spans three distinct areas as depicted in Figure 2.2, referred to as the Western Arm, Port Arm, and Extension. Nestboxes numbered 1 through 100 are placed along the Western Arm, 101 through 120 along the Extension and 121 through 150 along the Port Arm. Weekly or biweekly (that is, every two weeks) nestbox checks were performed from 4 July to 2 September, after which the monitoring frequency increased to once per day. Daily monitoring took place from 3 September until 6 November, after which the original monitoring pattern resumed until 3 February. For brevity, these periods of less-frequent monitoring are referred to as ‘weekly checks’.

Data recorded at each nestbox included the number and identity of adult Little Penguin individuals, as well as the number of chicks and eggs. Individuals were identified using a handheld reader to scan previously-implanted microchips. Note that penguins were not microchipped as part of the current study, but were tagged for other purposes by Penguin Trust personnel under their own Department of Conservation permits. Incidental data was also noticed and recorded, including events such as the discovery of new nesting material, digging of soil, or fresh faeces inside nestboxes.

To help determine nestbox activity in cases where individual birds were not sighted during a monitoring check, a gating method was employed in the style of Chiaradia & Kerry (1999). Empty nestboxes were marked with a short wooden stick placed upright — a gate — blocking the entrance to the nestbox. ‘Gate up’ then refers, in subsequent checks, to an undisturbed, upright stick — conversely, ‘gate down’ refers to instances where stick has been moved and/or is no longer standing. This method provided information on whether a penguin had entered a nestbox.

As an additional note — nestboxes are labelled in the results for this chapter (and the next) as either ‘breeding’ or ‘non-breeding’, referring to nestboxes that either did or did not contain eggs or chicks. Birds are also referred to as ‘breeding’ or ‘non-breeding’ based on their observed reproductive output over the course of the study, but may separately be named ‘single’ when they are found to be the sole adult individual (that is, with or without eggs or chicks) occupying a nestbox.

2.2.2 Assignment of sex

A total of 205 unique individuals were found in nestboxes from 1 July 2022 to 31 January 2023. 104 males and 101 females were recorded, with 93 breeding pairs present during the breeding season. Morphometric data, including beak shape and the proportion of upper and lower mandibles, had been used to determine individuals’ sexes prior to the study’s commencement, with multiple reassessments taking place over several preceding years. Inconsistencies in recorded individual sexes were rectified where possible during the study, primarily through live observation of breeding pairs in nestboxes.

2.2.3 Lunar phase data

Lunar phase data were mapped to observation days post hoc, using data from the online service at www.timeanddate.com/moon/phases/. Each day from 4 July to 28 November 2022 was assigned a corresponding ‘moon day’ with a number from 1 to 30, with Day 1 referencing a new moon. Moon days were divided into six groups of five days each, specifically: 1–5, 6–10, 11–15, 16–20, 21–25, 26–30.

2.2.4 Statistical analysis

Data in this chapter were analysed and plotted using GraphPad Prism 10 software, as well as the SciPy Python package v. 1.13.1 running in a Jupyter Notebook within the Google Colaboratory cloud environment. Welch’s t -test was performed to determine differences in the numbers of single females and single males present during the weekly nestbox checks in July. Additionally, the Kruskal-Wallis non-parametric test was used to find any significant difference between the mean number of non-breeding birds recorded across the lunar cycle. An alpha level of 0.05 was used for all statistical tests.

The period between peaks of non-breeding bird attendance was estimated by fitting a sum of Gaussian functions to data-points between 4 July and 19 September.

The general formula for the Sum of Gaussians is:

$$y(x) = \sum_{i=1}^N a_i \exp\left(-\frac{(x - \mu_i)^2}{2\sigma_i^2}\right) + d$$

where N is the number of Gaussian peaks (3, as is observable later in Figure 2.10), and for the i th peak:

- a_i is the amplitude
- μ_i is the mean, or centre
- σ_i is the standard deviation, or spread
- d is the baseline offset.

This formula serves as a model to input into SciPy, which can then fit a curve to the relevant data with `scipy.optimize.curve_fit` and plot the result. The Python script to perform this plot can be found in Appendix A.

2.3 Results

2.3.1 Little Penguin nestboxes

2.3.1.1 Occupied nestboxes

The total number of nestboxes with one or two penguins — referred to as occupied nestboxes — increased from 0 in early July to a peak of 72 in mid-July, declined to 7 in late July, then increased again in August (Figure 2.3). The frequency of nestbox checks in August and early September was too low to indicate whether a similar peak and subsequent decline occurred in August. On 3 September, when daily checks began, there were 57 occupied nestboxes. The number of occupied nestboxes sharply increased to around 85 in mid-September, then slowly rose to the low 90s, remaining consistent until the last daily check on 6 November. Weekly checks from mid-November until mid-December revealed a steady decline in the total number of occupied nestboxes, with 41 on 13 December. The number of occupied nestboxes declined further to 22 in mid-January and early February.

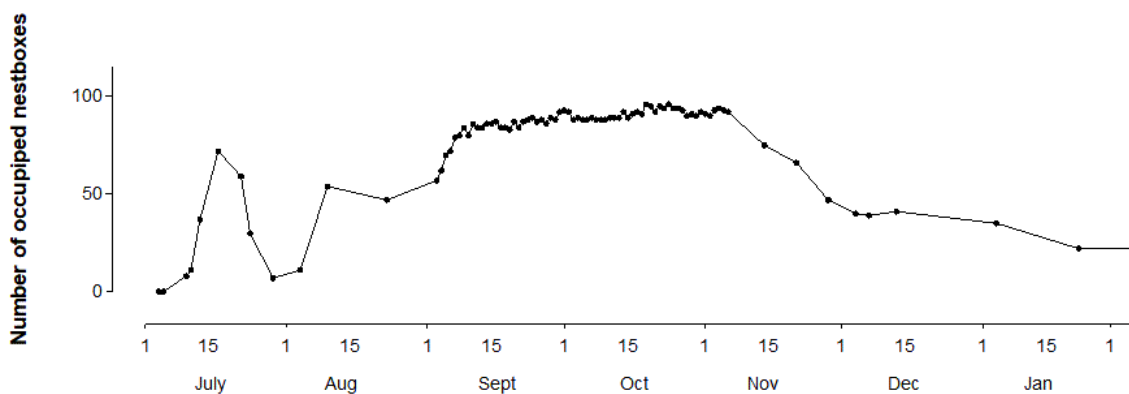


Figure 2.3: Total numbers of occupied nestboxes from July 2022 to February 2023.

The total numbers of occupied nestboxes that were classified as non-breeding (only adults present) or breeding (contained eggs or chicks) are shown in Figure 2.4. The first nestboxes with eggs were found on 22 July. The first chicks were found on 3 September, and eggs or chicks were present in nestboxes until 3 February. Non-breeding and breeding nestboxes are considered in detail below.

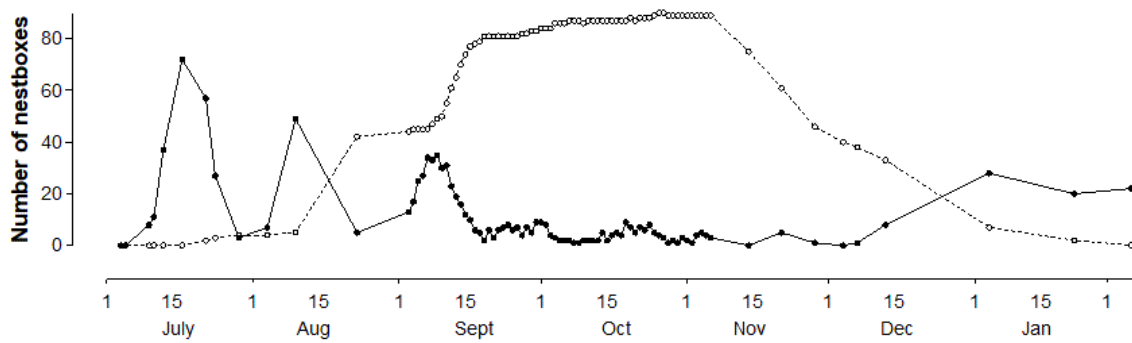


Figure 2.4: Total numbers of nestboxes occupied by non-breeding —●— and breeding ---○--- birds from July 2022 to February 2023.

2.3.1.2 Non-breeding nestboxes

There were regular peaks and troughs in the total number of non-breeding nestboxes — that is, nestboxes with one or two adults and no eggs or chicks; see Figure 2.5. The number of non-breeding nestboxes increased from 0 at the beginning of July to a peak of 72 nestboxes within a fortnight, then declined to three nestboxes in late July. While there were only three nestbox checks in August, the available data indicates that it is likely that another wave occurred.

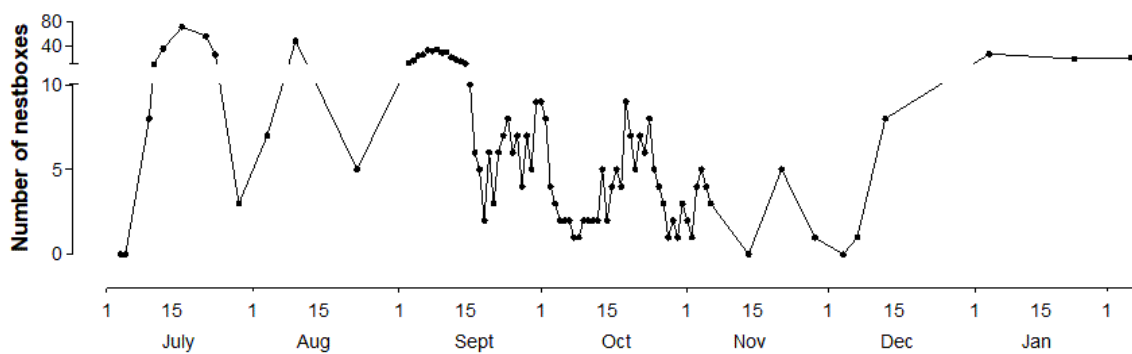


Figure 2.5: Total numbers of non-breeding nestboxes from July 2022 to February 2023.

Daily nestbox checks from 3 September revealed cycles involving steady increases in the number of non-breeding nestboxes over approximately 5 days, peaking at around 30 to 34 nestboxes, followed by steep declines to a minimum of two nestboxes approximately 10 days afterwards. These low-amplitude cycles continued through October and into early November. Irregular nestbox checks from early November until mid-December indicated that there may have been another peak in late November. The number of non-breeding nestboxes increased from mid-December into January as penguins likely returned to moult after breeding.

The total numbers of non-breeding nestboxes with one adult and with two adults are shown in Figure 2.6. There were more nestboxes occupied by a pair of birds than by one bird in the July and August peaks, and roughly equal numbers in the September peak. The quantities of non-breeding nestboxes with one bird and with two birds demonstrate synchronised low-amplitude, high-frequency cycles in late September and October. In contrast, from late November until early February, there were more non-breeding nestboxes with one adult than two adults.

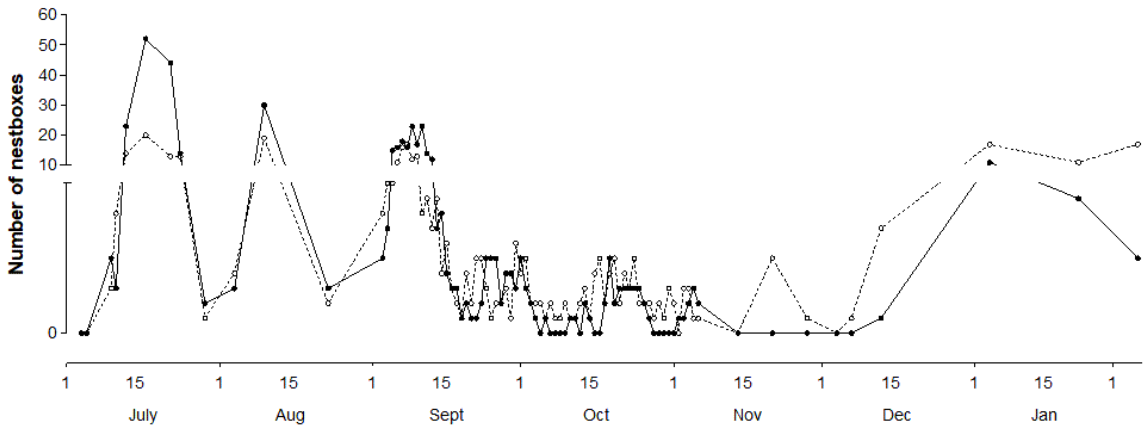


Figure 2.6: Total numbers of non-breeding nestboxes with one bird —●— or two birds ---○--- from July 2022 to February 2023.

2.3.1.3 Breeding nestboxes

In 2022, egg-laying at the Port Tarakohe Little Penguin colony began in July. The first two eggs were laid in separate nestboxes on 21 July, with two more eggs being found in other nestboxes on 23 and 24 July. Five nestboxes contained eggs on 10 August, then at the next nestbox check on 23 August, 42 nestboxes contained eggs (Figure 2.7). These nestboxes contained eggs from the first two periods of egg-laying. At the next nestbox check, on 3 September, there were 41 nestboxes with eggs. The number of nestboxes with eggs remained constant for four days, then increased to a peak of 75 nestboxes on 18 September. The number of nestboxes with eggs then declined for 10 days, remained relatively constant for 18 days, until 15 October, then declined to another plateau 10 days later. The plateau in numbers of nestboxes with eggs continued until the last daily nestbox check on 6 November, followed by a steady decline until no eggs were present in nestboxes on 7 December.

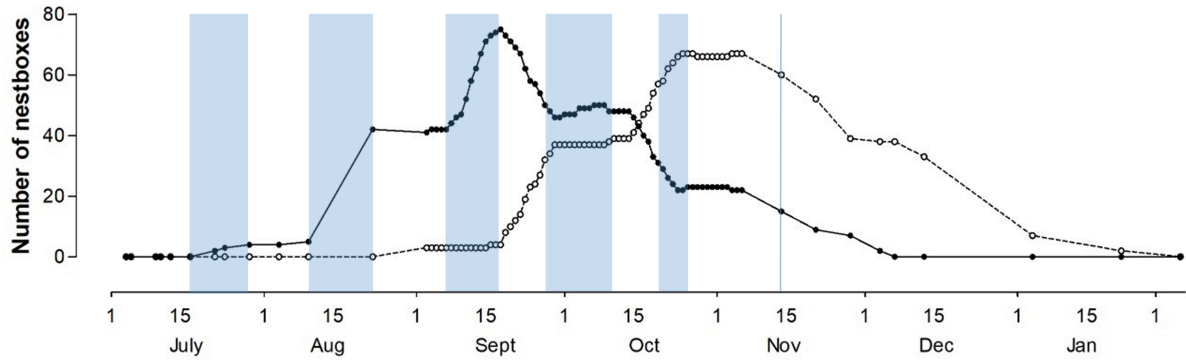


Figure 2.7: Total numbers of nestboxes with eggs —●— or chicks ---○--- from July 2022 to February 2023. Blue-shaded areas indicate new clutches being laid.

As indicated by the blue-shaded areas in Figure 2.7, distinct waves of egg-laying occurred over 17 July to 29 July, 10 August to 23 August, 7 September to 18 September, 27 September to 11 October, and 20 October to 9 November — more simply, a sequence of one small wave, two big waves, two small waves. The blue line in November signifies the laying of a final replacement clutch.

Predicted hatch dates for the first four clutches of the season were calculated to be from 28 August to 1 September (see Figure 2.7). Although the chicks from one clutch died, the other three nestboxes contained chicks by 3 September. A fourth nestbox contained chicks on 18 September, after which there was a steady rise to 37 nestboxes containing chicks from 18 September to 29 September. These nestboxes contained chicks from the first two waves of egg-laying. The number of nestboxes with chicks rose again in mid-October, followed by a plateau that continued until daily checks ceased on 6 November. The number of nestboxes with chicks declined from mid-November through December, with seven nestboxes containing chicks on 4 January. The first date after all chicks had fledged and no nestboxes contained chicks was 3 February.

One or both penguins of a pair may be present in a nestbox during egg-laying, but during most stages of the breeding season it is usual for only one parent to be found in a nestbox at a time. The total number of breeding nestboxes with one adult bird present generally indicates the total number of nestboxes where an adult was either incubating eggs or guarding chicks. The first day where birds were found to be incubating eggs was 22 July (see Figure 2.8). The number of breeding nestboxes with one adult increased to 5 by 10 August, then to 42 at the subsequent check on 23 August. At the next nestbox check, on 3 September, the number of breeding nestboxes with one adult had decreased to 41,

indicating that one breeding attempt had failed. The number of nestboxes with one bird increased to 78 on 18 September, remained relatively constant for approximately two weeks before a steady decline until mid-November. All nestboxes were found to be empty by 4 January 2023.

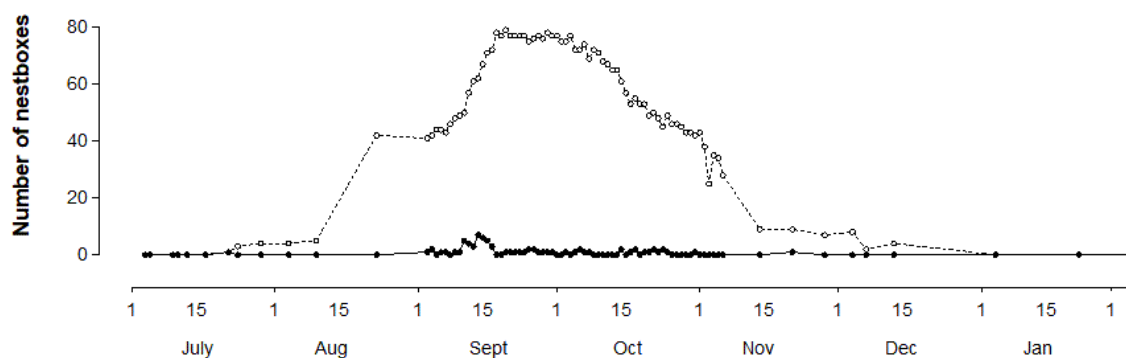


Figure 2.8: Total numbers of breeding nestboxes with one ---○--- or two —●— adults from July 2022 to February 2023.

The numbers of breeding nestboxes with two adults present remained low throughout the breeding season, apart from a five-day period in mid-September when there were three to seven breeding nestboxes with both birds.

2.3.2 Non-breeding and breeding birds

2.3.2.1 Total number of birds

Between July and August there were two cycles in attendance at the colony, with numbers increasing from 0 on 4 July to 124 birds on 17 July, then decreasing to 9 on 29 July (Figure 2.9). The peak of 124 birds was the greatest number of penguins found in nestboxes in 2022. Although nestbox checks were infrequent in August, there is likely another peak in attendance during mid-August, followed by a trough and then an increase again from late August up until the start of daily checks at the beginning of September. After a peak in early September, the total number of birds declined steadily until mid-November, remained relatively constant until early December, increased from the last December nestbox check on 13 December to the next check on 4 January (39 penguins), then remained relatively constant until early February 2023. The total number of birds shown in Figure 2.9 has a similar overall pattern to the total number of occupied boxes shown in Figure 2.3.

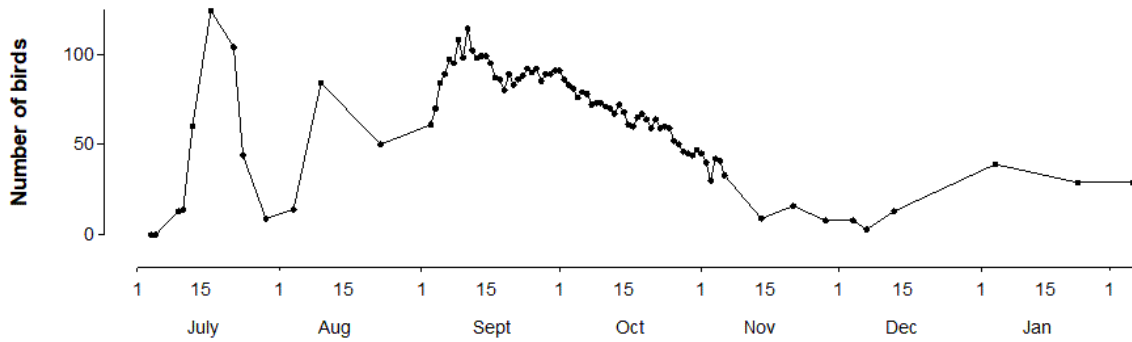


Figure 2.9: Total numbers of birds from July 2022 to February 2023.

2.3.2.2 Non-breeding birds

The total numbers of non-breeding birds and breeding birds are shown in Figure 2.10. There was a clear cycle in the numbers of non-breeding birds, with peaks of 124, 79 and 58 in birds in July, August, and September respectively. Nestbox checks were infrequent in August, so it cannot be assumed that the maximum number of birds in August was lower than in July. After the peak in early September, the number of non-breeding birds declined steeply to three on 19 September, increased to a broad peak of 11–13 birds in late September, then declined again to one bird on 8 and 9 October. Numbers of non-breeding birds increased to a broad peak from 19 to 24 October, declined to from 1 to 3 birds from 28 October to 2 November, then started increasing again. After daily checks ended on 6 November, the limited data indicates that there may have been small peaks in numbers of non-breeding birds in November and December, then numbers increased in January when birds had returned to the colony to moult.

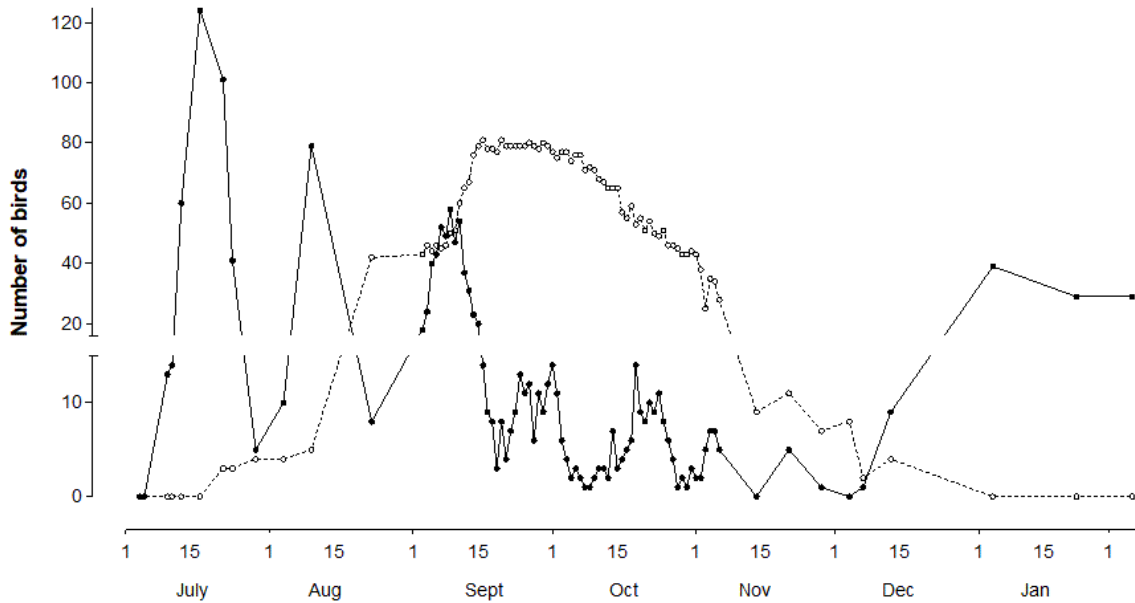


Figure 2.10: Total numbers of non-breeding —●— and breeding ---○--- birds from July 2022 to February 2023.

2.3.2.3 Breeding birds

The presence of breeding birds was first recorded on 22 July (three birds, see Figure 2.10) when eggs were first found in nestboxes (see Figure 2.7). The number of breeding birds remained low at weekly nestbox checks until 23 August, when 42 breeding birds were recorded. After daily nestbox checks began on 3 September, the number of breeding birds rapidly increased to 81 by 16 September and then remained relatively constant through the end of the month. A gradual decline occurred throughout the daily nestbox checks in October and November, and then further with weekly checks in December and January. The varying number of breeding birds present overall mirrors the number of nestboxes with one breeding bird (Figure 2.8) — most of the breeding birds recorded at any given time were occupying a nestbox with no other adults present.

2.3.2.4 Males

After weekly checks early in July found no birds present, an initial peak of 62 male birds was recorded at the colony on 17 July, with a subsequent drop to 6 male birds on 29 July (see Figure 2.11). While nestbox checks in August demonstrated fluctuating attendance, the low data resolution in that period obscures any potential patterns. After daily nestbox checks began on 3 September, the number of male birds steadily increased to 58 birds on 9 September, then gradually decreased as daily checks

continued to 6 November. Daily checks showed that the number of male birds rose and fell every two days from mid-September onwards. On 14 November, there were three male birds present in the colony. The number of birds increased to 13 birds before decreasing to zero on 7 December. There were 12 to 15 male birds present at weekly checks in January and early February.

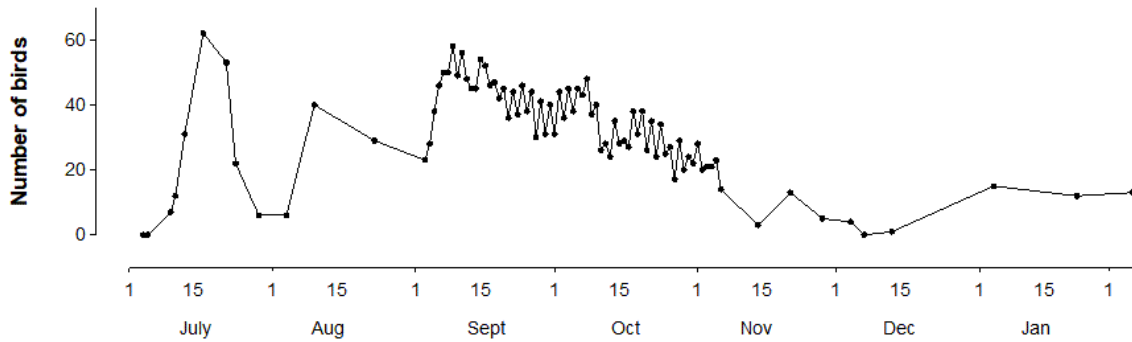


Figure 2.11: Total numbers of male birds from July 2022 to February 2023.

Figure 2.12 depicts the number of single males (that is, male adults observed to be alone in a nestbox) present. By comparison with Figure 2.10 and Figure 2.11, it is plain that the majority of males present during the attendance peak in July were recorded with a female counterpart. From late-August until January, most male birds present were single birds (e.g. 26 of 29 birds on 23 August). Daily nestbox checks revealed a small peak in the number of single male birds (8 and 9 September), a broader peak 10 days later, then another peak in early October. The number of single male birds then mirrors the total number of male birds from November through to January 2023.

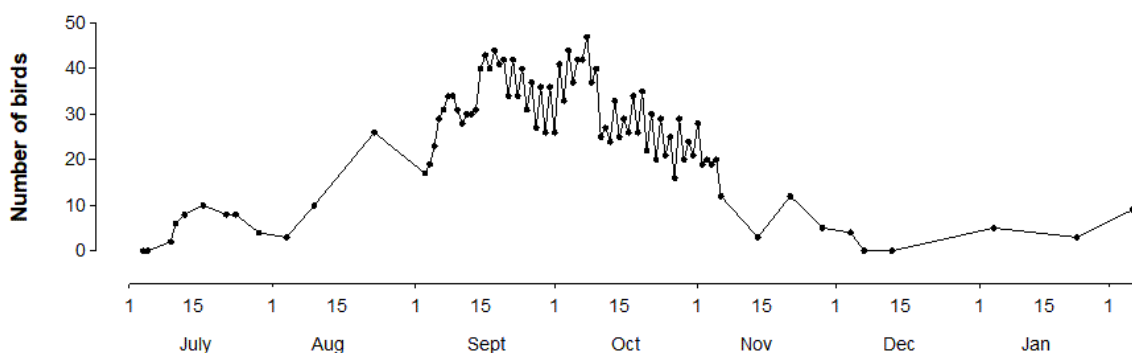


Figure 2.12: Total numbers of single male birds from July 2022 to February 2023.

2.3.2.5 Females

Figure 2.13 depicts the total number of female birds present during the weekly and daily nestbox checks from July 2022 to February 2023. In July and August, female attendance mirrors male attendance as seen previously in Figure 2.11. After daily checks begin on 3 September, the pattern of female attendance diverges from that of male attendance. Three distinct waves are recorded, with peaks on 11 September, 1 October, and 11 October.

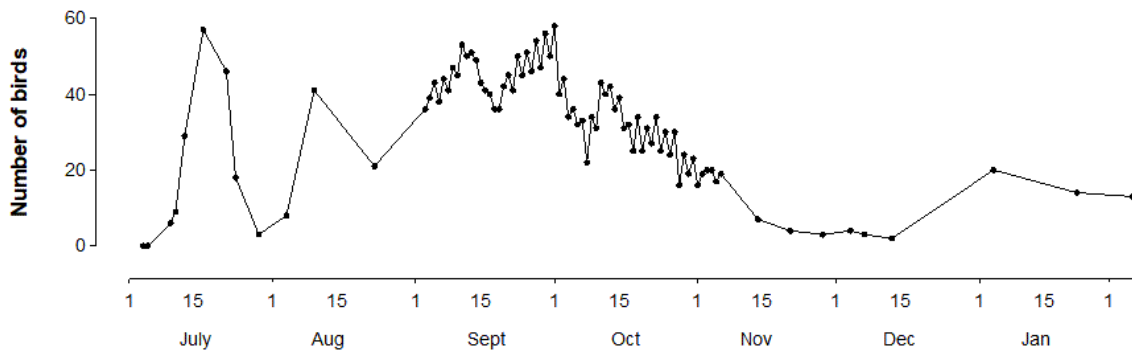


Figure 2.13: Total numbers of female birds from July 2022 to February 2023.

Figure 2.14 depicts the colony attendance of single females — that is; females present in a nestbox alone. When comparing this pattern with Figure 2.9, Figure 2.11, Figure 2.12, and Figure 2.13, it is evident that most females present during the attendance peak in mid-July were recorded with a male counterpart. During infrequent nestbox checks from early August to early September, single female attendance appears to increase gradually, contrasting with the marked peak and subsequent trough in overall female attendance shown in Figure 2.13.

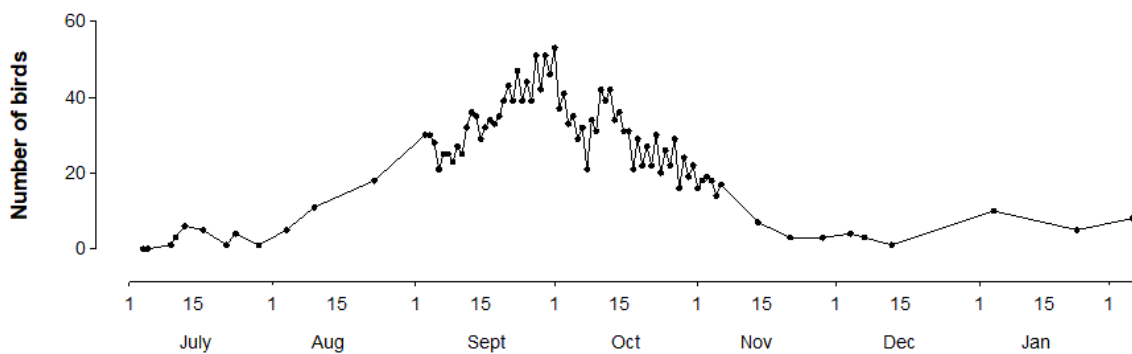


Figure 2.14: Total numbers of single female birds from July 2022 to February 2023.

2.3.2.6 Comparing males and females

Figure 2.15, which shows single male and female attendance numbers plotted against each other, reveals significant synchronisation in attendance patterns. After daily checks start on 3 September, the low-amplitude high-frequency variations in attendance mentioned earlier in Section 2.3.1.3 demonstrate inversion between sexes — that is, as the attendance numbers for one sex increase, the other decreases correspondingly and vice-versa. The frequency of this alternating pattern decreases to a single day in late October, and is visible through to the end of daily monitoring. Another significant difference to note is a spike in the attendance of single males in late November that is not also present for single females.

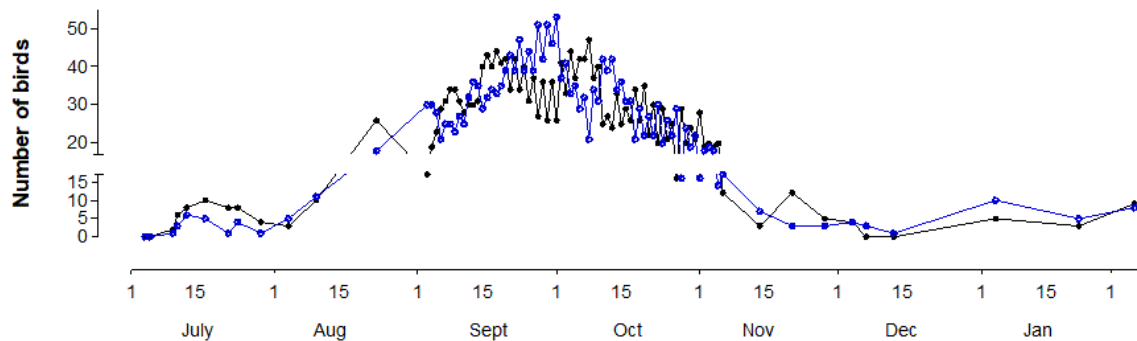


Figure 2.15: Total numbers of single male —●— and single female —●— birds from July 2022 to February 2023.

2.3.2.7 Breeding pairs

Figure 2.16 depicts the total number of pairs of Little Penguins present in nestboxes. Three large peaks are visible in July, August and early September. From late September onwards, fewer pairs were observed, with low-amplitude shifts visible until the end of daily monitoring. From mid-November through to mid-December, almost no pairs were recorded during weekly checks. Monitoring in January and February revealed an increase in pair attendance around the end of the breeding season.

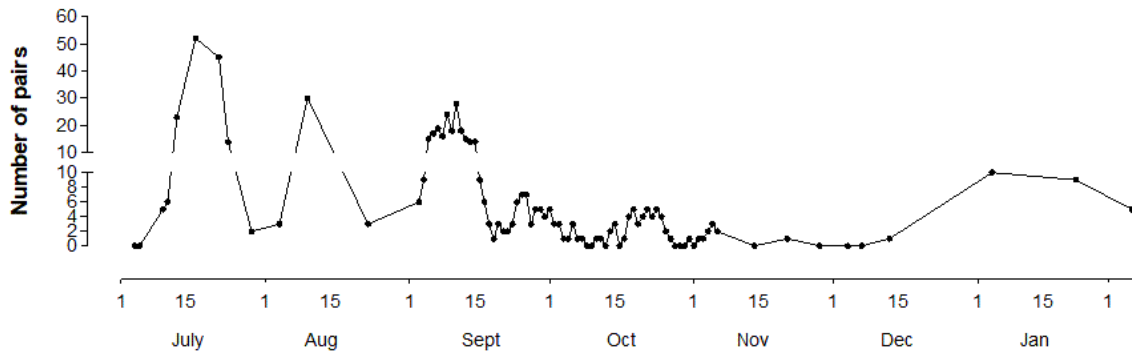


Figure 2.16: Total numbers of nestboxes containing two birds from July 2022 to February 2023.

2.3.3 Cycles of nestbox attendance of non-breeding birds

Five waves in non-breeding bird attendance were observed during nestbox checks from 4 July to 6 November (see Figure 2.10 and Table 2.2).

Table 2.2: Peaks and troughs in nest attendance for non-breeding birds from 4 July 2022 to 6 November 2022.

Date	Number of birds present	
	Trough	Peak
17 July		124
29 July	5	
10 August		84
23 August	8	
7 September		52
19 September	3	
1 October		14
8 & 9 October	1	
19 October		14
28 October	1	

Nestboxes were not checked daily before 3 September, so the timing and amplitude of peaks and troughs in non-breeding bird attendance cannot be precisely determined through July and August.

Period lengths for initial cycles in the nestbox attendance of non-breeding birds was estimated as in Section 2.2.4, resulting in Figure 2.17. The estimated average period over the three waves depicted is therefore 26 days (rounded to whole days).

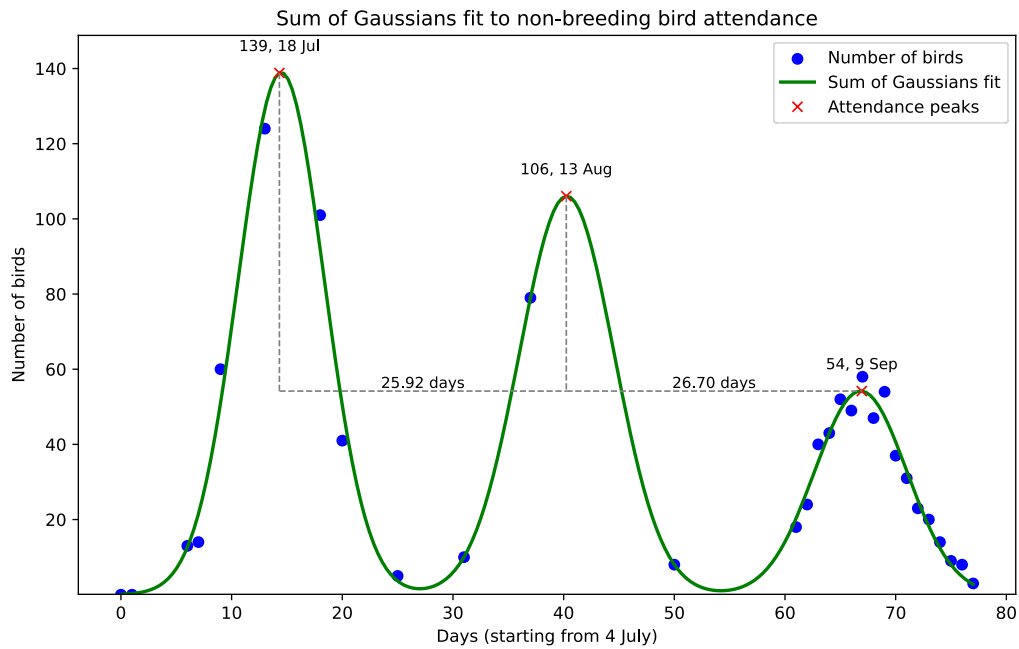


Figure 2.17: Total numbers of breeding birds for the first 77 days after 4 July, with an optimised sum of Gaussians fit.

2.3.4 Attendance of non-breeding birds in relation to lunar phases

As previously stated in Section 2.2.3, this study considers the new moon to occur on Day 1 of the 30-day lunar cycle. The number of non-breeding birds present at the colony ranged from 0 to 124 across all days of the lunar cycle (Figure 2.18). Peaks occurred in July (lunar days 15 to 26), August (infrequency of nestbox checks prevents accurate timing of the peak during lunar days 7 to 26), September (lunar days 8 to 24) and late September/early October (lunar days 26 to 30, then 1 to 10). The estimated period of the cycle in numbers of non-breeding birds present in nestboxes was 26 days (see Section 2.3.3), so each peak in numbers of birds would be expected to be earlier during the lunar cycle than the previous peak, as seen for the three peaks in Fig. 2.19.

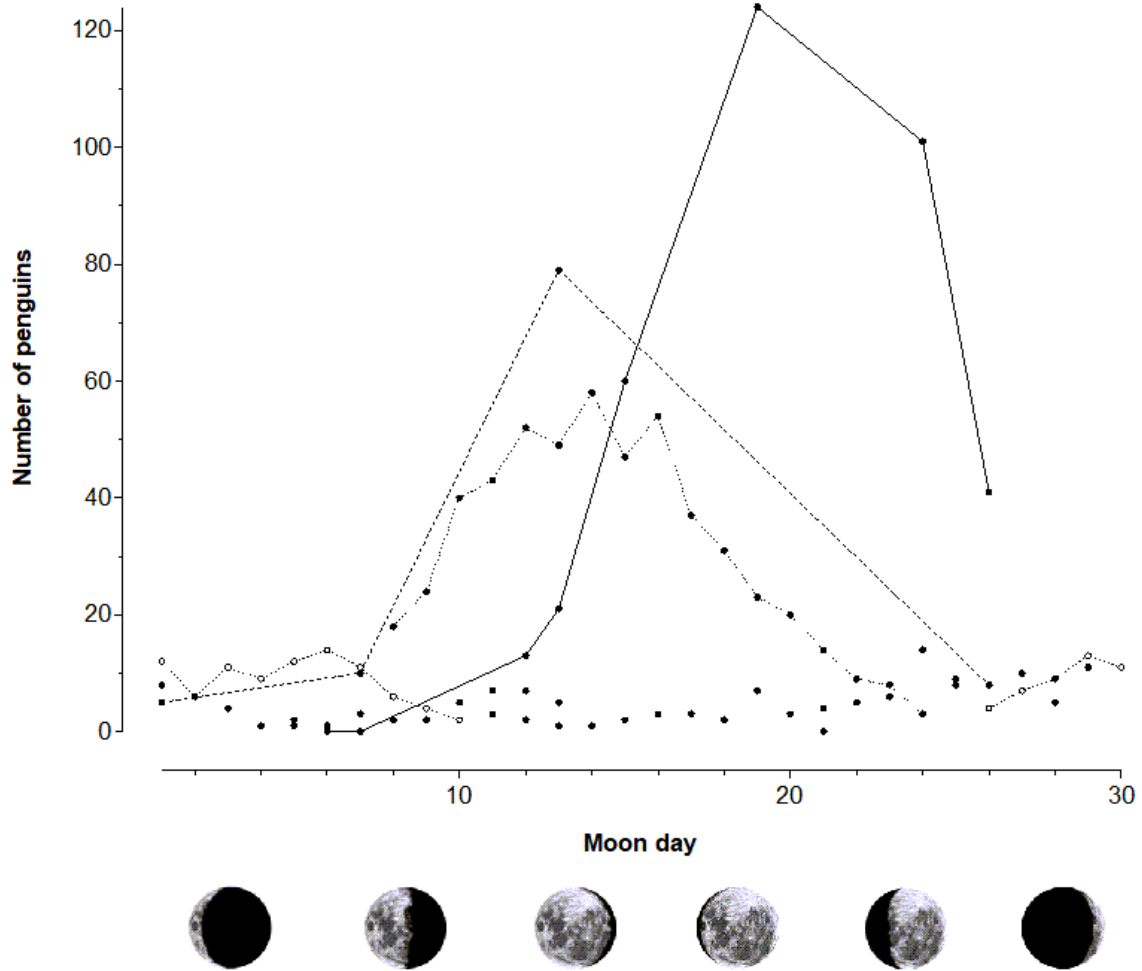


Figure 2.18: Total numbers of non-breeding birds in relation to lunar phases from July to November 2022. Peaks in numbers of birds are shown by lines in July —●—, August ---●---, mid-September ...●... and late September/early October ...○... Unlinked dots ● represent numbers of birds throughout October to November. Note that the peak in late September/early October began towards the end of the lunar cycle, so is shown on the graph as a discontinuous line.

The total numbers of non-breeding birds in relation to the day of the lunar cycle, grouped into five-day periods, are shown in Figure 2.19 and Figure 2.20. There were no significant differences between five-day periods in the mean numbers of non-breeding birds (Kruskal-Wallis test, $K5 = 6.516, p = 0.2592$).

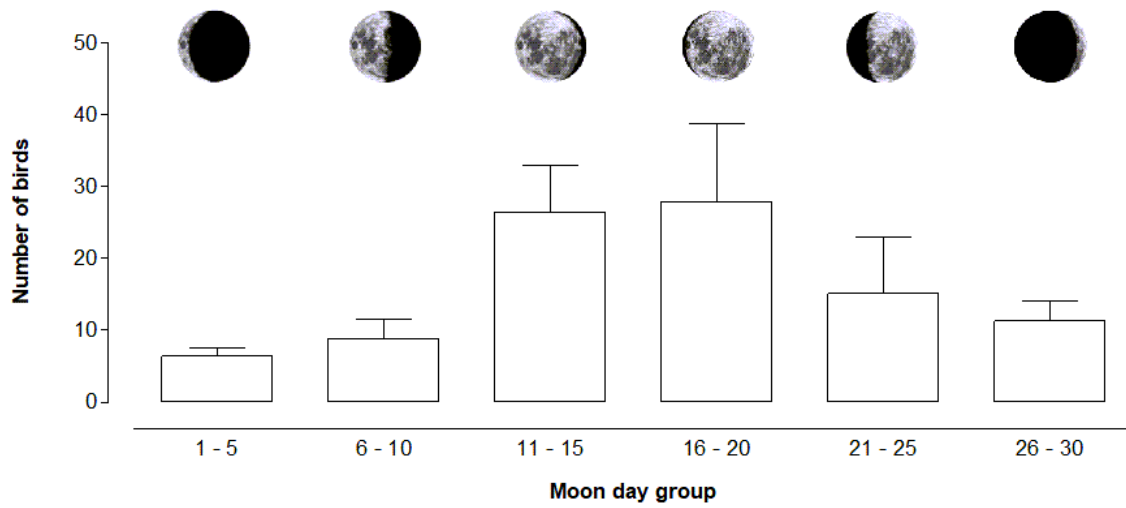


Figure 2.19: Total numbers of non-breeding birds present (mean + SE) in relation to five-day sections of the lunar cycle from July 2022 to November 2022.

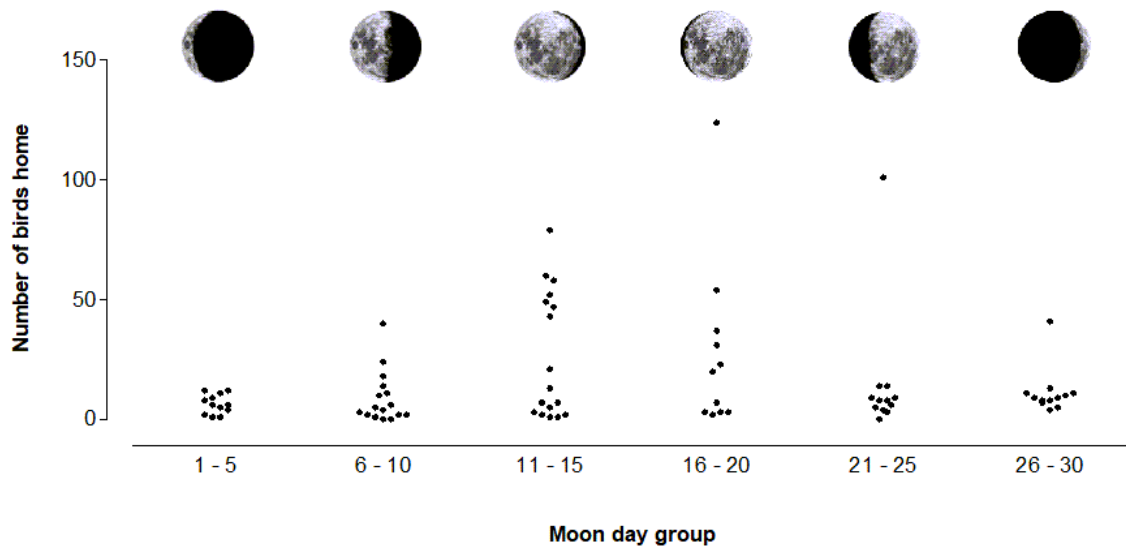


Figure 2.20: Total numbers of non-breeding birds present in relation to five-day sections of the lunar cycle from July 2022 to November 2022.

2.4 Discussion

This is the first study to examine the daily and weekly nestbox attendance of different sex and breeding status categories of Little Penguins present in nestboxes during the breeding period. During the three months before egg-laying, the number of non-breeding birds present in the colony fluctuated on a four-week cycle, in which birds consistently arrived at and departed from the colony simultaneously. These results were consistent with a previous study by Reilly & Cullen (1981). Furthermore, breeding pairs displayed differing attendance patterns, particularly during the incubation period. These patterns provide more insight into the movement of Little Penguins both en masse and individually during different stages of their life cycle. This discussion covers trends in attendance at the overall colony level, while Chapter 3 will cover individual attendance patterns, as well as the incubation and guard stages in more detail.

2.4.1 Breeding bird attendance

2.4.1.1 Breeding nestboxes

Figure 2.7 reveals distinct waves of egg-laying occurring in each month, demonstrating that Little Penguins synchronise their egg-laying with others in the colony. This finding is consistent with the synchronised egg-laying reported by Robinson et al. (2005) at the Little Penguin colony on Phillip Island in 2000. However, the timing of waves at the Phillip Island colony differed significantly — the majority of eggs were laid between late October to late November, with a much smaller wave in mid-December. Penguins at the Phillip Island colony were also observed to have better average body condition during 2000 compared to 2001, when egg-laying dates were more spread out (Robinson et al., 2005). In both colonies, the small wave of eggs laid at the end of the studied seasons may be generally comprised of replacement clutches.

In this study, no breeding pairs produced double broods — that is, the case where a pair lays a second clutch of eggs after the first is successful. However, three replacement clutches were identified. One was the result of a second breeding attempt by a breeding pair. The other two replacement clutches were laid by the same female bird, who selected a new male for the first replacement clutch before

switching back to the original partner for the second replacement clutch. The three replacement clutches were observed on 22 October, 27 September, and 9 November respectively.

2.4.1.2 Breeding individuals

Figure 2.8 graphs attendance at breeding nestboxes over the colony monitoring period, split between instances where either one or two adults are recorded. There was a low occurrence of both adults being simultaneously present at a nestbox, due to the majority of breeding birds at any given time undergoing either the incubation or guard phase. The notable exception to this pattern is a week in the middle of September in which three to seven pairs were observed to be jointly occupying their nestboxes each day. As this time overlaps with the peak of the largest wave of egg-laying, it can be assumed that most pairs concerned were about to lay eggs.

2.4.2 Non-breeding bird attendance

Weekly nestbox checks conducted at the Little Penguin colony in Australia's Penguin Parade in 1960 and 1970 revealed a three-weekly cycle in the number of occupied nestboxes in the winter months before breeding (Reilly & Cullen, 1981). Data from this chapter demonstrates a similar pattern in the three months before the first large wave of egg-laying. Peaks in non-breeding bird attendance in July, August, and September are evident in Figure 2.10. These peaks are replotted with a fitted curve in Figure 2.17, allowing for the estimation of the cycle's frequency. The number of days calculated between estimated peaks and troughs averages to 26 whole days. This cycle corroborates results from Reilly & Cullen (1981), albeit with a period closer to four weeks than three.

It should be noted that attendance results from Reilly & Cullen (1981) use the term 'breeding birds' to refer to all birds that made breeding attempts during the season, even if they had not yet laid eggs at the time of observation. Other results refer to the total number of birds present at the colony. This differs from the nomenclature in this thesis, where 'non-breeding birds' refer to all the birds present in nestboxes without eggs and chicks for a given day of monitoring. This results in instances where birds recorded as non-breeding early in the season can later be found with eggs or chicks and therefore be reclassified as a breeding bird from then onwards, but continue to be classified as non-breeding before that period.

A potential reason for the phenomenon described above can be found when comparing the attendance patterns of non-breeding and breeding birds against each other. Most non-breeding birds found to be present during the early attendance peaks in July and August were most likely birds that had returned to the colony to initiate courtship. This is clear from Figure 2.6, which records 52 nestboxes containing pairs during the July peak, while only 20 contained just one bird.

Figure 2.4 depicts the beginning of courtship and egg-laying stages for the season. Notably, there are two instances of an approximate one-month interval between a peak in non-breeding bird attendance and the midpoint of a subsequent rise in the number of breeding birds — these instances are labelled below in Figure 2.21. We can surmise that these are peaks in birds initiating courtship, and birds returning to nestboxes to begin egg-laying, respectively.

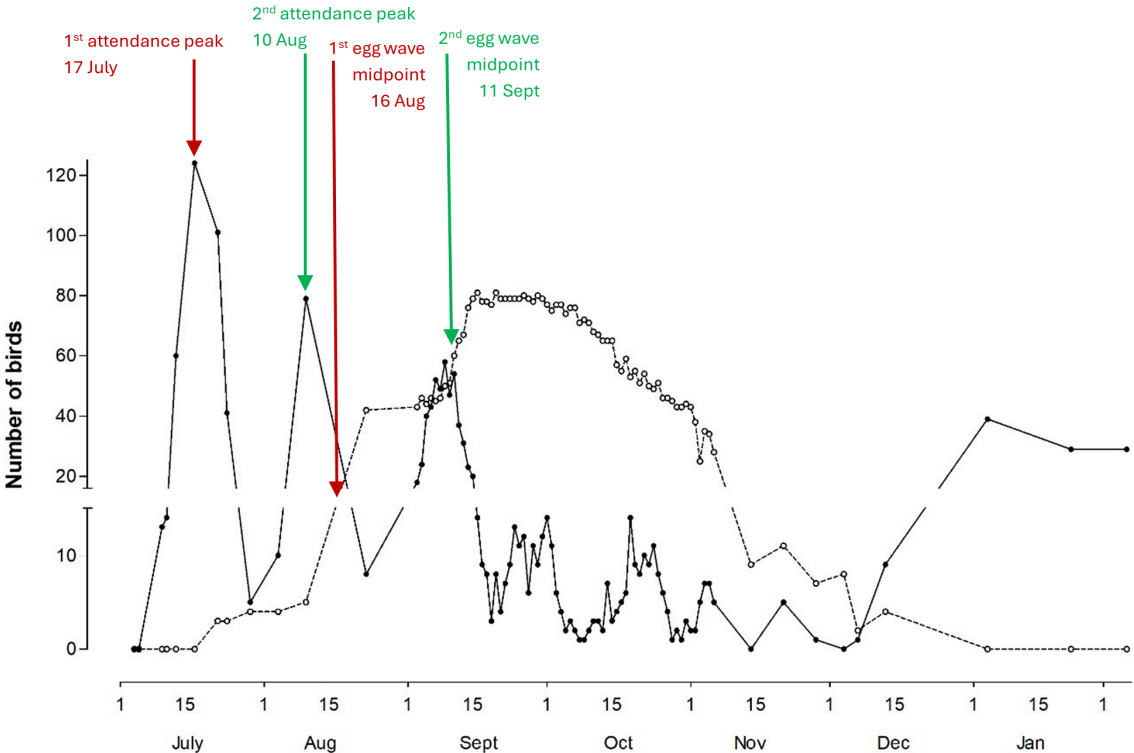


Figure 2.21: Total numbers of non-breeding —●— and breeding ---○--- birds from July 2022 to February 2023. Attendance peaks are labelled in red and midpoints of initial egg-laying waves are labelled in green.

The first observed peak in non-breeding bird numbers occurred on 17 July (Figure 2.21). The midpoint of the first egg-laying period — as best as can be estimated with the limited data resolution — is 16 August; almost exactly a month later. This phenomenon repeats itself with a second peak

in non-breeding bird attendance on 10 August, followed by another clear egg-laying wave with a midpoint that falls on 11 September — again, almost exactly another month later. This corroborates the observation from Chiaradia & Kerry (1999) that Little Penguins return to lay eggs approximately one month after courtship.

Previous studies examining Little Penguin behaviour during the breeding season have focused on participating birds — that is, breeding birds. As such, the following observations of non-breeding birds after the start of the egg-laying period are novel. Figure 2.10 shows a simultaneous rise in the attendance of breeding birds and fall in the attendance of non-breeding birds in the middle of September. This can be attributed to previously non-breeding pairs laying eggs and beginning the incubation phase. In turn, this means that non-breeding individuals recorded after this period are likely not to breed at all during the season.

The low overall attendance of non-breeding birds from the middle of September through to early November indicates that most birds in the colony are participating in breeding. Nevertheless, low-amplitude fluctuations with a frequency mirroring the earlier, larger waves are still visible, indicating that the pattern previously observed by Reilly & Cullen (1981) still holds for non-breeding individuals after the breeding season properly begins.

In December and January, newly hatched chicks fledge and leave their nestboxes. This drives a sharp increase in the number of non-breeding birds, many of whom were previously recorded to be breeding. At the same time, the end of daily monitoring and return to much more intermittent nestbox checks obscures any additional insight into the patterns of non-breeding birds, especially those that did not attempt to breed at any point during the season.

2.4.3 Attendance of both sexes

Male and female Little Penguins share parental responsibilities fairly equally (Dann & Cullen, 1990). Figures 2.11 through 2.14 reveal early peaks in attendance for pairs of birds as opposed to single pairs, likely linked to the initial courtship and egg-laying phases. A lower proportion of single female birds appear at the colony during the July wave compared to males, with a subsequent increase in August. This relative absence in July may be caused by some females foraging for a longer period before starting

courtship later in the season, while elevated numbers in August may correspond to females returning after their courtship to lay eggs and begin incubation.

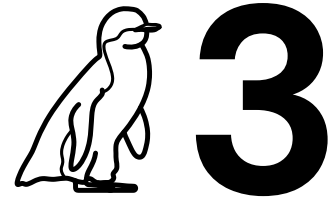
Figure 2.16 illustrates the attendance patterns of both single male and single female birds, starting with small increases in colony attendance for both during July. Slightly more single males seem to be present than single females, an observation in line with past findings where males arrive back to the colony to secure breeding sites first (Chiaradia & Kerry, 1999; Reilly & Cullen, 1981). Welch's *t*-test ($t(13) = 1.906, p = 0.079$) was performed for the data set in July, but was not able to demonstrate statistical significance.

The attendance patterns of single male and female birds fluctuate synchronously (Figure 2.16) between early September and late October, coinciding with the incubation and guard phases — it seems that male penguins are away from the nest while females are present, and vice versa. While this is consistent with prior notions around the incubation and guard phases in regards to individual breeding pairs, where parents alternating between foraging and egg/chick care, it is significant that multiple breeding pairs synchronise their attendance, even to the point of same-sex parents from differing breeding pairs arriving and departing from the colony synchronously. From November onwards, the attendance of single male and female birds drops off, except for a spike in male parents visiting their nestboxes just prior to fledging in late November (Figure 2.16).

2.4.4 Non-breeding bird attendance in relation to lunar phases

Figure 2.19, which depicts the attendance of non-breeding birds in relation to lunar phases, records lower attendance on darker, less moonlit nights — that is, nights close to or with a new moon. That being said, the pattern does not reach statistical significance. Conversely, Figure 2.18 shows peaks in non-breeding bird attendance for the months of July, August and September that all coincide with brighter, more moonlit nights close to or at the time of the full moon. This observation sits in contrast to a finding from Rodriguez et al. (2016) that fewer Little Penguins came ashore during full-moon nights at the Phillip Island colony. However, Iasiello & Colombelli-Négrel (2025) records no variation in attendance in regard to moonlight, and Rodriguez et al. (2018) did observe penguins to prefer well-lit paths when traversing between the ocean and their nests, so it seems the role of light in influencing Little Penguin attendance requires further research.

In contrast, the number of non-breeding birds present from 6 October to 28 November remained low despite differing lunar phases. Most birds recorded at the colony during this period were breeding birds, which of course corresponds with a sharp decrease in the number of non-breeding birds compared to the months before. This in turn makes it difficult to identify any significant patterns in attendance. It is also important to note another potential confounding factor — attendance during days around the full moon may be affected by cloud cover, fog, or other phenomena that decrease the moon's perceived luminance (Chiaradia et al., 2007).



Breeding Pair Attendance of the Little Penguin

3.1 Introduction

Little Penguins (*Eudyptula minor*) are the smallest extant penguin species, standing approximately 30 cm high and weighing about one kilogram when fully grown. The Little Penguin is known as the *kororā* in Māori – in Australia it is called the *fairy penguin*. This species is found along the west coast of Australia, as well as the coasts of mainland New Zealand and surrounding islands. They have a slate-blue plumage with a white underside (Marchant & Higgins, 1990).

3.1.1 The breeding season

3.1.1.1 Courtship and egg-laying

The breeding season of Little Penguins usually runs through winter and into summer. Breeding begins with courtship, with Little Penguins returning to the colony approximately a month before egg-laying begins (Chiaradia & Kerry, 1999). Egg-laying occurs from as early as May until as late as December (Reilly & Cullen, 1981). Approximately a month after courtship, individuals will return

to their nest site in preparation for laying eggs. Males have been found by Chiaradia & Kerry (1999) to arrive at the nest site before females, in preparation for egg-laying. Little Penguins typically lay two eggs in a clutch, but occasionally just a single egg (Reilly & Cullen, 1981).

3.1.1.2 The incubation period and spells

Once eggs are laid, males and females take turns to incubate them. One parent undertakes an incubation spell — that is to say, they are present at the nest, ensuring eggs are protected and maintaining an optimal temperature, while the other parent is out at sea foraging. Incubation periods recorded previously have a mean length of 35 days, ranging from 31 to 40 days (see Table 3.1) (Chiaradia & Kerry, 1999; Kato et al., 2008; Kemp & Dann, 2001). During this time, each penguin will exhibit about five to six incubation spells that last around three to six days, as depicted in Table 3.2 and Table 3.3.

Incubation spells soon after egg-laying are relatively short for both male and female parents (Numata et al., 2000; Weavers, 1992). The length of spells increases as the midpoint of the incubation period is reached as found by Kato et al. (2008) (see Figure 3.1). After this, incubation spell length varies (Numata et al., 2000; Weavers, 1992). Kato et al. (2008) corroborates this with results showing that females exhibited significantly longer spells in the middle of incubation than males (again, see Figure 3.1).

As shown by Kato et al. (2008) in Figure 3.1, Little Penguins begin to shorten their incubation spells as egg hatch nears. Spells in the days immediately preceding egg hatch are usually a single day in length (Numata et al., 2000). This overall incubation pattern observed in Little Penguin pairs may suggest a form of synchronisation between the parents. Additionally, this pattern is present in breeding pairs across locations, indicating some sort of intrinsic behaviour within the species. The transition to one-day incubation spells closer to hatch may be caused by parents observing egg movement or pipping.

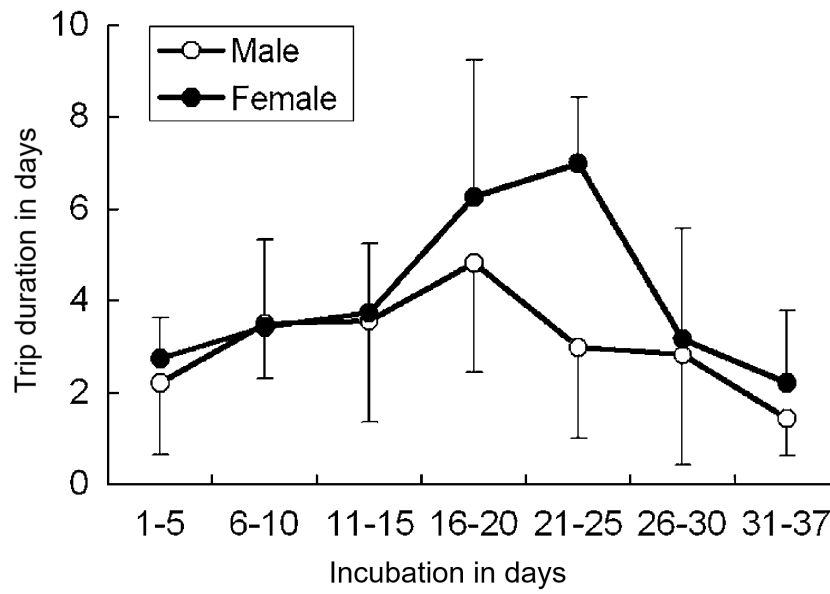


Figure 3.1: Change of trip duration in relation to timing of departure within the incubation stage of male and female Little Penguins. Vertical bars indicate standard deviation (SD). Adapted from Kato et al. (2008).

Table 3.1: Mean lengths (days) of Little Penguin incubation periods recorded in previous papers.

Mean	Incubation period				Nest check frequency	Number of birds	Number of nests	Location	Year	Reference
	SE	<i>n</i>	Min	Max						
35.50	0.25	48	31	40	Daily	106	53	Phillip Island, AUS	1995	Chiaradia & Kerry (1999)
35.40		142	33	44	Daily		105	Phillip Island, AUS	1998	Kemp & Dann (2001)
35.10	0.32	10			Every 2 days	20	10	Phillip Island, AUS	2004	Kato et al. (2008)

Table 3.2: Mean numbers of incubation spells undertaken within an incubation period, as recorded in previous papers.

Number of incubation spells						Nest check frequency	Location	Year	Reference
Male			Female						
Mean	SE	<i>n</i>	Mean	SE	<i>n</i>				
5.6	0.27	54	5.7	0.28	52	Daily	Phillip Island, AUS	1995	Chiaradia & Kerry (1999)
5.3	0.41	10	4.8	0.47	10	Every 2 days	Phillip Island, AUS	2004	Kato et al. (2008)

Table 3.3: Mean lengths (days) of incubation spells for sexes individually and cumulatively recorded in previous papers.

Incubation spell (Both sexes)			Male incubation spell			Female incubation spell			Nest check frequency	N° of birds	N° of nests	Location	Year	Reference
Mean (days)	SE	<i>n</i>	Mean (days)	SE	<i>n</i>	Mean (days)	SE	<i>n</i>						
4.8	1.20	17									Phillip Island, AUS	1992	Collins et al. (1999)	
3.9	0.60	16									Phillip Island, AUS	1993	Collins et al. (1999)	
3.4			3.5	0.17	54	3.4	0.32	49	Daily	106	53	Phillip Island, AUS	1995	Chiaradia & Kerry (1999)
			3.0	0.22	10	4.1	0.38	10	Every 2 days	20	10	Phillip Island, AUS	2004	Kato et al. (2008)
			3.2	0.01		4.0	0.01		Daily	222		Phillip Island, AUS	2001- 2011	Saraux et al. (2016)
			2.9	0.30	18	3.2	0.40	20	Daily	64	34	Oamaru, NZ	1998	Numata et al. (2000)
			6.2	0.60	23	5.2	0.50	15	Daily	74	39	Motuara Island, NZ	1998	Numata et al. (2000)

Figure 3.2 depicts the incubation spells of male and female parents recorded in two example nestboxes, one at the Oamaru colony and one at the Motuara Island colony. Distinct variation is recorded in overall incubation spell length between breeding pairs at each location. The breeding individuals at Motuara Island were observed during the study to have poorer body condition on average, compared to those at Oamaru — this is suggested by Numata et al. (2000) to correlate with the incubation spell lengths depicted.

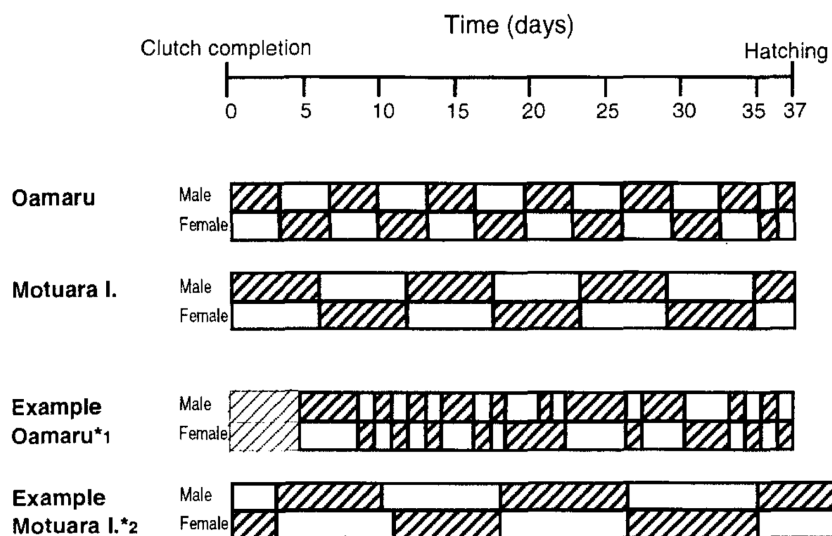


Figure 3.2: Schematic diagrams and observed examples of nest attendance patterns in Little Penguins at Oamaru and Motuara Island during the incubation period in the 1998/99 breeding season. Shaded areas show periods of attendance. Adapted from Numata et al. (2000).

3.1.1.3 The guard period

After chicks have hatched, the guard period begins. During this time, one adult bird will remain in the nest during the day, while the other parent forages at sea. This mirrors the dynamic that began in the incubation period, but with the foraging parent having the additional objective of acquiring food for the newly-hatched chicks. During the guard period, all spells are around a single day in length (Chiaradia & Kerry, 1999). Table 3.4 records the lengths of guard periods which range from around 15 to 21 days, with significant outliers recorded for both the minimum of 8 days (Chiaradia & Kerry, 1999) and maximum of 39 days (Braidwood, 2009).

As consistently shown by Table 3.5, as well as Braidwood (2009) in Figure 3.3, the guard period length for one-egg clutches is longer than that for two-egg clutches. Braidwood (2009) demonstrated

a significant difference in length with a Mann–Whitney U test. However, no significant differences in average weight were recorded between chicks of either one-egg or two-egg clutches (Braidwood, 2009). With only one mouth to feed, it may be that parents of single chicks experience less pressure to acquire food, thus allowing more time to be spent guarding the chick.

Table 3.4: Mean lengths of Little Penguin guard periods recorded in previous papers.

Mean (days)	SE	<i>n</i>	Minimum	Maximum	Nest check frequency	Location	Year	Reference
15.1	1.00	12	10	22		Motuara Island, NZ	1998	Numata et al. (2004)
20.0	1.00	14	16	28		Oamaru, NZ	1998	Numata et al. (2004)
21.3	1.60	23	14	39		South Westland, NZ	2008	Braidwood (2009)
14.5	3.6		8	25		Phillip Island, AUS	1995	Chiaradia & Kerry (1999)
15.0	0.54	54			Daily	Phillip Island, AUS	1995	Chiaradia & Nisbet (2006)
19.0	0.54	54			Daily	Phillip Island, AUS	1996	Chiaradia & Nisbet (2006)
20.0	0.75	44			3 times a week	Phillip Island, AUS	2000	Chiaradia & Nisbet (2006)
16.0	0.69	52			3 times a week	Phillip Island, AUS	2001	Chiaradia & Nisbet (2006)
20.0	0.57	50			3 times a week	Phillip Island, AUS	2002	Chiaradia & Nisbet (2006)

Table 3.5: Mean lengths of guard periods (days) for one-egg and two-egg Little Penguin clutches recorded in previous papers.

Guard period (1 chick)			Guard period (2 chicks)			Location	Year	Reference
Mean	SE	<i>n</i>	Mean	SE	<i>n</i>			
18.8	1.50	4	13.3	0.70	8	Motuara Island, NZ	1998	Numata et al. (2004)
26.0	0.70	3	18.4	0.50	11	Oamaru, NZ	1998	Numata et al. (2004)
28.6	2.60	8	17.4	1.00	15	South Westland, NZ	2008	Braidwood (2009)

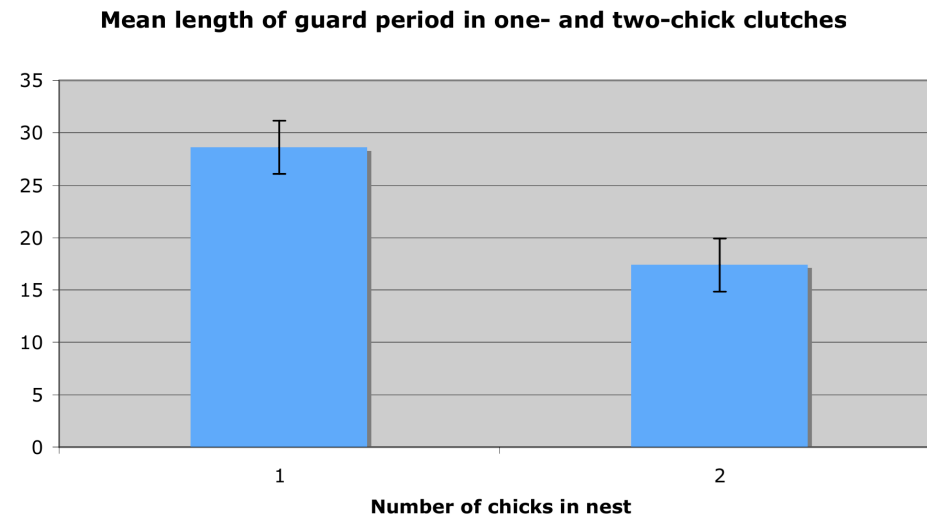


Figure 3.3: Mean (SE) length in days of guard period in one-egg and two-egg clutches. Adapted from Braidwood (2009).

3.1.2 Aims of Chapter 3

The goal of this chapter is to investigate the daily nestbox attendance of Little Penguin breeding pairs present during the 2022 breeding season at the Port Tarkohe colony. Data on Little Penguin nest attendance at this resolution has never before been collected from a New Zealand-based colony.

The data presented reveal patterns in incubation attendance for individuals within breeding pairs. Additionally, the lengths of various breeding season stages, as exhibited by pairs and individuals, are compared and contrasted with results from previous studies. Overall, this chapter aims to build upon the high-level results from Chapter 2, focusing on data collected specifically from daily nestbox checks to yield detailed insights.

3.2 Materials and methods

3.2.1 Study site and physical monitoring

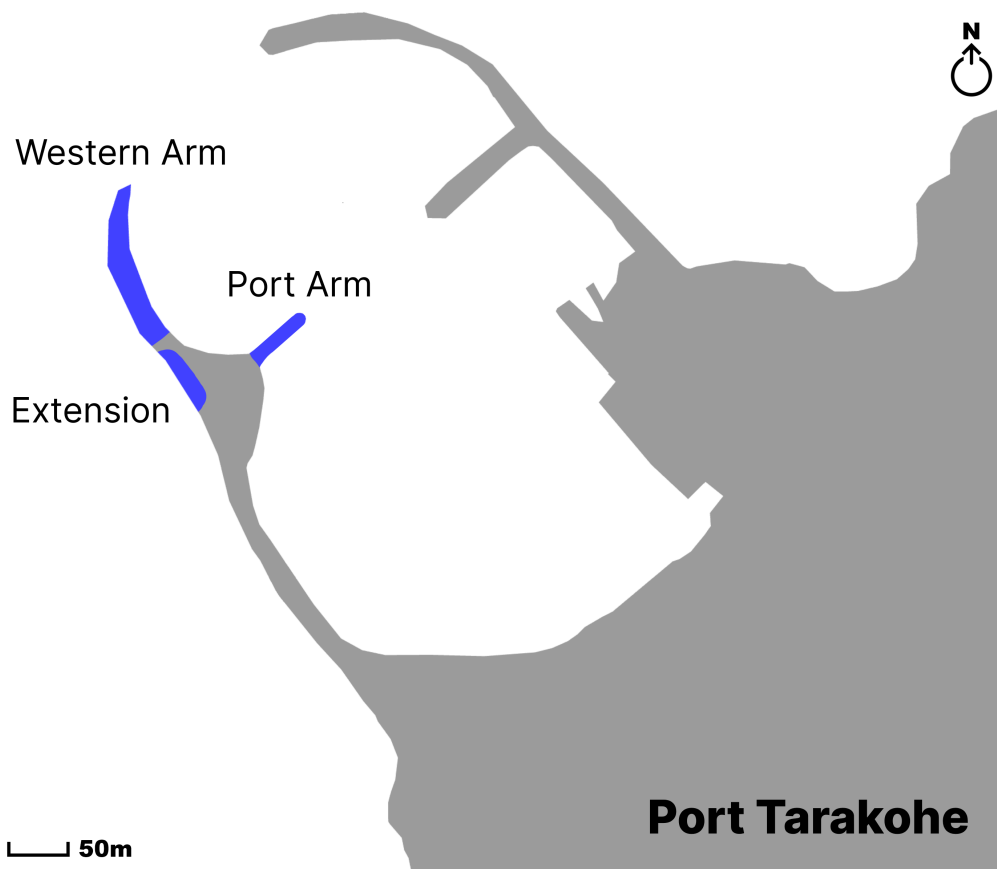


Figure 3.4: Map of Port Tarakohe, Golden Bay, New Zealand. The three coloured and labelled segments indicate areas of nestbox placement.

This study was conducted from July 2022 to January 2023 at Port Tarakohe, Golden Bay in New Zealand, under a protocol approved by the Massey University Animal Ethics Committee (09/76) and the Department of Conservation (Permit ECHB-23237-RES). The Little Penguin colony present there spans three distinct areas as depicted in Figure 3.4, referred to as the Western Arm, Port Arm, and Extension. Nestboxes numbered 1 through 100 were placed along the Western Arm, 101 through 120 along the Extension and 121 through 150 along the Port Arm. Weekly or biweekly (that is, every two weeks) nestbox checks were performed from 4 July to 2 September, after which the monitoring frequency increased to a daily cadence. Daily monitoring took place from 3 September until 6 November, after which the original monitoring cadence resumed until 3 February. For brevity, these periods of less-frequent monitoring are referred to as ‘weekly checks’.

Data recorded at each nestbox included the number and identity of adult Little Penguin individuals, as well as the number of chicks and eggs. Individuals were identified using a handheld reader to scan previously-implanted microchips. Note that penguins were not microchipped as part of the current study, but were tagged for other purposes by Penguin Trust personnel under their own Department of Conservation permits. Incidental data were also noticed and recorded, including events such as the discovery of new nesting material, digging of soil, or fresh faeces inside nestboxes.

To help determine nestbox activity in cases where individual birds were not sighted during a monitoring check, a gating method was employed in the style of Chiaradia & Kerry (1999). Empty nestboxes were marked with a short wooden stick placed upright — a gate — blocking the entrance to the nestbox. ‘Gate up’ then refers, in subsequent checks, to an undisturbed, upright stick — conversely, ‘gate down’ refers to instances where stick has been moved and/or is no longer standing. This method provided information on whether a penguin had entered a nestbox.

As an additional note — nestboxes are labelled in the results for this chapter (and the next) as either ‘breeding’ or ‘non-breeding’, referring to nestboxes that either do or do not contain eggs or chicks. Birds are also referred to as ‘breeding’ or ‘non-breeding’ based on their observed reproductive output over the course of the study, but may separately be named ‘single’ when they are found to be the sole adult individual (that is, with or without eggs or chicks) occupying a nestbox.

3.2.2 Assignment of sex

A total of 205 unique individuals were found in nestboxes from 1 July 2022 to 31 January 2023. 104 males and 101 females were recorded, with 93 breeding pairs present during the breeding season. Morphometric data, including beak shape and the proportion of upper and lower mandibles, had been used to determine individuals’ sexes prior to this study, with multiple reassessments taking place over several preceding years. Inconsistencies in recorded individual sexes were rectified where possible during the study, primarily through live observation of breeding pairs in nestboxes.

3.2.3 Statistical analysis

Data in this chapter was analysed and plotted using GraphPad Prism 10 software. The two-way ANOVA test was used to investigate the effect of sex and start date on incubation spell lengths. The

Šídák correction was subsequently applied to analyse differences in incubation spell lengths in respect to specific groups of start dates. Welch's *t*-test was performed to analyse nestbox attendance during incubation for male and female parents, guard period lengths for one-chick and two-chick clutches, and guard period lengths for two-chick clutches with different onsets. An alpha level of 0.05 was used for all statistical tests.

3.3 Results

3.3.1 Preliminary observations from daily nestbox checks

At the onset of daily nestbox checks on 3 September, most nestboxes did not yet contain eggs. The majority of eggs laid during daily monitoring were laid in clutches of two, with the exception of three single eggs laid in Nestboxes 40, 78, and 84. The second breeding pair to occupy Nestbox 113 also laid only a single egg inside the nestbox, but a second egg was also discovered just outside the box during the check.

All breeding pairs observed during the daily monitoring period laid a single clutch, except for the pair occupying Nestbox 104, which laid two successive clutches of eggs. Neither of these breeding attempts were successful.

An unusual scenario was observed during the monitoring of Nestbox 113 (previously mentioned), in which two breeding pairs were consistently observed at different times. Events are illustrated in Figure 3.5 below. The line colours indicate the lengths of time over which individuals and pairs were present. Three eggs were laid inside the nestbox — two from the first pair in September, and one from the second pair on November 1. A fourth egg, tentatively attributed to the second pair, was discovered outside the nestbox on November 4, but parentage could not be confirmed. From 24 November onwards, all four birds of both pairs occupied the nestbox at different times. No eggs were observed to hatch — all were prematurely cracked.

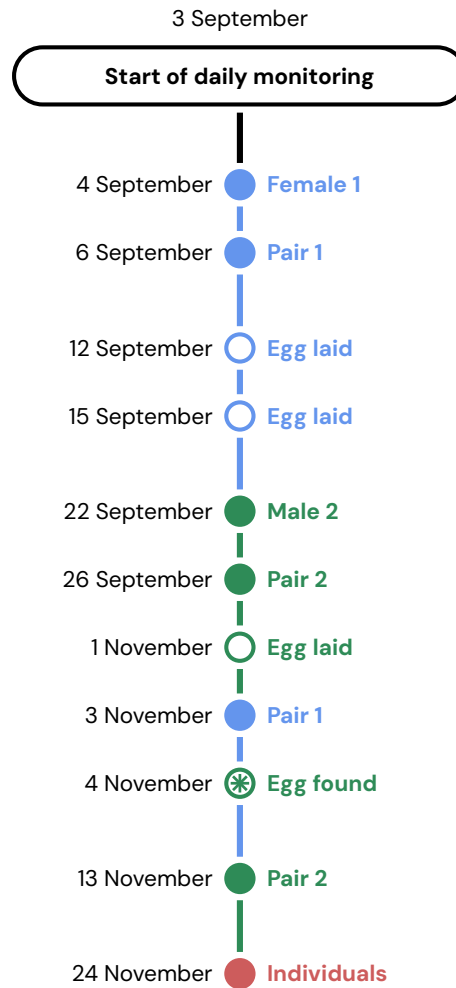


Figure 3.5: Timeline of Little Penguin attendance at Nestbox 133. Coloured lines indicate pair occupancy. The egg laid on 4 November has tentatively been attributed to Pair 2.

In another notable case, Nestbox 2 was occupied by three different birds during the daily monitoring period — two males and one female. Two eggs were present before the start of daily monitoring, along with the first male bird and the female bird. On 21 September, the second male bird began to occupy the nestbox alongside the female bird. On 27 September and 29 September, two new eggs were discovered, after which point all three birds occupied the nestbox individually on different days, with gaps where the nestbox was empty. Both breeding attempts were observed to have failed, as no eggs hatched.

3.3.2 Incubation periods

Raw attendance data are available for reference in Appendix B. The following results are generated from processing these data.

Figure 3.6 depicts the range of incubation period lengths for breeding pairs that began incubation in September 2022. Apart from three early incubation periods starting in the first week of September, the majority began between 11 and 21 September. All incubation periods had lengths between 33 and 37 days total. Values may overlap — that is to say, incubation periods that begin on the same dates and have the same length occupy the same dot plotted in Figure 3.6.

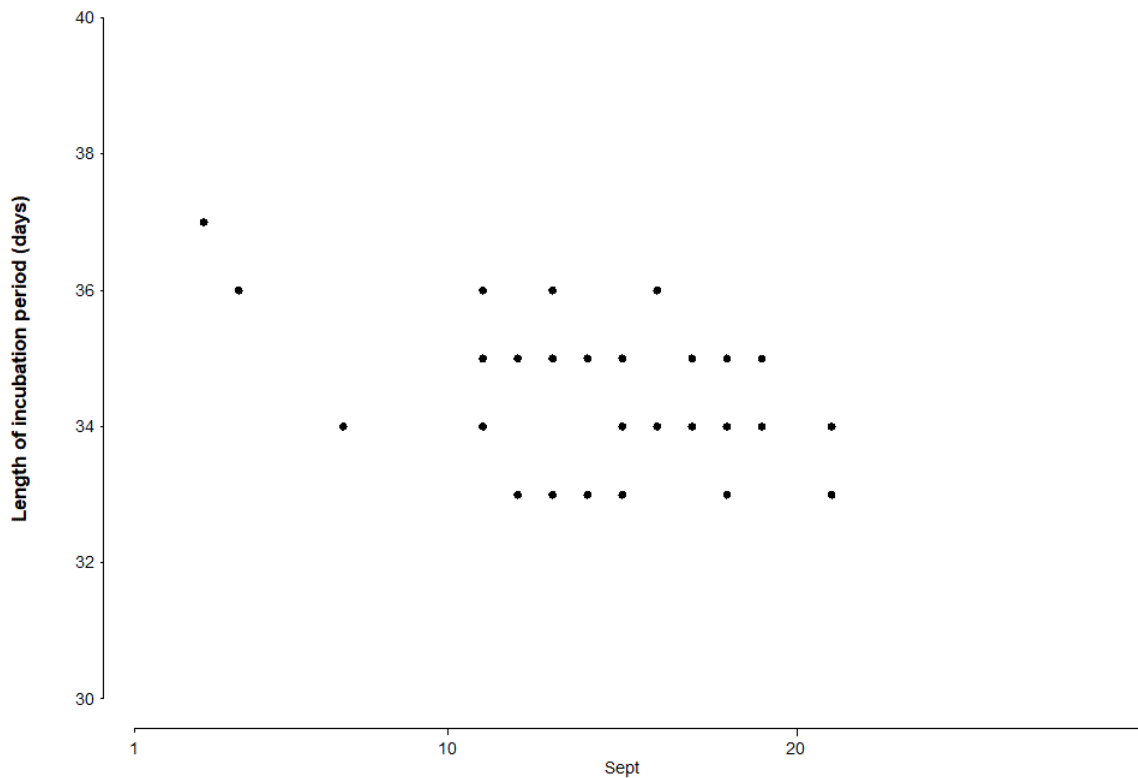


Figure 3.6: Incubation period lengths for Little Penguin breeding pairs that began incubation in September 2022.

A total of 32 incubation periods were recorded during daily nestbox checks. The mean length of incubation periods was found to be 34.41 ± 0.19 ($n = 32$) days. Table 3.6 records the mean number of days that male and female parents were observed attending nestboxes during their incubation periods. Welch's t -test was performed to compare male and female variance in these data, and found that the number of days each parent incubated was not significantly different: $t(61) = 1.221$, $p = 0.2268$.

Table 3.6: Mean cumulative durations of nestbox attendance for male and female Little Penguins during incubation periods beginning in September 2022.

Attending parent	Mean (days)	SE	<i>n</i>	Minimum length (days)	Maximum length (days)	Range
Female	17.38	0.27	32	13	21	8
Male	16.91	0.27	32	14	20	6
Both	0.06	0.04	32	0	1	1

3.3.3 Incubation spells

Two variations of an attendance pattern were observed in respect to individual breeding pairs during their incubation periods, as depicted in Figures 3.7, 3.8 and 3.9. Both variations are of identical structure, where incubation begins with shorter spells, increases to longer spells, and then decreases to end with short spells that are usually a single day long. The major difference between variations is the general length of incubation spells overall. Figure 3.7 depicts nestboxes with shorter, more frequent spells, whereas Figures 3.8 and 3.9 depict nestboxes with longer, less frequent spells. This difference is particularly apparent within the first 10 days after the second egg is laid.

Figures 3.7, 3.8 and 3.9 all require the same legend as in the raw data figures in Appendix B to specify the meanings of coloured glyphs. The legend has been reproduced below in Table 3.7 for convenience:

Table 3.7: Legend for nestbox attendance plots.

Symbol	Event
■	Egg laid
▲	Eggs hatched
▼	Post-guard
◆	Fledge
×	Eggs lost
×	Chicks lost

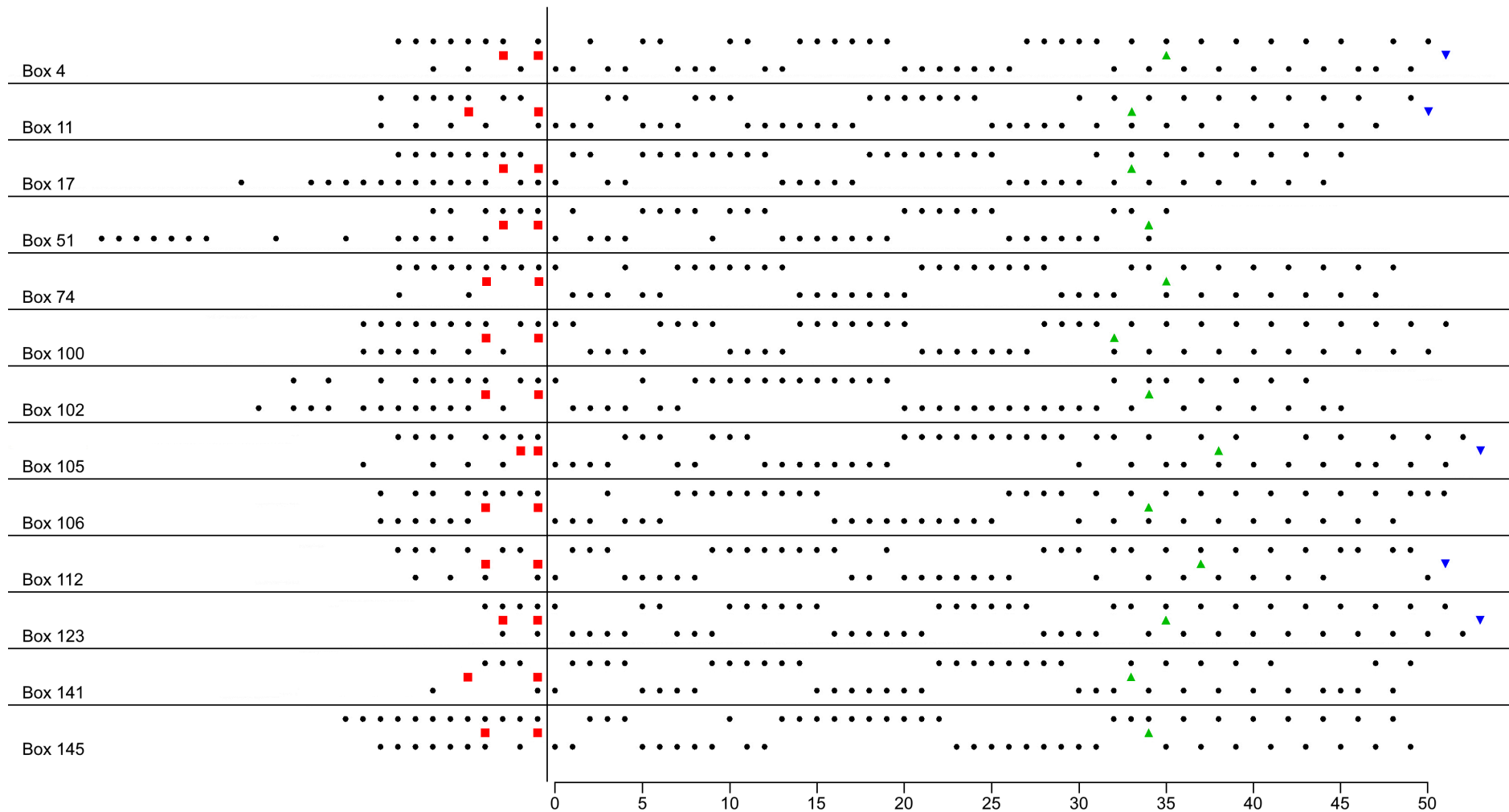


Figure 3.7: Variation 1. Nestbox attendance of breeding birds that undertook relatively short incubation spells. The top row of dots for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox. The vertical line at Day 0 denotes days before and after the second egg was laid.

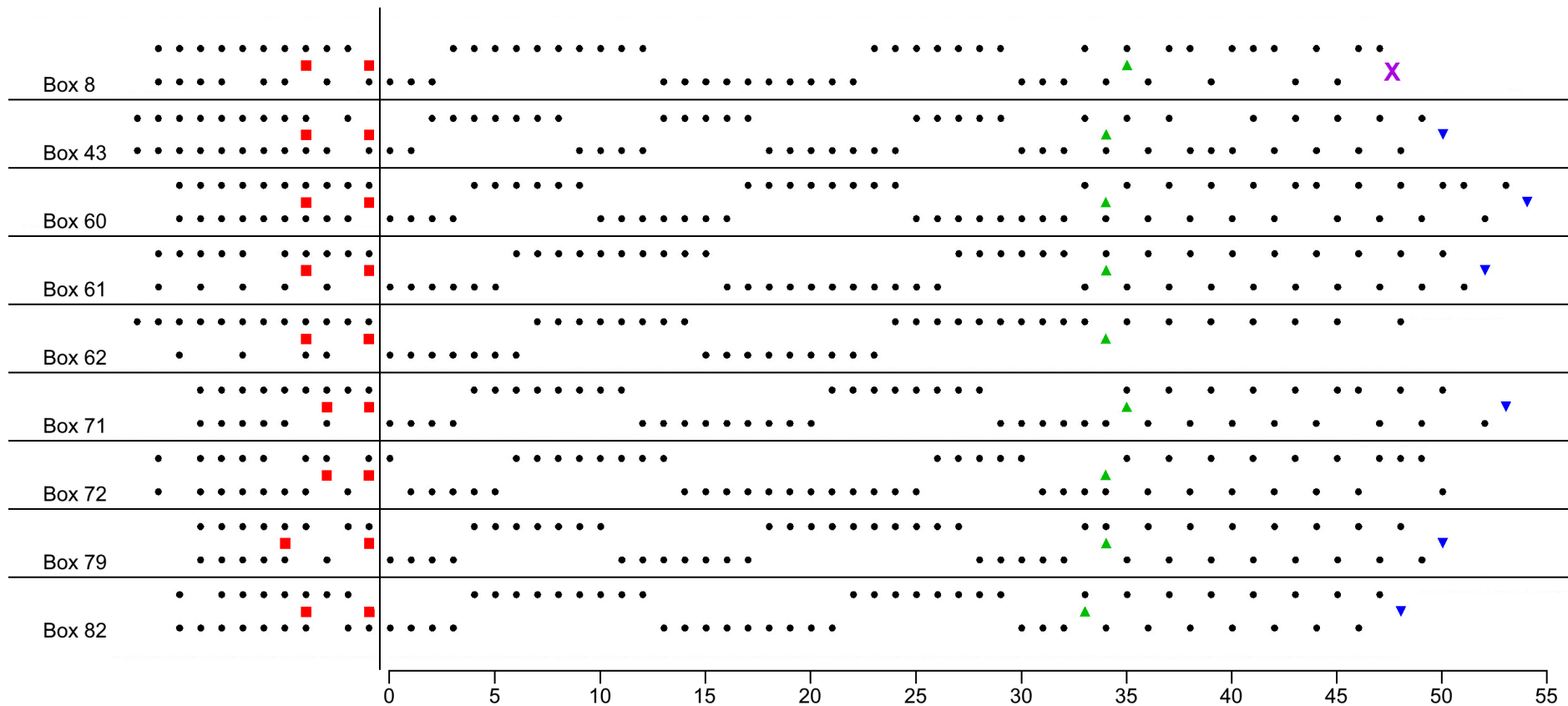


Figure 3.8: Variation 2, Part 1. Nestbox attendance of breeding birds that undertook relatively long incubation spells. The top row of dots for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox. The vertical line at Day 0 denotes days before and after the second egg was laid.

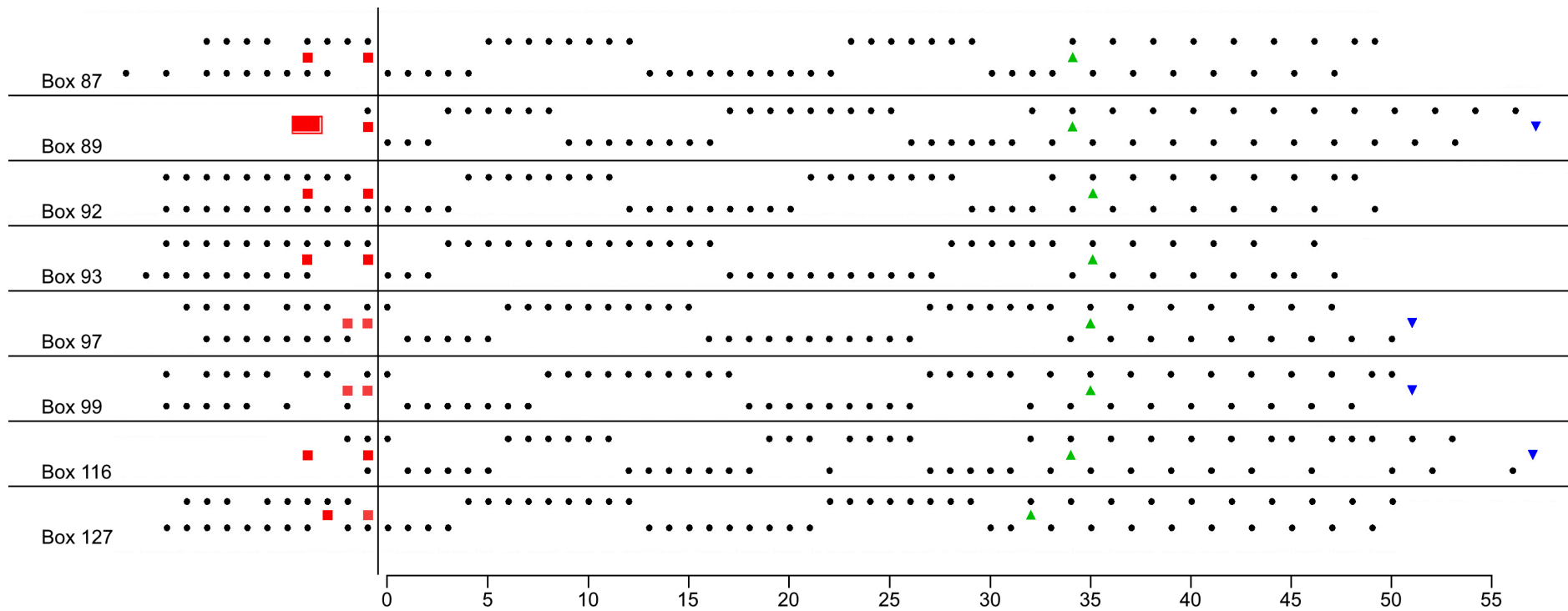


Figure 3.9: Variation 2, Part 2. Nestbox attendance of breeding birds that undertook relatively long incubation spells. The top row of dots for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox. The vertical line at Day 0 denotes days before and after the second egg was laid.

Figure 3.10 shows the range of lengths of incubation spells undertaken by the individual birds of breeding pairs that incubated eggs until hatch between 3 September and 6 November. Days were numbered from 1 to 37, with Day 1 being the first day of incubation for any recorded individual. As with the previous dot plot, values may overlap.

Incubation spells beginning on the first day of the incubation period ranged from 1 to 5 days in length, increasing rapidly to a peak length of 14 days. Incubation spells undertaken close to the midpoint of the incubation period had a higher average minimum length. Incubation spells near to the end of incubation decreased in maximum length, shortening to a single day just before the end of the plot (Figure 3.10).

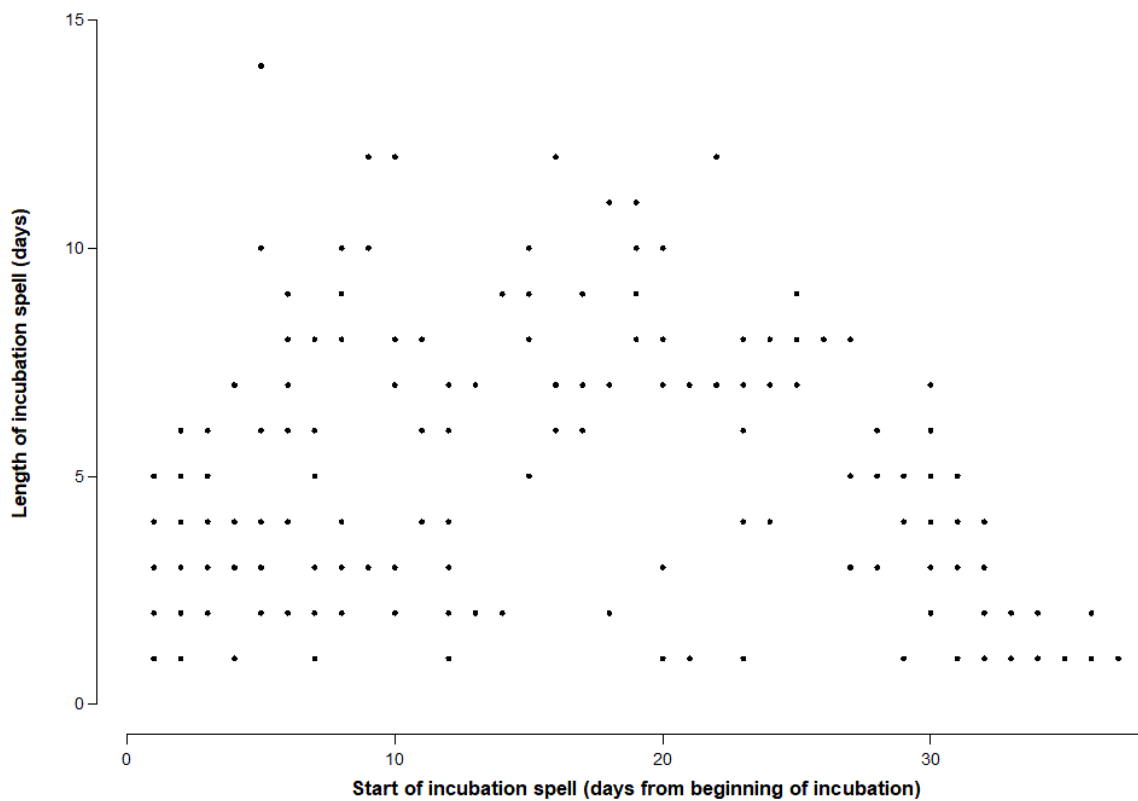


Figure 3.10: Lengths of incubation spells undertaken by individual Little Penguins that incubated eggs until hatch between 3 September 2022 and 6 November 2022. The x -axis numbers days from 1 to 37.

Figure 3.11 and Figure 3.12 split Figure 3.10 into two separate plots, one for each sex. This clarifies slight differences in the ranges of incubation spell lengths between female and male parents, particularly within the first 10 days of incubation.

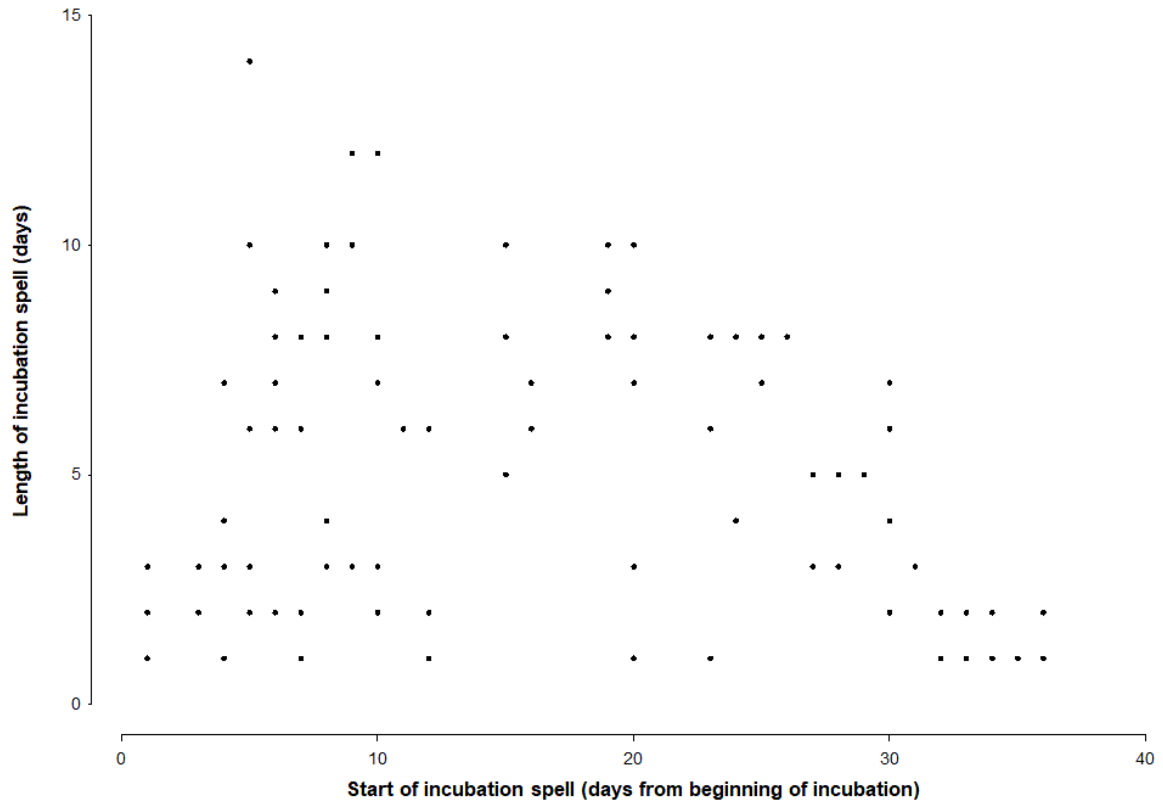


Figure 3.11: Lengths of incubation spells undertaken by female Little Penguins that incubated eggs until hatch between 3 September 2022 and 6 November 2022. The x -axis numbers days from 1 to 37.

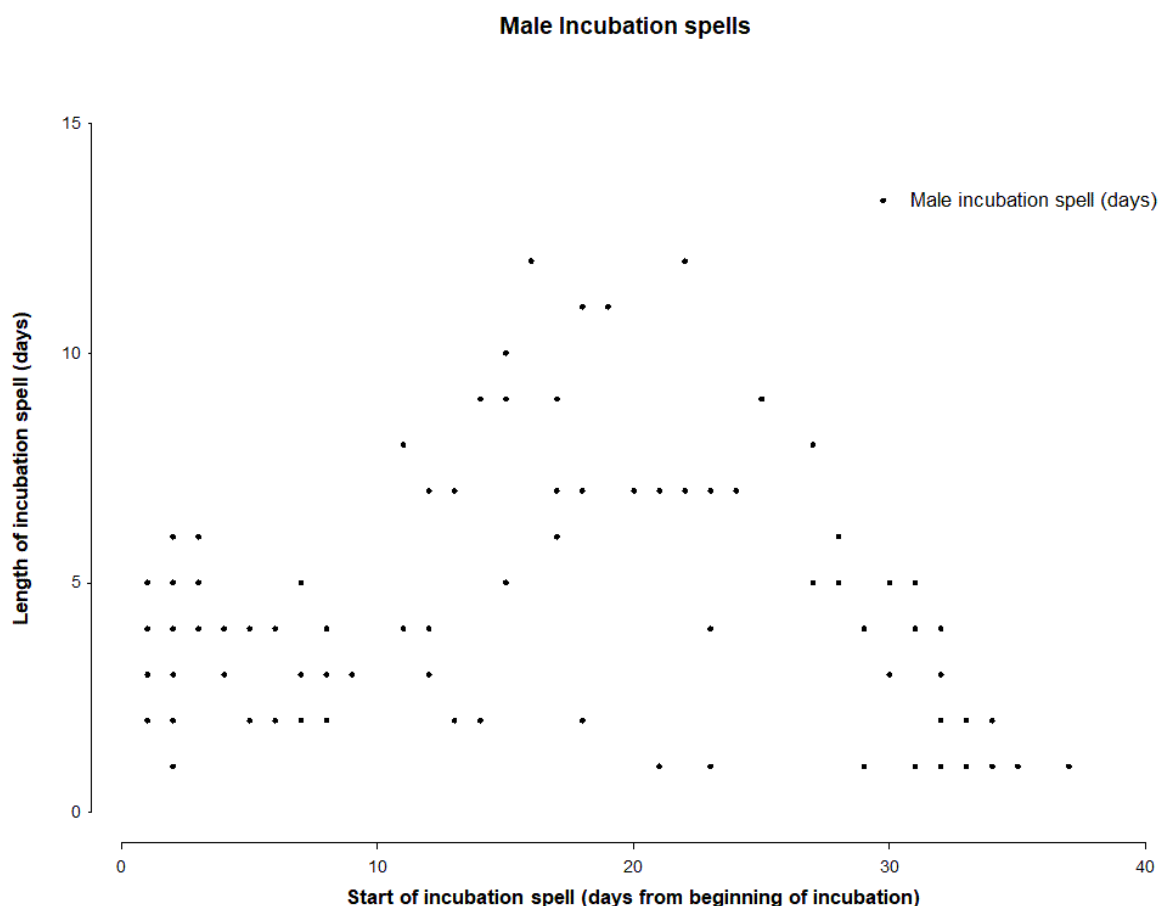


Figure 3.12: Lengths of incubation spells undertaken by male Little Penguins that incubated eggs until hatch between 3 September 2022 and 6 November 2022. The x -axis numbers days from 1 to 37.

The dot plots for Figures 3.10 through 3.12 are useful to illustrate the varying ranges of incubation spell lengths, but obscure average lengths due to overlapping values. It is therefore helpful to present mean data separately. The mean length of incubation spells undertaken by both male and female birds was 4.34 ± 0.19 ($n = 253$) days. Table 3.8 records the average incubation spell lengths plotted in Figure 3.10, split into three groups by start day: Week 1, Weeks 2-4, and Week 5. The shortest incubation spell was a single day long — noting that the true length in hours is obscured by the frequency of checks. The longest recorded incubation spell was 14 days long.

Table 3.8: Mean lengths of Little Penguin incubation spells between 3 September 2022 and 6 November 2022, grouped temporally.

Temporal group	Mean (days)	SE	<i>n</i>	Minimum length (days)	Maximum length (days)	Range
Week 1	3.41	0.25	90	1	14	13
Weeks 2-4	6.15	0.29	109	1	12	11
Week 5	2.24	0.21	54	1	7	6

The mean length of incubation spells undertaken by females was 4.34 ± 0.28 ($n = 128$) days, almost identical to that of the males: 4.34 ± 0.25 ($n = 125$) days. Table 3.9 and Table 3.10 record the average incubation spell length of females and males respectively. Incubation spells are again split into three groups by start day: Week 1, Weeks 2-4, and Week 5. The same data are also presented in Figure 3.13, which illustrates a similar rise and fall in incubation spell length for each sex. A secondary variant of this plot, presented in Figure B10 in Appendix B, examines individual data points in more detail. It has been omitted in this section to minimise repetition.

Table 3.9: Mean lengths of female Little Penguin incubation spells between 3 September 2022 and 6 November 2022, grouped temporally.

Temporal group	Mean (days)	SE	<i>n</i>	Minimum length (days)	Maximum length (days)	Range
Week 1	3.30	0.43	50	1	14	13
Weeks 2-4	6.26	0.39	54	1	12	11
Week 5	2.21	0.37	24	1	7	6

Table 3.10: Mean lengths of male Little Penguin incubation spells between 3 September 2022 and 6 November 2022, grouped temporally.

Temporal group	Mean (days)	SE	<i>n</i>	Minimum length (days)	Maximum length (days)	Range
Week 1	3.55	0.20	40	1	6	5
Weeks 2-4	6.04	0.42	55	1	12	11
Week 5	2.27	0.24	30	1	5	4

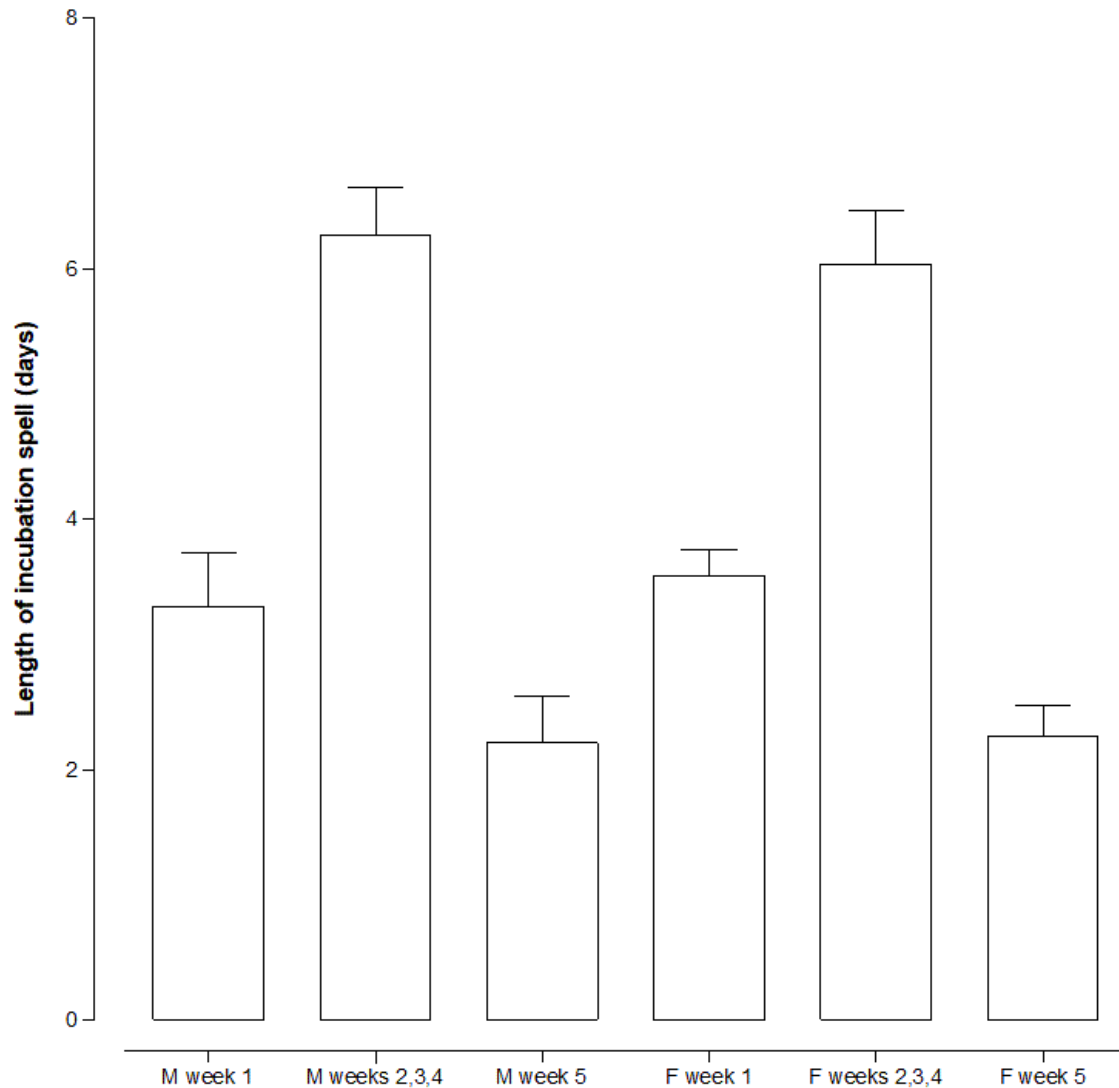


Figure 3.13: Mean (SE) lengths of male and female Little Penguin incubation spells between 3 September 2022 and 6 November 2022, grouped temporally and by sex.

A two-way ANOVA test was performed to identify any statistically significant variation in incubation spell length in regards to sex and start date, using the three temporal groups described above. The main effect of sex did not reach statistical significance $F_{1,247} = 0.0072, p = 0.9325$. However, the main effect of start date was found to be statistically significant $F_{2,247} = 51.42, p < 0.0001$. No interaction effect between sex or start date was found $F_{2,247} = 0.2150, p = 0.8067$.

The Šídák correction was applied to the above results to further compare incubation spell lengths within each temporal group. The p -values for comparisons between spell lengths in Week 1 and Weeks 2-4, and between spell lengths in Week 5 and Weeks 2-4, were found to be < 0.0001 for both male and

female subgroups, demonstrating statistical significance. Comparisons between spell lengths in Week 1 and Week 5 did not yield statistical significance.

3.3.4 Guard periods

Figure 3.14 depicts the guard periods of breeding pairs that hatched either one or two chicks between 16 September and 19 October, plotted by duration. Data were not included for broods with chicks that began post-guard after the end of daily checks, since their guard period lengths could not be determined. Two waves of hatching are visible, the first occurring from 16 to 29 September, and the second occurring from 10 to 19 October. The length of all guard periods recorded ranged from 16 to 33 days. Four guard periods after the first wave of hatching continued for 27 or more days, with the remainder having lengths between 17 and 25 days. Guard periods after the second wave of hatching had lengths ranging from 16 to 22 days.

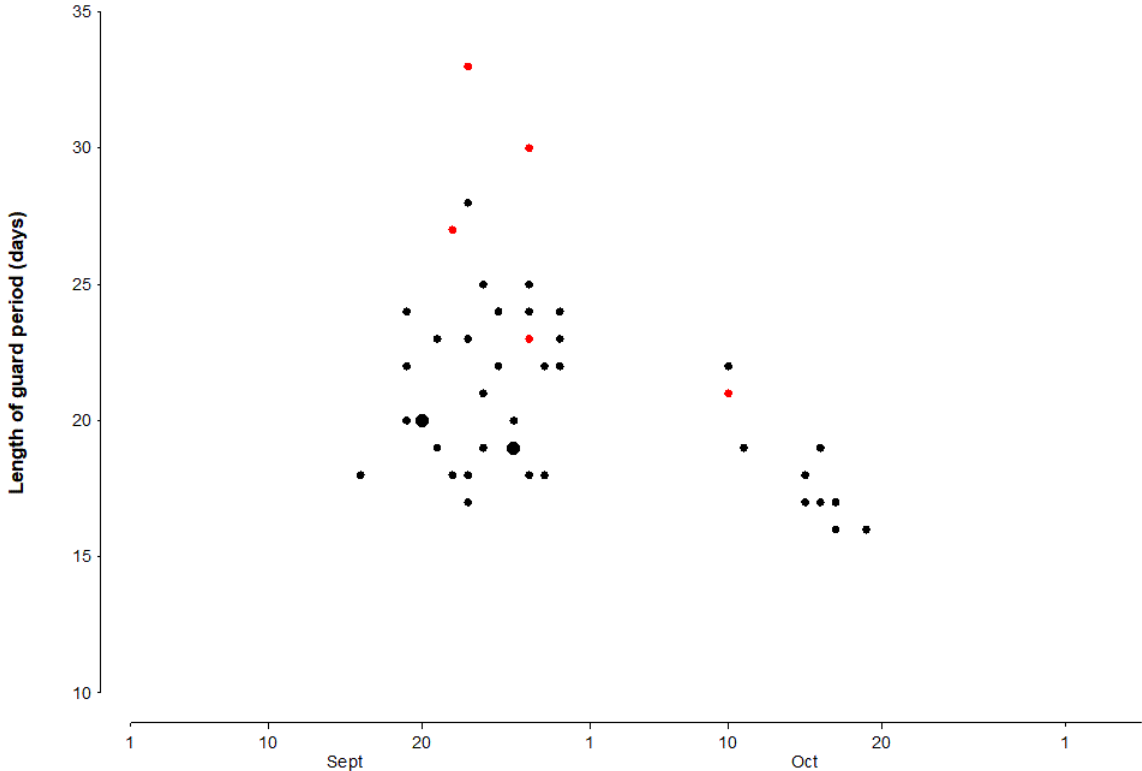


Figure 3.14: Guard periods of Little Penguin breeding pairs that hatched one ● or two ● chicks, plotted by duration between 16 September 2022 and 19 October 2022. Large dots represent two guard periods with the same duration and start date overlapping.

In the case of Figure 3.14 (in contrast to previous dot plots), each dot represents the guard period of a specific breeding pair, with the exception of two large dots which each denote two breeding pairs that began their guard period on the same date, and concluded on the same date.

The mean length of guard periods undertaken by breeding pairs observed was 21.16 ± 0.57 ($n = 43$) days. Table 3.11 records the mean lengths of guard periods for one-chick and two-chick clutches. A Welch's t -test was performed on these data, revealing that the guard periods for one-chick clutches are significantly longer on average than the guard periods for two-chick clutches: $t(4) = 2.834$, $p = 0.042$. It must be noted that only five one-chick clutches were observed, leading to a large discrepancy in sample sizes.

Table 3.11: Mean guard period lengths of one-chick and two-chick Little Penguin clutches that hatched between 16 September 2022 and 19 October 2022.

Clutch size	Mean (days)	SE	n	Minimum length (days)	Maximum length (days)	Range
1	26.80	2.20	5	21	33	12
2	20.42	0.48	38	16	28	12

As previously stated, Figure 3.14 depicts two distinct waves. Excluding one-chick clutches, breeding pairs within the earlier wave had guard periods with a mean length of 21.21 ± 0.51 ($n = 29$) days. Breeding pairs within the later wave had guard periods with a mean length of 17.89 ± 0.63 ($n = 9$) days. Welch's t -test demonstrates that the length of two-chick guard periods in the second wave is significantly shorter than that in the first wave: $t(19.49) = 4.074$, $p = 0.0006$.

3.4 Discussion

The daily nest attendance of individual Little Penguins within breeding pairs has previously been observed only in the Australian colony at Port Phillip by Chiaradia & Kerry (1999). This chapter presents patterns identified from observing the Port Tarakohe colony in New Zealand at a similar level of detail. Some unique findings are discussed below, especially in regards to patterns in incubation spell length. Incubation period and guard period length will also be discussed.

3.4.1 Commentary on preliminary observations

The analysis in Chapter 3 was done under the assumption that only a single breeding pair was present in each nestbox. However, two unusual cases are described in Chapter 3.3.1 where more than one breeding pair occupied a nestbox. These exceptions highlight that there is more variation in Little Penguin breeding behaviour than can be included in this analysis. Future studies could explore these less common breeding arrangements to better understand the full range of behaviours present during Little Penguin breeding seasons. Further limitations are considered in Chapter 4.3.

3.4.2 Incubation periods

The incubation period lengths described in Section 3.3.2 demonstrate consistency with previous findings — the Port Tarakohe colony had a mean incubation period length of 34.41 ± 0.19 days, compared to the mean of previous results in Table 3.1; 35.33 days. Incubation period lengths fell within a very tight band of 33 to 37 days, as seen in Figure 3.6. Noted that this figure only plots the incubation period lengths for breeding pairs that successfully hatched chicks — failed egg incubation was not included, as incubation periods become indefinable after eggs dies.

The cumulative days that male and female parents attended their nestbox during their incubation periods was also recorded in Section 3.3.2. No statistical significance was found between the number of days each parent incubated. Although sources (Chiaradia & Kerry, 1999; Dann, 2013) agree that Little Penguins share parental responsibility, there is no consensus on the exact proportion of breeding duties during the incubation period - only Kinsky (1960) was found to make any mention of this at

all. Saraux et al. (2011b) appears to conflict with these results, but in fact only examines parental care at the post-guard stage.

3.4.3 Incubation spells

The data on incubation spells described in Section 3.3.3 are particularly interesting. Variance in incubation spell length throughout the incubation period appears to take a general form for the majority of breeding birds — it begins with short initial spells, shifts to longer spells in the midsection, and returns to short spells at the end of incubation. This pattern is clearly evident for both male and female parents in Figure 3.13, and is confirmed to be statistically significant through the two-way ANOVA and Šídák method performed in Section 3.3.3. This phenomenon is consistent with previous findings on incubation spell length (Kato et al., 2008; Numata et al., 2000; Weavers, 1992). However, two distinct variations are recorded in the Port Tarakohe results. Figure 3.7 depicts the first variation, recording breeding pairs that preferred to undertake shorter incubation spells overall. Figures 3.8 and 3.9 depict the second variation, recording breeding pairs that preferred to undertake longer incubation spells overall.

To the author's knowledge, these two variations in incubation spell length have not previously been noted in regards to the breeding pairs in a single colony. However, Numata et al. (2000) does make note of (as in Figure 3.2) a similar discrepancy between incubation spell lengths at the Oamaru and Motuara Island Little Penguin colonies. Numata et al. (2000) suggests that this aligns with differences in the average body condition of the population at each colony — specifically; that individuals at Motuara Island were reported to have relatively poorer body condition, necessitating longer foraging trips, and by extension, longer incubation periods from the attending parent. It is likely that a similar phenomenon is at least partially responsible for the variations seen at Port Tarakohe, but further investigation on how body condition affects incubation spell length is necessary for confirmation.

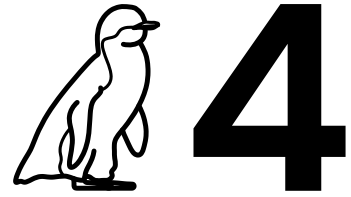
3.4.4 Guard periods

The mean length of guard periods for the breeding pairs at Port Tarakohe — 21.16 ± 0.57 ($n = 43$) days, as recorded in Section 3.3.4 — aligns well with results from previous studies at other colonies, which are listed in Table 3.4. Braidwood (2009) records the most similar mean length of 21.3 ± 1.6

($n = 23$) days for breeding pairs at colonies along the coastline of South Westland, roughly 350 km from Port Tarakohe. The colony on Motuara Island is even closer, only 120 km or so away, but a mean guard period length of only 15.1 ± 1.0 ($n = 12$) days has been recorded there (Numata et al., 2004). As referenced above in regard to incubation period lengths, Numata et al. records in their 2000 paper that Motuara Island breeding pairs were in particularly poor body condition, and suggest in their 2004 paper that this may result in a shortened guard period. This is posited to occur because of the increasing energy demands of growing chicks — in cases where parents are not individually productive enough (due to their own needs, or other factors) to feed their brood, both parents must leave the nest simultaneously to forage, triggering the post-guard period.

Guard period lengths for one-chick and two-chick clutches at Port Tarakohe were found to be significantly different, as demonstrated in results from Welch's t -test in Section 3.3.4. One-chick clutches were observed to have extended guard periods compared to two-chick clutches, a finding that corroborates those from other colonies. Table 3.5 and Figure 3.3 demonstrate the same pattern in South Westland, Oamaru and Motuara Island colonies. It must be noted that the number of one-chick clutches observed at each colony is relatively low, which diminishes the credibility of any one result in isolation — the mean sample size of past papers is five (Table 3.5), and the number of one-chick clutches observed at Port Tarakohe is also five (Table 3.11).

The last notable pattern observed is in relation to the onset of guard for two-chick clutches. Figure 3.14 depicts two waves of hatched chicks: a larger wave with longer guard periods overall, and a smaller, later wave with shorter guard periods overall. The discrepancy in mean guard period length is statistically significant, as noted at the end of Section 3.3.4 — as with other patterns, the lower mean guard period length in the second wave could be attributed to parents' poor body condition.



Conclusions

4.1 Thesis overview

This study is the first to look closely at Little Penguin nest attendance specifically during the breeding season. Though breeding pair attendance and annual individual attendance have previously been reported, mainly at the Port Phillip colony in Australia (Chiaradia & Kerry, 1999; Reilly & Cullen, 1981), this thesis investigates nest attendance through multiple lenses. The cumulative findings in Chapter 2 and Chapter 3 represent the second-ever published investigation into the daily nest attendance patterns of Little Penguins during the breeding season, and the first-ever New-Zealand-based study to examine nest attendance from day to day. This study is also the first to record and analyse data on Little Penguins at the Port Tarakohe colony.

Chapter 2 investigates nestbox attendance through the categories of breeding and non-breeding birds, defined here as individual birds that are present in their nestbox either with or without offspring (eggs or chicks). Analysis in this chapter first focused on the fluctuating number of occupied (and unoccupied) nestboxes within the colony as it moved through waves of egg-laying, incubation, and guard. The second point of focus was on the birds themselves, categorised by gender and breeding status. Special attention was paid to the behaviour of non-breeding birds during the breeding season,

both in relation to early-stage breeding and to the lunar cycle. Observations made throughout Chapter 2 about breeding birds were generally consistent with several prior studies, with several novel insights in regards to egg-laying, breeding pair attendance, and non-breeding bird attendance.

Chapter 3 delves more deeply into data from the daily nestbox monitoring to uncover patterns in the nestbox attendance of breeding pairs. Analysis first focused on incubation periods, and the meta-patterns of attendance within those, before shifting to look closely at the length of incubation spells for males and females. Guard period lengths and timing were the final point of discussion in the chapter. The high frequency of data collection in this study enabled the observation of more specific variations in incubation and guarding compared to prior studies, and provided greater resolution and context for previously-recorded patterns.

4.2 Notable findings

The goal of Chapter 2 was to examine overall colony attendance during the breeding season by examining breeding and non-breeding nestboxes and birds, with a secondary focus on attendance in relation to lunar phases. Observations within this section include:

1. Pairs of Little Penguins synchronised their nestbox attendance within July, August, and September, corresponding to the courtship, egg-laying and incubation phases respectively.
2. Egg-laying occurred in distinct, synchronised waves. Synchronisation in egg-laying is also apparent in Robinson et al. (2005), but this study notably records distinct, separated periods of egg-laying within a single season.
3. Courtship was observed to occur one month prior to egg-laying for multiple waves (as mentioned above). This corroborates an identical one-month gap between courtship and egg-laying observed by Chiaradia & Kerry (1999).
4. The nestbox attendance of parents in differing breeding pairs was recorded to synchronise over the incubation and guard periods with parents of the same sex arrived at and departed from the colony at the same time. This finding is novel, to the author's knowledge.
5. Non-breeding penguins exhibited a cycle of nestbox attendance that fluctuated over approximately four weeks. This pattern was evident during daily and weekly nestbox checks, and strongly indicates synchronised behaviour among colony members. This finding mirrors the results of Reilly & Cullen (1981), which record a three-weekly cycle in overall colony attendance in the months before breeding commences.

The nestbox attendance of non-breeding penguins in relation to the lunar cycle was another topic of exploration. During the early months of the breeding season, non-breeding individuals were observed in slightly greater numbers close to the times of full moons, but this effect did not reach statistical significance.

The goal of Chapter 3 was to investigate breeding pair attendance in regards to incubation periods, incubation spells, and guard periods observed during the greater breeding season. Observations within this section include:

1. The mean incubation period length for breeding pairs at Port Tarakohe was found to align with those recorded at other colonies (Chiaradia & Kerry, 1999; Kato et al., 2008; Kemp & Dann, 2001).
2. Male and female parents within observed breeding pairs displayed similar cumulative nestbox attendance over their incubation periods. This extends the general notion that Little Penguin parents share parental duties (Chiaradia & Kerry, 1999; Dann, 2013) to the incubation period specifically.
3. The lengths of incubation spells exhibited by breeding pairs rose and fell predictably during the greater incubation period, in a manner similar to previously described patterns (Kato et al., 2008; Weavers, 1992). However, two differing variations of this pattern were seen — one with relatively shorter incubation spell lengths, and the other with relatively longer ones. This is similar to observations from two different colonies made by Numata et al. (2000).
4. The mean guard period length for breeding pairs at Port Tarakohe was found to align with those recorded at other colonies (Braidwood, 2009; Chiaradia & Nisbet, 2006; Chiaradia & Kerry, 1999; Numata et al., 2004).
5. One-chick clutches were observed to be guarded for longer than two-chick clutches, which supports prior observations by Numata et al. (2004) and Braidwood (2009) at other colonies.
6. Start times for the guard periods of two-chick clutches were observed to occur in two distinct waves. The larger, earlier wave had significantly longer average lengths than the smaller, later wave.

4.3 Learnings, limitations, and future studies

This thesis aims to provide more insight into Little Penguin breeding behaviour, in the hopes that knowledge of their comings and goings will help us learn how to conserve and protect *Eudyptula minor* parents and offspring during the breeding season and beyond.

Several constraints and limitations in this study should be acknowledged. The first category is in regard to the general data collection protocol employed:

- The intermittent nestbox checks described as ‘weekly’ in prior sections reduce data resolution and introduce ambiguity into the observed patterns.
- Variation in the timing of nestbox checks throughout each day may have introduced inconsistency into attendance data, as recorded ‘days’ may have been intermittently shorter or longer than exact 24-hour periods.
- Technical difficulties with microchip reading occasionally led to prolonged amounts of time spent at certain nestboxes over the course of observation. Increased interaction with penguins present at these nestboxes could have elevated stress levels or otherwise influenced behaviour, potentially leading to nest abandonment.
- All data for this study were collected within a single breeding season, making the dataset susceptible to environmental anomalies.
- The study site is relatively enclosed by a car barrier and gate and is not known as a recreational area. However, occasional human activity has been observed, including dogs being walked nearby, people fishing and at least one instance of attempts to open nestboxes.

These first limitations may be overcome through the use of a more rigorous data collection protocol and by increasing temporal coverage. The timing of future studies may also be increased in two ways. Beginning daily nestbox checks earlier and/or ending them later would increase data resolution, and may reveal more detail in observed patterns. Extending future studies across multiple breeding seasons may enable future researchers to capture broader trends across annual variations in behaviour.

Moving to potential topics for future study, the first is a more in-depth analysis on how the lunar cycle (and other sources of light) affect Little Penguin colony attendance. A strong follow-up to this

study would be to assess the effect of the lunar cycle on colony attendance, both inside and outside the breeding season. Another potential avenue for future study would be the selection of a broader set of environmental factors, and subsequent data collection on the influence of those factors upon colony attendance. Distinguishing the effects of environmental variability from general reproductive behaviours would provide a clearer picture of central drivers behind Little Penguin colony attendance. A third research recommendation, particularly relevant to this study's findings on incubation spell and guard period variation, is to assess the effect of body condition on nest attendance within and of breeding pairs. Finally, an area of particular interest is the unexplained synchrony between the nestbox attendance of male and female members within separate breeding pairs. The identification of synchronised patterns of incubation spells — both short (more frequent) and long (less frequent) — across multiple breeding pairs presents an opportunity for further research into the mechanism allowing this synchronisation, potentially yielding valuable insights into Little Penguin socialisation.

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<https://doi.org/10.1371/journal.pone.0016098>

Appendix A: Statistical analysis in Python

```
from re import X
import numpy as np
import matplotlib.pyplot as plt
from scipy.optimize import curve_fit
from scipy.signal import find_peaks
from datetime import datetime, timedelta
# Import the dataset
x_original = np.array([185, 186, 191, 192, 194, 198, 203, 205, 210, 216,
                       222, 235, 246, 247, 248, 249, 250, 251, 252, 253,
                       254, 255, 256, 257, 258, 259, 260, 261, 262])
y = np.array([0, 0, 13, 14, 60, 124, 101, 41, 5, 10, 79, 8, 18, 24, 40,
              43, 52, 49, 58, 47, 54, 37, 31, 23, 20, 14, 9, 8, 3])
# Shift x values so that the minimum starts at zero
x_shifted = x_original - np.min(x_original)
# Define the sum of Gaussians function
def gaussian_model(x, a1, mu1, sigma1, a2, mu2,
                  sigma2, a3, mu3, sigma3, d):
    return (a1 * np.exp(-((x - mu1) ** 2) / (2 * sigma1 ** 2)) +
            a2 * np.exp(-((x - mu2) ** 2) / (2 * sigma2 ** 2)) +
            a3 * np.exp(-((x - mu3) ** 2) / (2 * sigma3 ** 2)) + d)
# Estimate initial peak positions based on rough observations
mu_initial = [20, 50, 80]
gaussian_initial_guesses = [50, mu_initial[0], 10,
                             40, mu_initial[1], 10,
                             30, mu_initial[2], 10, 5]
# Fit the model to the data
try:
    popt_gaussian, _ = curve_fit(gaussian_model, x_shifted, y,
                                p0=gaussian_initial_guesses, maxfev=10000)
    y_gaussian_fit = gaussian_model(np.linspace(min(x_shifted),
                                                max(x_shifted), 200), *popt_gaussian)
except RuntimeError: y_gaussian_fit = np.zeros_like(x_shifted)
```

```

# Generate smooth x values for plotting the fitted curve
x_fit = np.linspace(min(x_shifted), max(x_shifted), 200)
# Find gaussian peaks
peaks, _ = find_peaks(y_gaussian_fit)
# Set the reference date (4th of July)
base_date = datetime(2022, 7, 4)
# Function to convert y-values to date
def y_to_date(y_value):
    return base_date + timedelta(days=int(round(y_value)))
# Plot the original data and fitted Gaussian curve
plt.figure(figsize=(10, 6))
plt.scatter(x_shifted, y, color='blue', label='Number of birds')
plt.plot(x_fit, y_gaussian_fit, 'g-',
         label='Sum of Gaussians fit', linewidth=2)
plt.plot(x_fit[peaks], y_gaussian_fit[peaks],
         'rx', label='Attendance peaks')
for peak in peaks:
    x_label = round(y_gaussian_fit[peak])
    y_label = y_to_date(x_fit[peak])
    # Format the date as D Mon (e.g., 1 Jan)
    date_str = y_label.strftime('%-d %b')
    # Adding the text label to the plot
    plt.text(x_fit[peak],
            y_gaussian_fit[peak] + 5,
            f'{x_label}, {date_str}',
            fontsize=9, verticalalignment='bottom',
            horizontalalignment='center')
plt.ylim(bottom=min(y_gaussian_fit), top=max(y_gaussian_fit) + 10)
# Draw lines between peaks and label the period in days
period = []
for i in range(1, len(peaks)):
    x1, x2 = x_fit[peaks[i-1]], x_fit[peaks[i]]
    y1, y2 = y_gaussian_fit[peaks[i-1]], y_gaussian_fit[peaks[i]]
    # Plot a line between consecutive peaks
    plt.plot([x1, x2], [y1, y1], 'gray', linestyle='--', lw=1)
    plt.plot([x1, x1], [y2, y1], 'gray', linestyle='--', lw=1)

```

```

# Calculate the period in days (difference in x-values)
period.append(abs(x2 - x1))
formattedPeriod = '{:.2f}'.format(round(period[i - 1], 2))
# Add label for the period between peaks
mid_x = (x1 + x2) / 2 # Midpoint of the line for the label
plt.text(mid_x, y1, f'{formattedPeriod} days',
         fontsize=9, verticalalignment='bottom',
         horizontalalignment='center')

# Log average period
# print(round(sum(period) / len(period)))
plt.xlabel('Days (starting from 4 July)')
plt.ylabel('Number of birds')
plt.legend()
plt.title("Sum of Gaussians fit to non-breeding bird attendance")
# Save as vector
plt.savefig("graph.svg")
plt.draw()

```

Appendix B: Raw daily nestbox check data

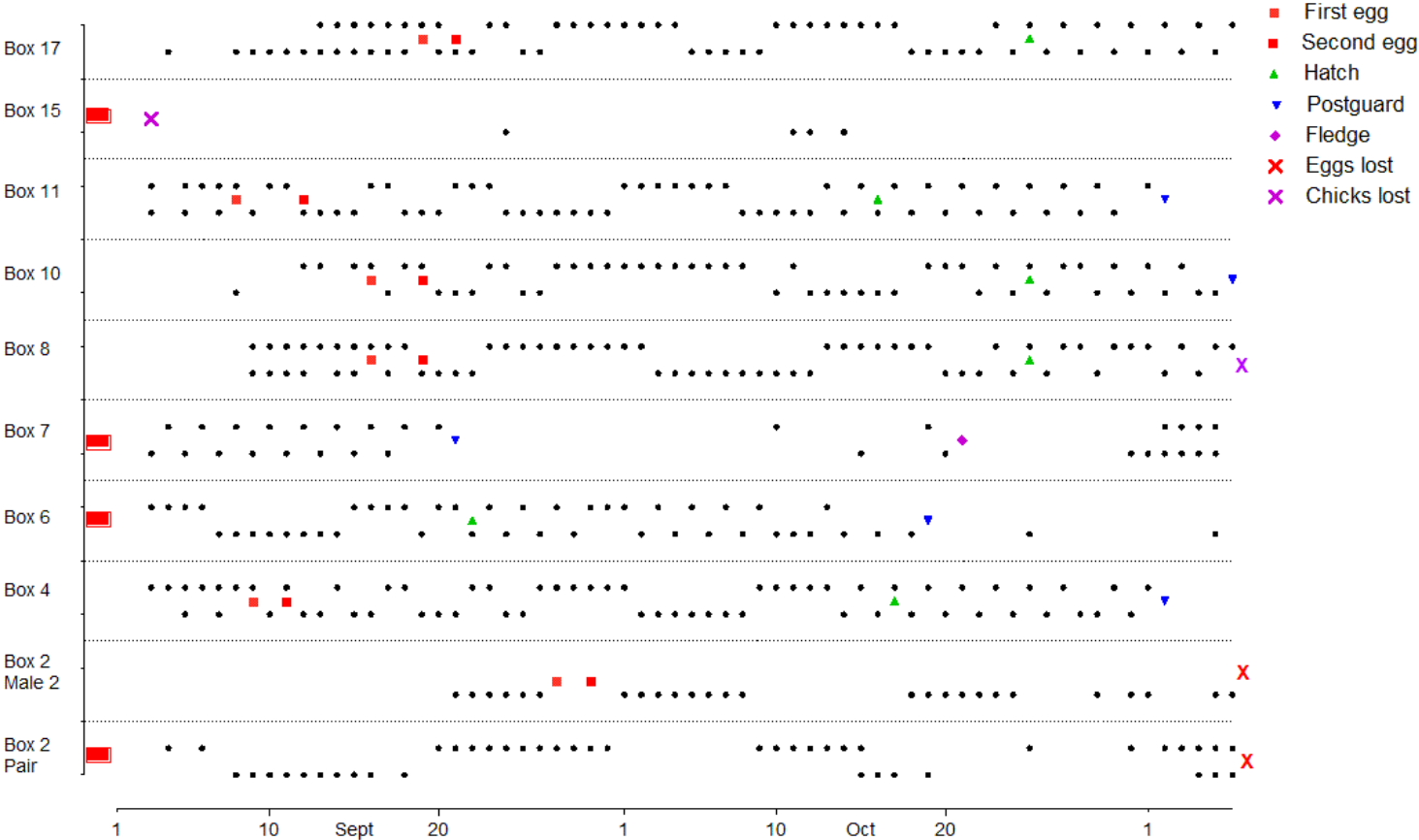


Figure B1: Attendance of birds in Nestboxes 2, 4, 6, 7, 8, 10, 11, 15 and 17 from 3 September 2022 to 6 November 2022. The top row of data points for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox during the day. Red boxes indicate that eggs had been laid before daily nestbox checks started.

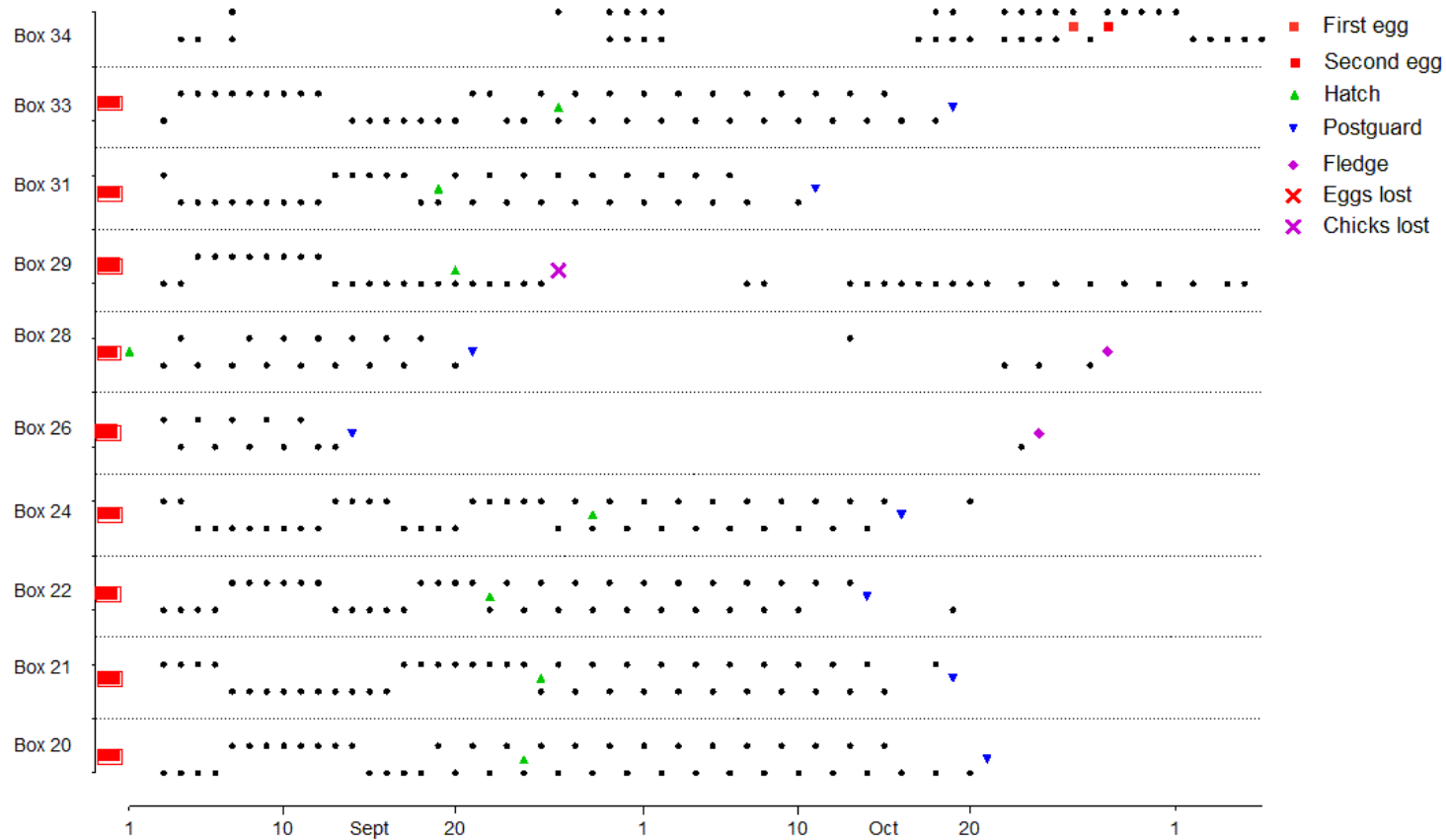


Figure B2: Attendance of birds in Nestboxes 20, 21, 22, 24, 26, 28, 29, 31, 33 and 34 from 3 September 2022 to 6 November 2022. The top row of data points for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox during the day. Red boxes indicate that eggs had been laid before daily nestbox checks started.

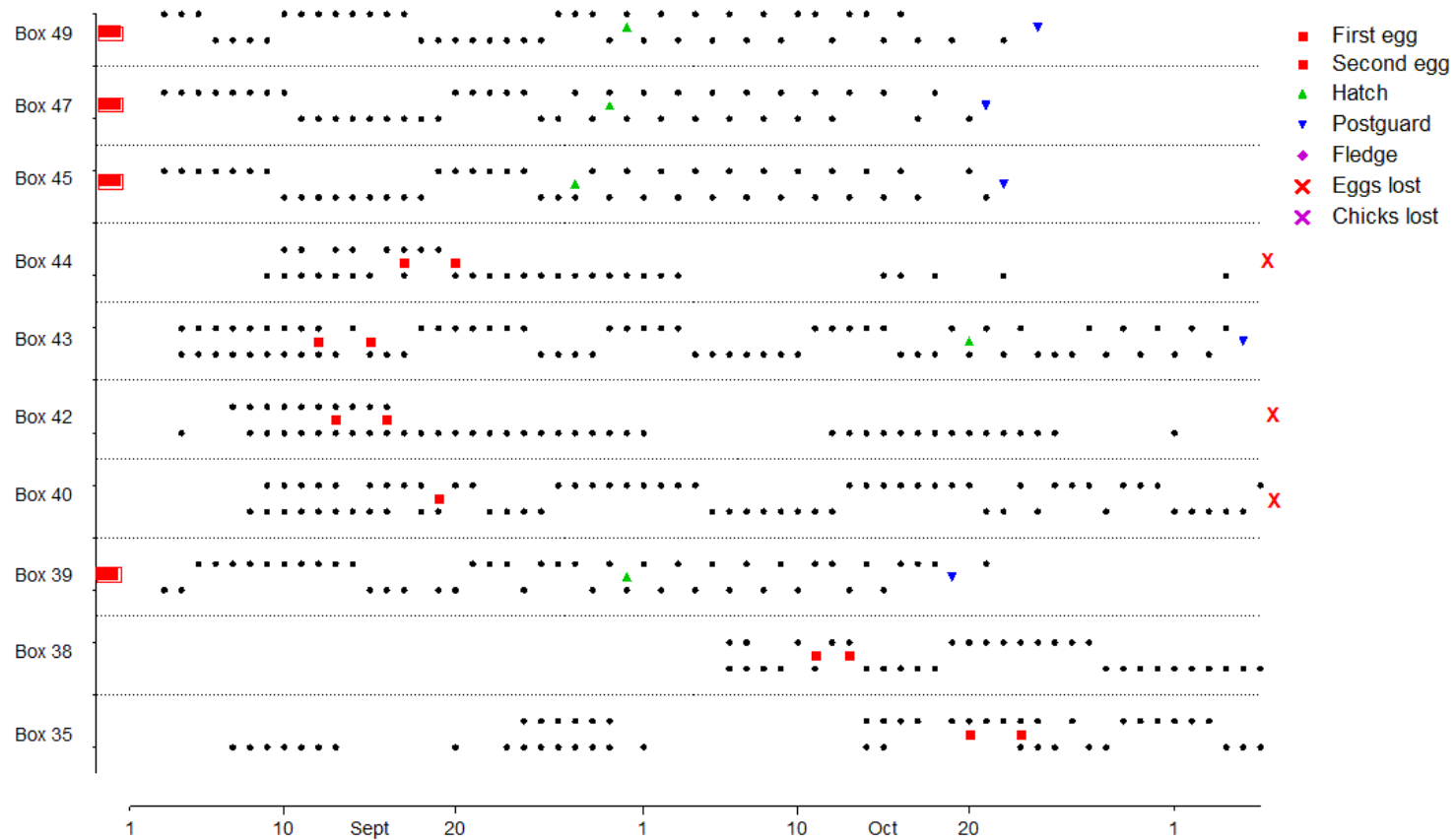


Figure B3: Attendance of birds in Nestboxes 35, 38, 39, 40, 42, 43, 44, 45, 47 and 49 from 3 September 2022 to 6 November 2022. The top row of data points for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox during the day. Red boxes indicate that eggs had been laid before daily nestbox checks started.

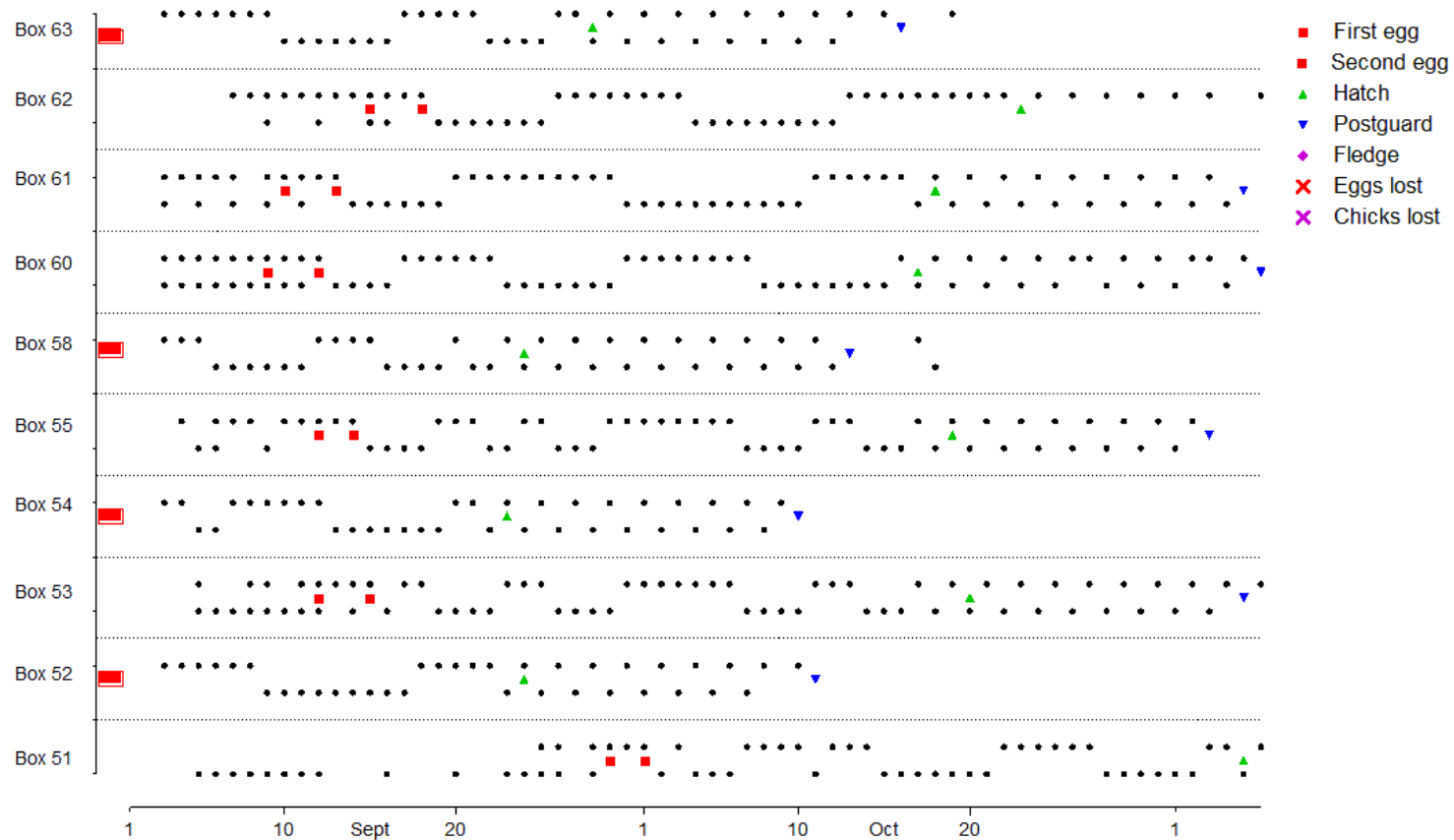


Figure B4: Attendance of birds in Nestboxes 51, 52, 53, 54, 55, 58, 60, 61, 62 and 63 from 3 September 2022 to 6 November 2022. The top row of data points for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox during the day. Red boxes indicate that eggs had been laid before daily nestbox checks started.

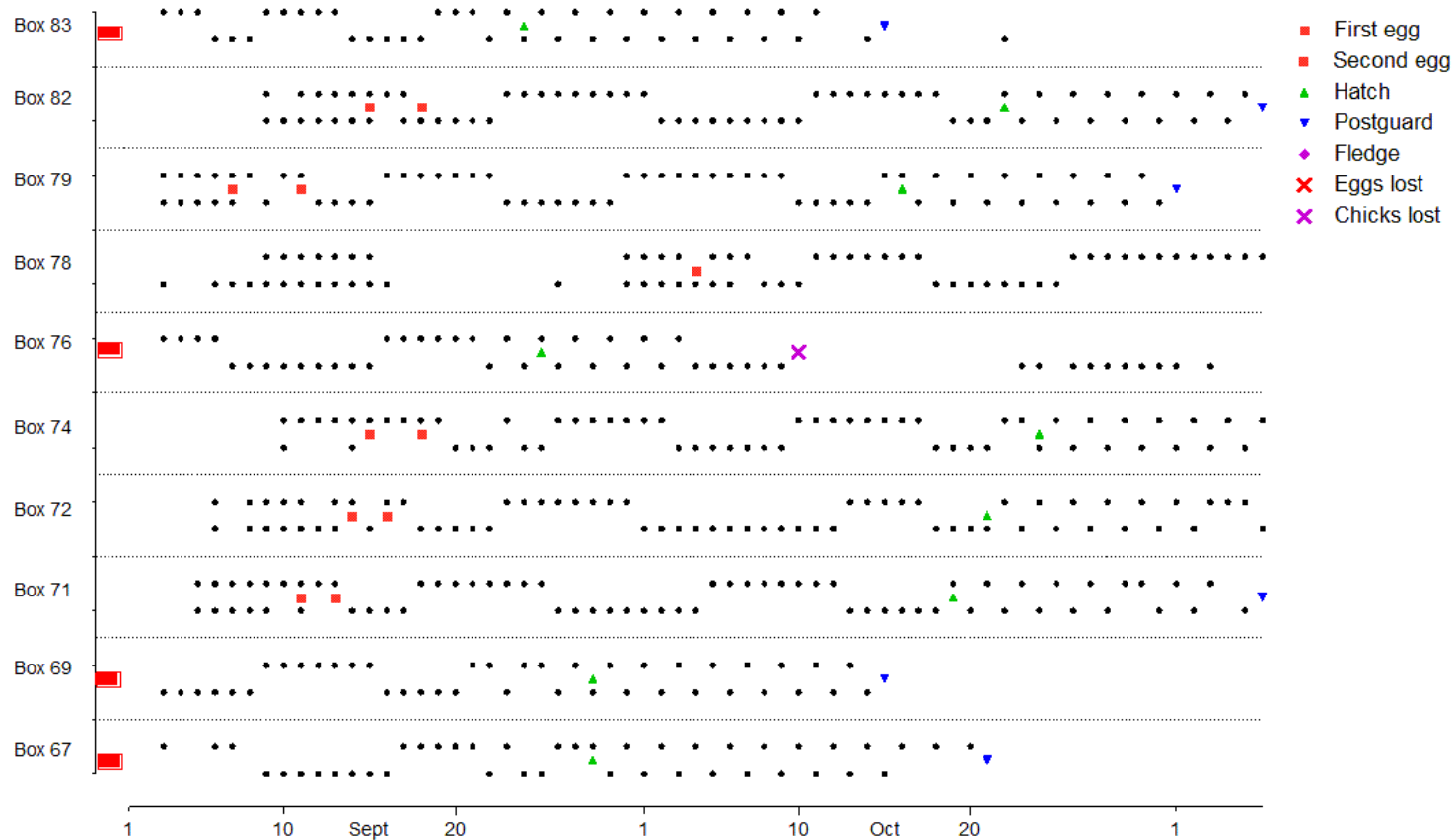


Figure B5: Attendance of birds in Nestboxes 67, 69, 71, 72, 74, 76, 78, 79, 82 and 83 from 3 September 2022 to 6 November 2022. The top row of data points for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox during the day. Red boxes indicate that eggs had been laid before daily nestbox checks started.

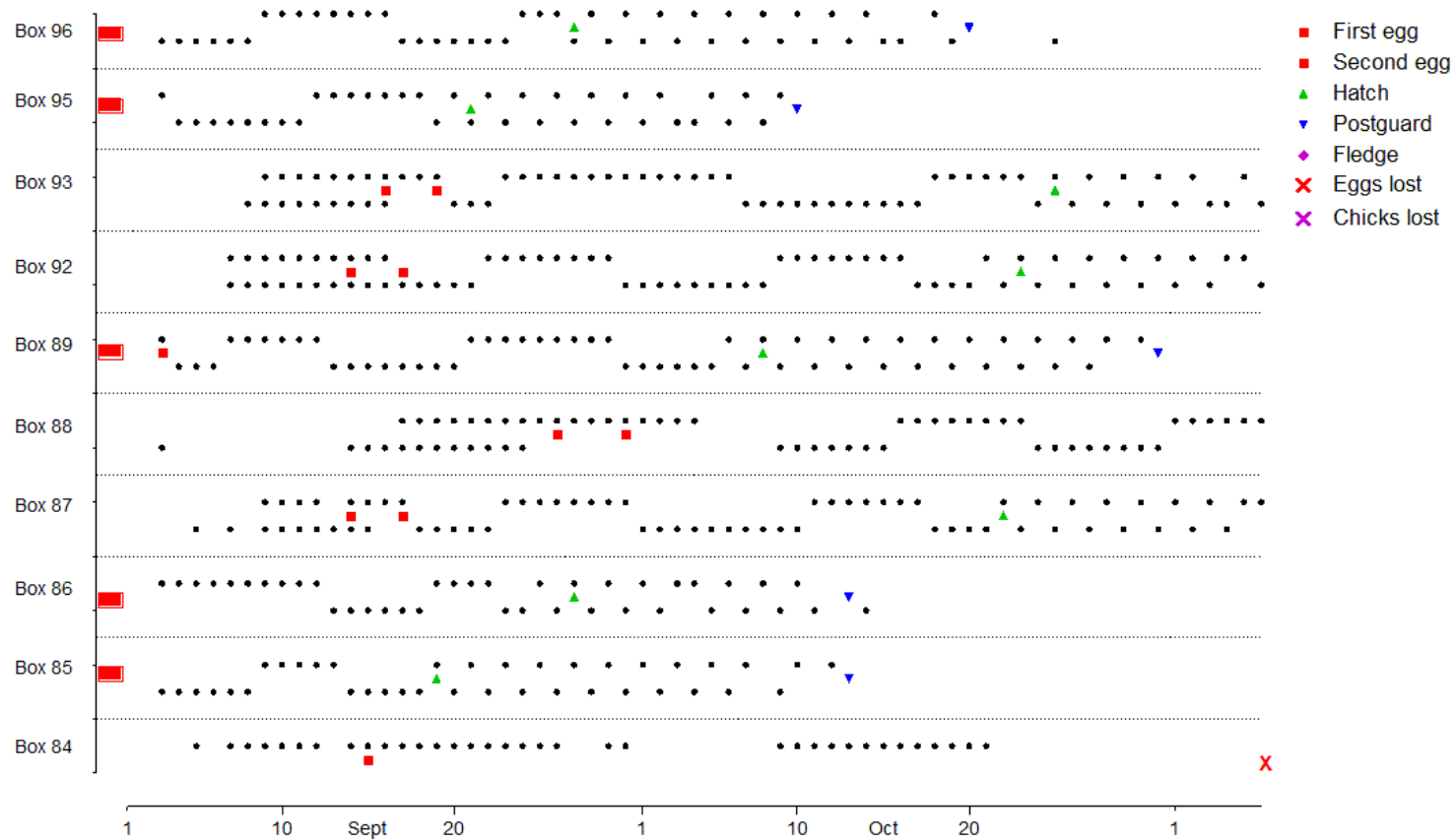


Figure B6: Attendance of birds in Nestboxes 84, 85, 86, 87, 88, 89, 92, 93, 95 and 96 from 3 September 2022 to 6 November 2022. The top row of data points for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox during the day. Red boxes indicate that eggs had been laid before daily nestbox checks started.

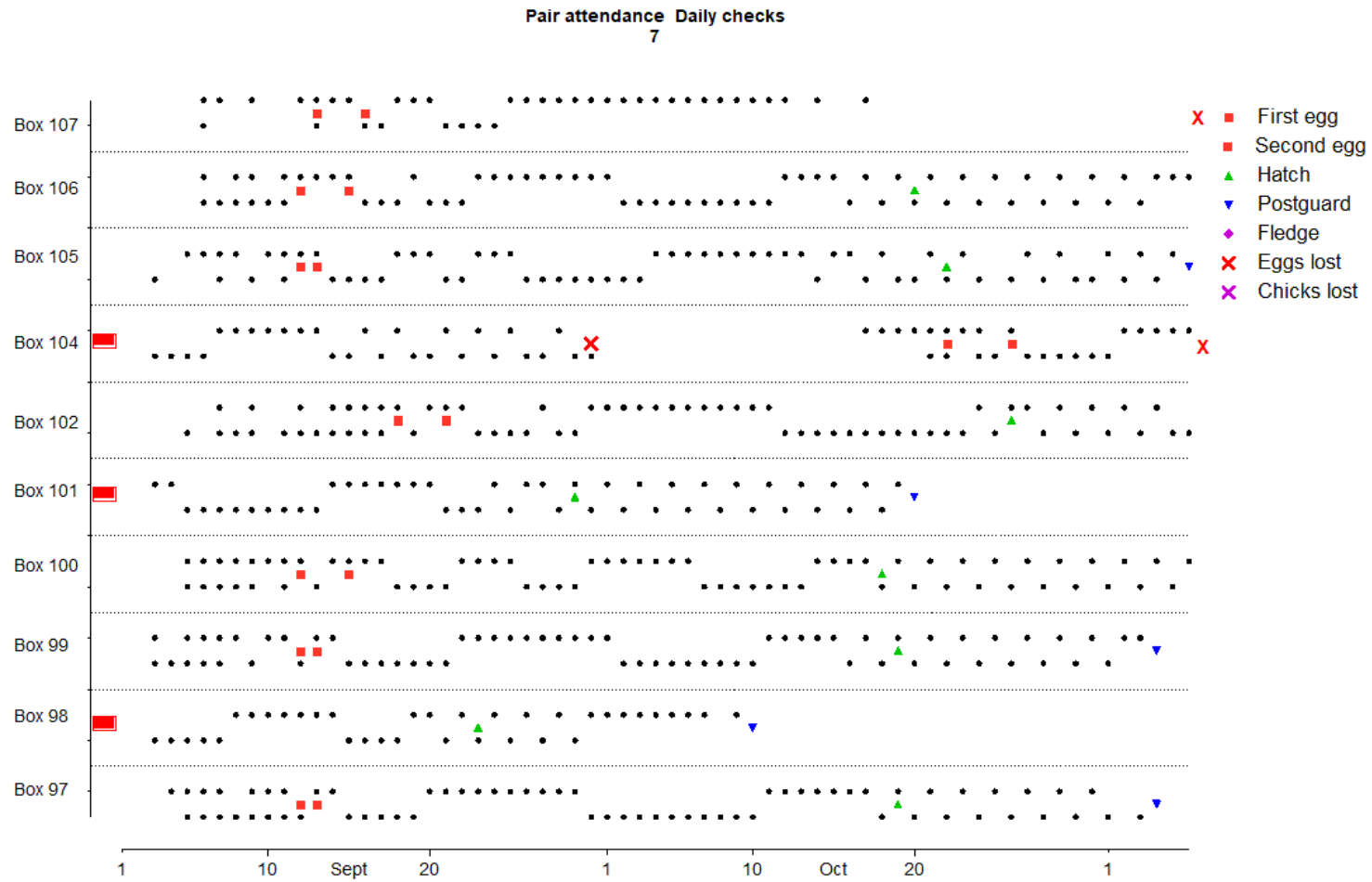


Figure B7: Attendance of birds in Nestboxes 97, 98, 99, 100, 101, 102, 104, 105, 106 and 107 from 3 September 2022 to 6 November 2022. The top row of data points for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox during the day. Red boxes indicate that eggs had been laid before daily nestbox checks started.

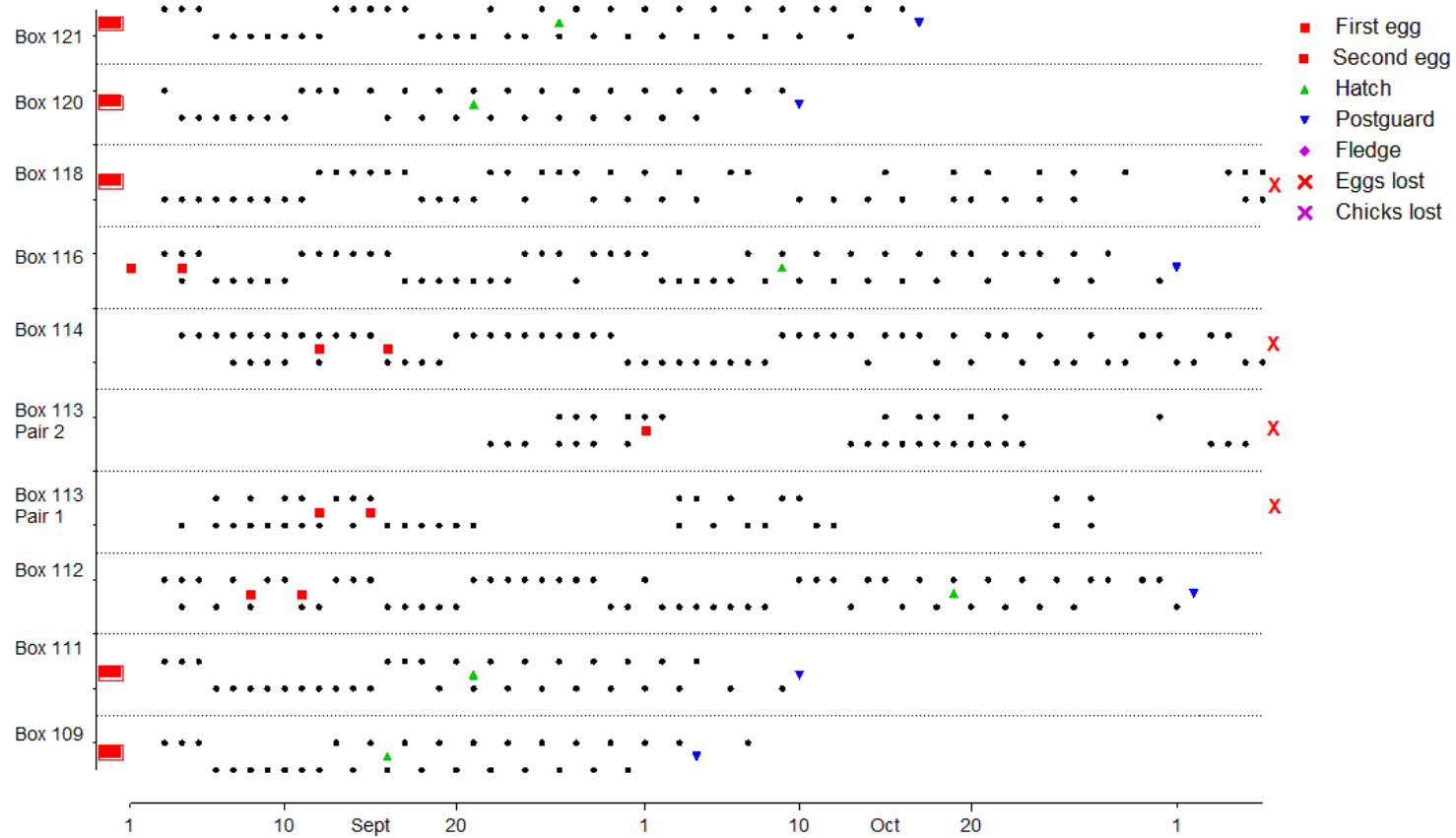


Figure B8: Attendance of birds in Nestboxes 109, 111, 112, 113, 114, 116, 118, 120 and 121 from 3 September 2022 to 6 November 2022. The top row of data points for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox during the day. Red boxes indicate that eggs had been laid before daily nestbox checks started.

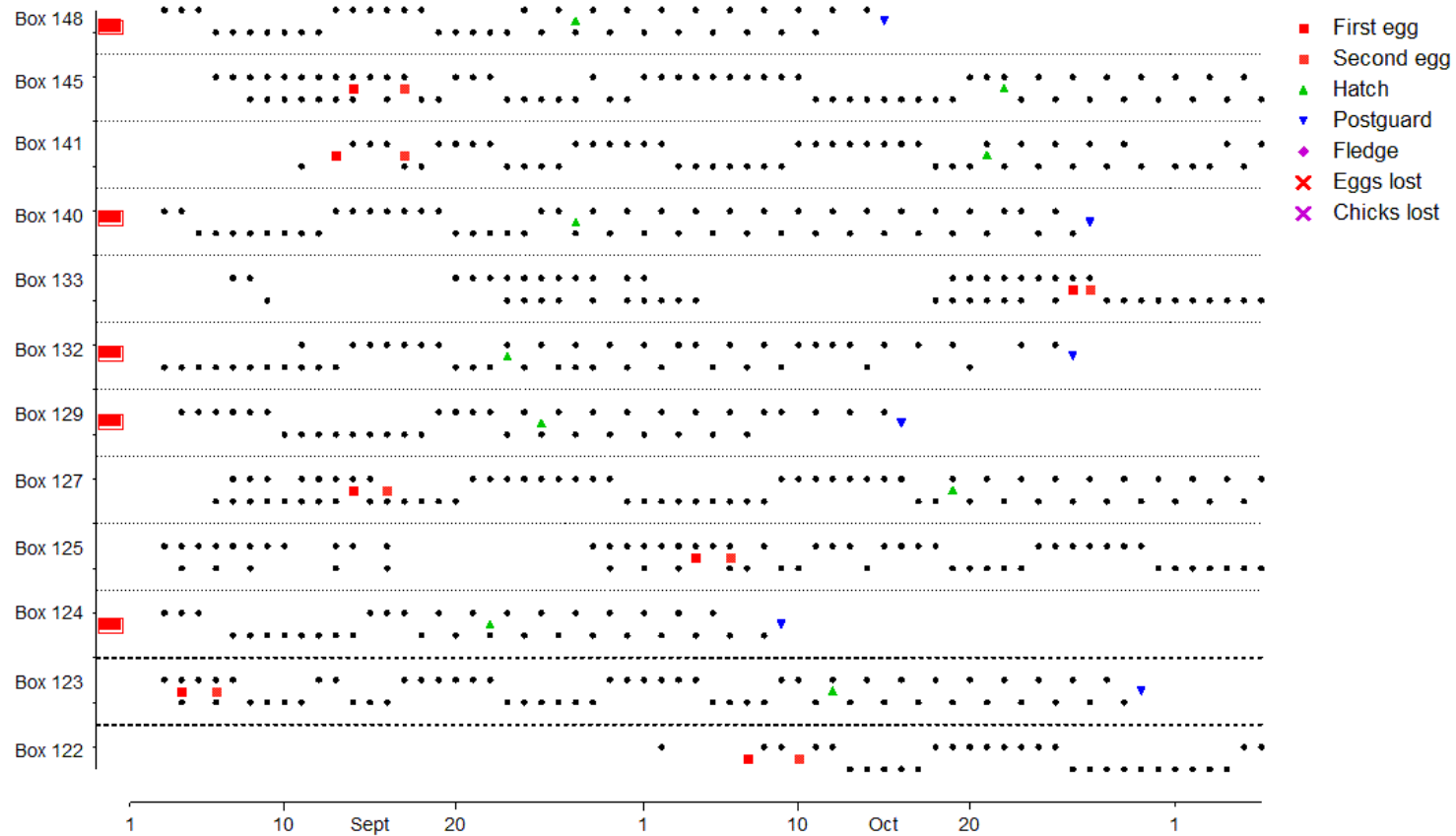


Figure B9: Attendance of birds in Nestboxes 122, 123, 124, 125, 127, 129, 132, 133, 140, 141, 145 and 148 from 3 September 2022 to 6 November 2022. The top row of data points for each nestbox represents the female bird, and the bottom row the male bird. Each black circle denotes a bird present in the nestbox during the day. Red boxes indicate that eggs had been laid before daily nestbox checks started.

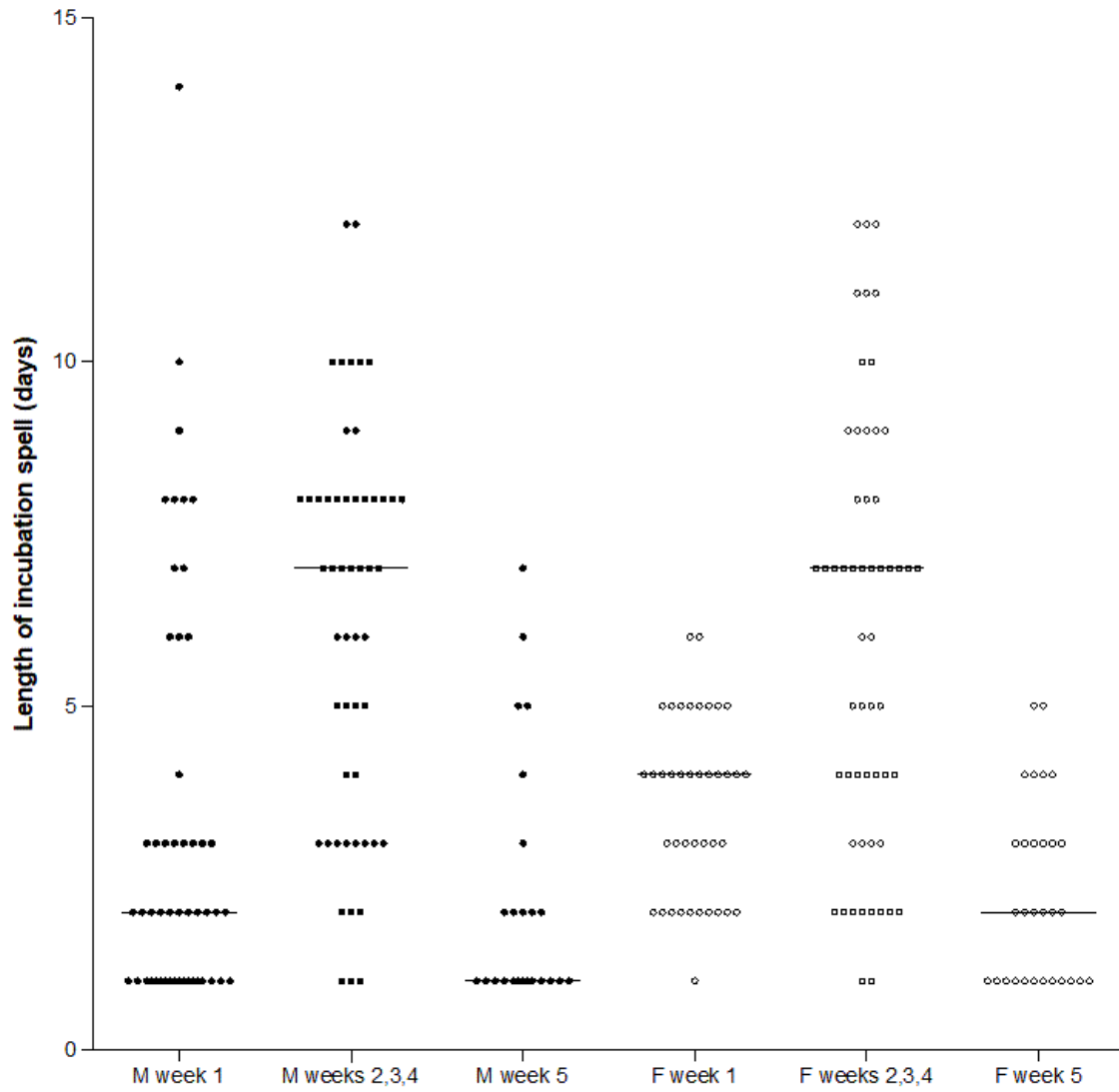


Figure B10: Quantities and lengths of male ● and female ○ Little Penguin incubation spells between 3 September 2022 and 6 November 2022, grouped temporally and by sex.