Autumn and winter patterns of nest site attendance and behaviour by little penguins (*Eudyptula minor*)

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Abstract

Little penguins are widespread around eastern and southern Australia, the coast of New Zealand and neighbouring islands, with various sized colonies distributed irregularly throughout these locations. There are many studies on little penguin colony attendance and behaviour during the breeding season, yet little is known about their autumn and winter behaviours at the colony. There have been varying reports of little penguin colony attendance, some with regular attendance patterns and others without. The present study was conducted to investigate colony attendance and behaviour of little penguins during autumn and winter. During April – July 2021, colony attendance, body condition, nestbox occupancy, individual colony attendance behaviours and penguin pairing of 205 little penguins (*Eudyptula minor*) were examined at the Port Tarakohe colony in Golden Bay on the South Island of New Zealand. Nestboxes were checked every two days during April and May and then twice a week during June and July. Previously published data of colony attendance and body weight was also analysed for comparison with Port Tarakohe data. I found a three-and-a-half-week cycle of colony attendance with 0 to 106 penguins being present at the colony at any given time. Body weights did not increase during these months, and the colony attendance cycle was not influenced by the lunar phase. A majority of penguins stayed loyal to one nestbox (60%) and one 'partner' (75.6%) during these months, but some individuals were sighted in anywhere up to seven different nestboxes or with four other penguins. Individual penguins displayed varying colony attendance patterns, with many penguins showing clear patterns of presence and absence, and some pairs showing signs of synchronisation. There was a significant difference in the time little penguins spent on land in their nestbox compared to at sea, with penguins spending, on average, one week on land and two weeks at sea. This is the first study to show that little penguins in the South Island of New Zealand have cyclic colony attendance patterns in autumn and winter. It is

also the first study to report individual differences in little penguin autumn and winter behaviours and can be used as a baseline for future studies.

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1. Introduction

1.1 General description

Kororā/Little penguin (also known as “blue penguin”, “little blue penguin” or “fairy penguin”) are the smallest penguin in the world, standing at around 30-40 cm tall and weighing about 1 kg (Davis and Renner, 2003; Gwatkin, 2025; Hadden *et al.*, 2020; Stahel and Gales, 1987). There is a substantial overlap in size between sexes, however male penguins tend to be slightly larger and heavier than females and have greater bill depths (Gales and Green, 1990; Klomp and Wooller, 1991; Reilly and Cullen, 1979). Little penguins are flightless and are the only penguin species that are nocturnal on land, where they breed and moult annually (Heber *et al.*, 2008; Peucker *et al.*, 2009). They have dense waterproof plumage which is dark in colour on their back and white on their chest (Stahel and Gales, 1987). This acts as camouflage and is a prevalent colour pattern across penguin species (Kooyman and Lynch, 2013). The colour varies from pale blue to dark grey-blue and is dependent on the penguins age and season of the year. Sometimes they may even have grey and brown colouration, especially around the face (Davis and Renner, 2003). The diet of little penguins mainly consists of fish such as pilchard, anchovies, and sprat, but they may also eat crustaceans and cephalopods such as krill and squid (Cullen *et al.*, 1991; Davis and Renner, 2003; Klomp and Wooller, 1988). Chiaradia *et al.* (2003) found that other fish species such as red cod, blue warehou and barracouta also play a vital role in little penguins’ diet when their usual food supply is in shortage. On average, little penguins live around six and a half to seven years of age, however many little penguins have lived well beyond their average life expectancy (Chiaradia, 2022; Dann *et al.*, 2005; Peucker *et al.*, 2009; Reilly and Cullen, 1979). They have been found to live up to 20 years or more with the oldest known little penguin living to be around 25 years and 8 months old (Dann *et al.*, 2005; Joly *et al.*, 2023).

1.2 Taxonomy

Little penguins belong to the family Spheniscidae (Order Sphenisciformes) and are the only living penguin species of the genus *Eudyptula* (Fowler and Fowler, 2001; Waas, 1990). The taxonomy of *Eudyptula* at the species level is still unclear. Based on the two little penguin specimens found, it was originally thought that there were two different species. *Eudyptula minor* was described by Forster in 1781 based on a specimen found in Dusky Sound in the South Island of New Zealand. The white-flippered penguin (*Eudyptula albosignata*) was described by Finsch in 1874 based on a specimen found at Akaroa Harbour, Banks Peninsula (Banks *et al.*, 2002; Grosser *et al.*, 2017). However, in 1976, Kinsky & Falla reclassified the *Eudyptula* penguins into one species with six subspecies by using morphometric data (Banks *et al.*, 2002; Grosser *et al.*, 2017; Ksepka and Ando, 2011). The six species they recognised were *E. m. iredalei* which breed around the northern North Island of New Zealand, *E. m. variabilis* which breed around the southern North Island and Cook Straight, *E. m. albosignata* which breed on Motunau Island and Banks Peninsula, *E. m. minor* which breed around Southland, Otago and the West Coast of the South Island, *E. m. chathamensis* which breed on the Chatham Island and *E. m. novaehollandiae* which breed in Australia (Banks *et al.*, 2002). More recent evidence suggests that there may be two clades (Grosser *et al.*, 2017; Ksepka and Ando, 2011). One being penguin populations from Australia and Otago and the other being populations from the rest of New Zealand, including the Chatham Islands (Banks *et al.*, 2002; Banks *et al.*, 2008; Grosser *et al.*, 2017). The classification of little penguins is still uncertain, so for now, until further clarification, they are all considered to be one species: *Eudyptula minor* (Rowe *et al.*, 2020).

1.3 Distribution and habitat

Little penguins are colonial, burrow-nesting seabirds that are widespread around eastern and southern Australia, the coast of New Zealand and neighbouring islands. Their colonies are distributed irregularly throughout these locations and colony size can vary greatly from a few pairs to thousands of individuals (Banks *et al.*, 2002; Peucker *et al.*, 2009; Ratz, 2019). Little penguins are the only penguin species that are strictly nocturnal on land, even though they are diurnal foragers, and they also use land for their annual moult as well as for breeding (Peucker *et al.*, 2009; Rodriguez *et al.*, 2016). They are highly philopatric, tending to return to their natal breeding sites, although, fledglings have been observed migrating to non-natal colonies to breed and have been known to travel hundreds of kilometres (Cargill *et al.*, 2022; Peucker *et al.*, 2009). Little penguin come ashore after dusk and return to the sea before sunrise (Klomp and Wooller, 1991; Stahel and Gales, 1987). They generally nest among sand dunes, under bushes or tussock, within caves or rock crevices, under driftwood, under buildings or other man-made structures, inside natural burrows or in artificial nestboxes (Heber *et al.*, 2008; Ropert-Coudert *et al.*, 2004; Stahel and Gales, 1987). It isn't easy to define what a typical little penguin burrow is like, but, many consist of a tunnel or entrance with a nest bowl at the end of it, often containing plant-based nesting material (Stahel and Gales, 1987). When nestboxes are provided, little penguins readily use them for breeding and moulting (Ratz, 2019). They have been found to improve breeding success and increase local penguin population numbers too (Sutherland *et al.*, 2014). Perriman and Steen (2000) found that breeding success was generally higher for penguins breeding in artificial nestboxes than in natural nests and Sutherland *et al.* (2014) found that survival rates and fledging weights of penguin chicks were higher when using nestboxes, making them a useful conservation tool.

1.4 Threats

The IUCN (International Union for Conservation of Nature) classify little penguin as ‘least concern - stable’, while in New Zealand, DOC (Department of Conservation) classifies little penguin as ‘at risk – declining’ (Rowe *et al.*, 2020). In Australia, most mainland colonies of little penguins have declined over time in both size and numbers, and many are now extinct. In New Zealand, little penguin populations on the mainland also appear to be declining, but there is no evidence in decreasing colony numbers on offshore islands. Predation on land, habitat modification, habitat destruction and being hit by cars are some of the main threats to little penguin on the New Zealand mainland (Priddel *et al.*, 2008). Other threats such as climate change (Dann and Chambers, 2013), predation at sea (Costello and Colombelli-Négrel, 2023) parasites/disease (Harrigan, 1991; Sijbranda *et al.*, 2017), lack of food (Dann *et al.*, 2000), and trauma (Cannell *et al.*, 2016) are also a problem.

1.5 Annual cycle

The annual cycle of little penguins consists of nest building, egg laying, incubation, chick raising (guard and post-guard stages), pre-moult foraging, annual moult and other non-breeding activities (Stahel and Gales, 1987). The cycle can be quite variable with the timing of breeding varying both within and between years and can reflect the seasonality of their food resources (Reilly and Cullen, 1981; Stahel and Gales, 1987). Little penguins at Port Tarakohe begin their annual cycle in autumn, after their moult. The first egg in 2021 was laid in June and the last egg was laid in October. Little penguins usually lay a two-egg clutch and can also lay more than one clutch during a breeding season. The average incubation time for little penguin eggs is approximately 33-35 days (Kemp and Dann, 2001; Reilly and Cullen, 1981; Stahel and Gales, 1987). The first egg at Port Tarakohe hatched in August and the last to hatch was in December. The ‘guard stage’ of chick rearing occurs for the first one to two

weeks after chicks hatch and is when one adult must always attend the nest to protect the newly hatched chicks (Sutton *et al.*, 2017). The 'post-guard stage' extends from when neither parent is present in the nest to the time the chicks fledge (Saraux *et al.*, 2011). Once the chicks are larger, both parents can leave the nest to forage for chick provisioning and self-maintenance (Sutton *et al.*, 2017). Little penguin chicks fledge at approximately eight weeks of age, after which, parents can forage for several weeks to attain suitable fat reserves required for their annual moult (Gales and Green, 1990). Moult at Port Tarakohe started early December and ended early February. Moulting takes approximately 10-14 days, with the penguin staying ashore for the entire moult duration (O'Brien, 1940). During the winter months, little penguins remain at their colony, foraging during the day and returning to the colony after sunset (Gales and Green, 1990).

1.6 Autumn and winter colony attendance and behaviour

Little penguins live a loosely colonial lifestyle and can be present at their colonies all year round (Reilly and Cullen, 1981; Stahel and Gales, 1987). While there have been many studies of little penguin colony attendance and behaviour during the breeding season, there is relatively little information for autumn and winter. Some studies have reported nightly counts of little penguins returning to their colonies, and have discussed factors that may affect the return of penguins to their colonies (Chiaradia *et al.*, 2007; Rodriguez *et al.*, 2018; Sutherland and Dann, 2014), but little is known about individual patterns of colony attendance or behaviour in autumn and winter.

Reilly and Cullen (1981) studied a colony of little penguins on Phillip Island (Victoria, Australia) in 1969 and 1970, recording the number of penguins in their study area once a week during daytime checks from April to September. They found that penguins continued

to visit the colony from time to time, occupying their former nest or one close by. During the autumn and winter months they saw about one eighth of the future breeding penguins at the colony during daytime checks and double that number during night checks. When they looked at total colony attendance, they found fluctuations in attendance numbers, with regular peaks and troughs occurring from April to September. Penguin numbers varied from approximately 1 to 48 in 1969 and 0 to 31 in 1970. During weekly night checks, Kinsky (1960) also found peaks and troughs of penguin colony attendance on Matiu Somes Island (Wellington Harbour) in 1957. Penguin numbers varied from approximately 60 to 220 from the end of March to the beginning of August.

Reilly and Cullen (1981) also looked at the nighttime colony attendance of individual penguin pairs for 35 days during June and July in 1978. They found that some pairs were synchronised, consistently attending their nests at the same time. The general pattern for these penguins was that they spent several consecutive nights at the colony before going out to sea for slightly longer. Penguin pairs showed some synchronisation of their arrival and departure times and if mates did not leave together on the same night, they usually left the colony on successive nights. If nest sites were swapped, mates usually stayed the same. Reilly and Cullen (1981) also discussed how some penguin pairs appeared to arrive at the colony together as though they had spent time at sea together, while other penguin pairs appeared to be able to locate each other after a separation and still synchronise their return to the colony. In contrast, Chiaradia and Kerry (1999) looked at colony attendance of 53 penguin pairs from 28 June 1995 until 30 January 1996 on Phillip Island (Victoria, Australia). During the winter months of their study, few penguins were sighted at the colony. When penguins were sighted it was usually a male penguin and there were no clear patterns of colony attendance during the winter months, which differed from the results of Kinsky (1960)

and Reilly and Cullen (1981). Penguins also appeared to arrive in winter in a more random fashion, with no synchronization, in comparison with clear patterns of colony attendance from September onwards until the end of fledging.

To my knowledge, there have not been detailed studies of individual little penguin attendance at the Port Tarakohe colony during autumn and winter, with no available information on variables such as the number of different nestboxes visited by a penguin, how many other penguins each penguin shares a nestbox with, and the approximate time penguins spent on land in nestboxes compared to time spent at sea.

1.7 Thesis outline

Most studies of little penguin have focused on their behaviour during the breeding season, but little is known about their behaviour during the autumn and winter months that lead up to egg laying. The present study was conducted to investigate colony attendance and behaviour of little penguins during autumn and winter at the Port Tarakohe colony in Golden Bay on the South Island of New Zealand. I collected data on little penguin during April, May, June and July 2021, with checks every second day in April and May and every third or fourth day in June and July. Data recorded included total colony attendance numbers, nestbox visitations by individual penguins, penguins seen with other penguins, individual penguin colony attendance patterns, paired penguin colony attendance patterns, and durations of time in nestboxes compared with time at sea. Each penguin was microchipped so I could identify individual penguin behaviours. Other data collected included flipper length, body weight and body condition index. In addition, some data on colony attendance and body weight were extracted from previously published papers for comparison with Port Tarakohe data.

Chapter 2 discusses total colony attendance patterns over the study period, and investigations of potential relationships between lunar phase and colony attendance. This chapter also considers body weight, flipper length and condition index changes in male and female penguins. Chapter 3 considers individual penguin behaviours at a finer scale, including nestbox use, penguin sightings with other penguins, individual penguin colony attendance patterns, colony attendance patterns for pairs of penguins, and duration of time individual penguins spent on land versus at sea. The fourth chapter provides a summary and general discussion of the findings of this study, together with suggestions for future research.

2. Patterns of colony attendance in little penguins in autumn and winter

2.1 Introduction

While little penguins frequently and predictably attend their colonies during the breeding season (Gales and Green, 1990), little is known about colony attendance patterns during the autumn and winter months that lead up to breeding. Little penguins have been reported to remain at their colony during the autumn and winter months (Gales and Green, 1990; Salton *et al.*, 2015), but these are not the months scientists usually focus on studying. To my knowledge, Reilly and Cullen (1981) and Kinsky (1960) are the only authors who have published data on autumn and winter colony attendance patterns for little penguins.

Reilly and Cullen (1981) studied a little penguin colony at Phillip Island (Victoria, Australia) for 11 years and noted that little penguins are present at their colonies all year round, with at least one quarter of the population in nests at night and one eighth of the population in nests during the day during the 'non-breeding' season. They found that little penguin colony attendance increased two or three months prior to the breeding season and that penguins had a three-week cycle of colony attendance. They considered whether external events, such as lunar phase, might act as a timer for penguins to synchronise their return to the colony, with no correlation found between colony return and lunar phase.

Kinsky (1960) studied little penguins on Matiu Somes Island (Wellington Harbour) from 30 March to 9 August in 1957 and found that little penguin numbers were not constant during the winter months. Little penguin numbers increased to a peak towards the end of April before dropping again in May. There was a second peak of penguins present on the island, with numbers increasing from late May and to a peak around mid-July.

It is important to note that Reilly and Cullen (1981) observed little penguins during the day while Kinsky (1960) observed little penguins during night visits. Little penguins wait until after dark to come ashore, and head out to sea before the sun rises (Stahel and Gales, 1987), therefore, study results may differ according to methods used to monitor the penguins. There are no other published studies of little penguin autumn and winter colony attendance. Nestbox checks throughout the year at Port Tarakohe have shown that the number of penguins ashore during the day can vary from no penguins to more than 100 penguins (J.F. Cockrem, pers. obs.). Higher numbers of penguins are found on land during the day during the breeding season than the non-breeding period of the year (Stahel and Gales, 1987).

In order to develop appropriate conservation measures, it is important that we can collect accurate measures of penguin population size (Colombelli-Négrel, 2023; Sutherland and Dann, 2014). Because penguins are one of the most threatened groups of seabirds, monitoring their population trends are essential to ensure populations don't decline (Colombelli-Négrel, 2023; Costello and Colombelli-Négrel, 2023). When construction work is needed at a site where little penguins may be present, the work is usually scheduled for outside the breeding and moulting months, so generally autumn and winter (Marker *et al.*, 2024). Because little penguins are present at the colony all year round, with winter breeding becoming a more frequent occurrence, it is important for penguin conservation that we know more about their colony attendance during this time.

Body weight and body condition of little penguins have rarely been studied in autumn and winter. Body condition is frequently used as a key health indicator and is calculated by the body mass (g) divided by the flipper length (mm) in little penguins (Robinson *et al.*, 2005; Wells *et al.*, 2025). Alternating periods of feeding and fasting occur in little penguins as they

forage exclusively at sea but come ashore at night to rest as well as spending long periods of time on land for breeding and moulting (Groscolas and Robin, 2001; Ropert-Coudert *et al.*, 2006; Stahel and Gales, 1987). Salton *et al.* (2015) measured body mass and predicted that little penguins would have a lower body mass in winter, when colony attendance was at its lowest, than at other times of the year. However, they found that winter body masses of both male and female penguins was equal to or higher than body mass at other times of the year, and suggested that this might be related to increasing body condition after moult. Kinsky (1960) also measured autumn and winter body weights of little penguins and found that male and female weights reached a slight peak at the start of April then remained relatively constant in winter before slightly dropping before the nesting season. Kinsky (1960) noted that the weights of individual penguins varied greatly between weighing occasions, mostly due to differences between occasions in how long a penguin had been on land fasting before being weighed. Johannesen *et al.* (2002b) also recorded consistent average body weights of penguins from April to July at Pilots Beach (Otago, New Zealand) in 2000.

In this chapter, I examine the patterns of total colony attendance and body condition of little penguins at Port Tarakohe in autumn and winter months. Based on the literature, it was anticipated that little penguins would be present at the colony during the autumn and winter months in low numbers, with potential cycles of peaks of attendance. Potential relationships between cycles of numbers of penguins on land at Port Tarakohe, and lunar cycles were investigated and data from Phillip Island (previously published results from Reilly and Cullen (1981)) were examined for comparison with Port Tarakohe data. I also used published data from Kinsky (1960) and Johannesen *et al.* (2002b) to see if there were changes in body weight in autumn and winter for comparison with Port Tarakohe data. Based on the

literature, it was expected that there would be no increase in body weight and body condition as penguins recovered from moult and prepared for the breeding season.

2.2 Materials and methods

2.2.1 Study site

This study was conducted at a newly established penguin colony in nestboxes at Port Tarakohe (40.8242°S, 172.8991°E) in the Tasman district of the upper South Island of New Zealand (see Fig. 2.1). Port Tarakohe is a small port east of Tākaka town on Abel Tasman Drive in Golden Bay. The port has two rock breakwaters that enclose a harbour area with a marina, moored recreational boats, and a commercial wharf. The breakwaters consist of large limestone rocks with gravel and earth on top of the breakwaters. There are western and eastern breakwaters (see Fig. 2.2), with 150 nestboxes on the western breakwater. The nestbox colony had been established in 2020 when new nestboxes were installed to replace old nestboxes, and additional new nestboxes were installed. There are 57 nestboxes on the outer side and 43 nestboxes on the inner side of the western breakwater, a further 20 nestboxes on the outer side of the western breakwater where it widens, and 30 nestboxes on an arm of the breakwater, known as the port arm, that extends into the harbour (see Fig. 2.2). Some nestboxes have been moved since their initial placement, either because of local flooding or because the nestboxes had not been used after several years, and several nestboxes on the port arm were decommissioned as they were flooded during stormy days.

The nestboxes (internal dimensions 450 mm long x 350 mm wide x 250 mm high; 25 mm thick timber; see Fig. 2.3) had been made by local volunteers. The nestboxes have side tunnels 500 mm long. Penguins enter the tunnels then make a 90° turn to go through a 150 mm wide entrance into the nestbox. Each nestbox has a lid that opens vertically, with a

simple locking mechanism of a nail in a hole through the front of the nestbox into wood of the nestbox lid. A magnet is used to draw the nail out during nestbox checks so that the lid could be opened to see into the nestbox. This locking system helped reduced tampering of nestboxes by members of the public who would otherwise lift nestbox lids. Large rocks were also placed on top of the nestbox lids to deter people from trying to open the lids. Each nestbox has a yellow identification tag with the box number on it or near it for easy identification. Some nestboxes were placed with their entrance facing the sea, while others had their entrances facing away from the sea and towards the flat top of the breakwater. Nestboxes were all placed at the top of the breakwater, with some hidden among flax bushes (*Phormium tenax*), some placed amongst rocks, and others in the open.

Fig. 2.1. Port Tarakohe located in the upper South Island in Golden Bay, New Zealand. Map was created using Google Earth Pro.

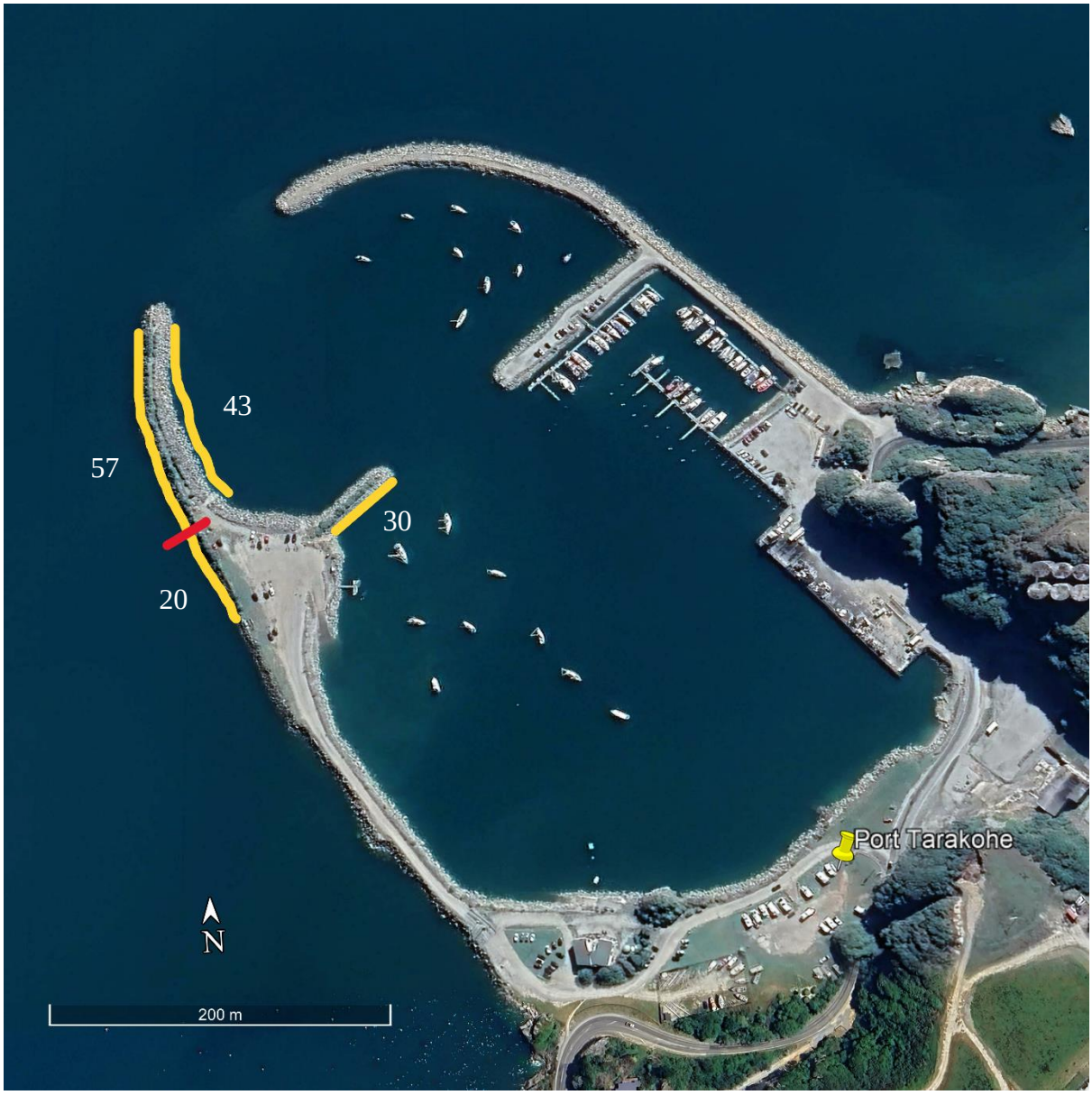


Fig. 2.2. Aerial view of Port Tarakohe. Nestboxes are located along the breakwaters in areas highlighted in yellow, with the number of nestboxes in each area shown on the figure.

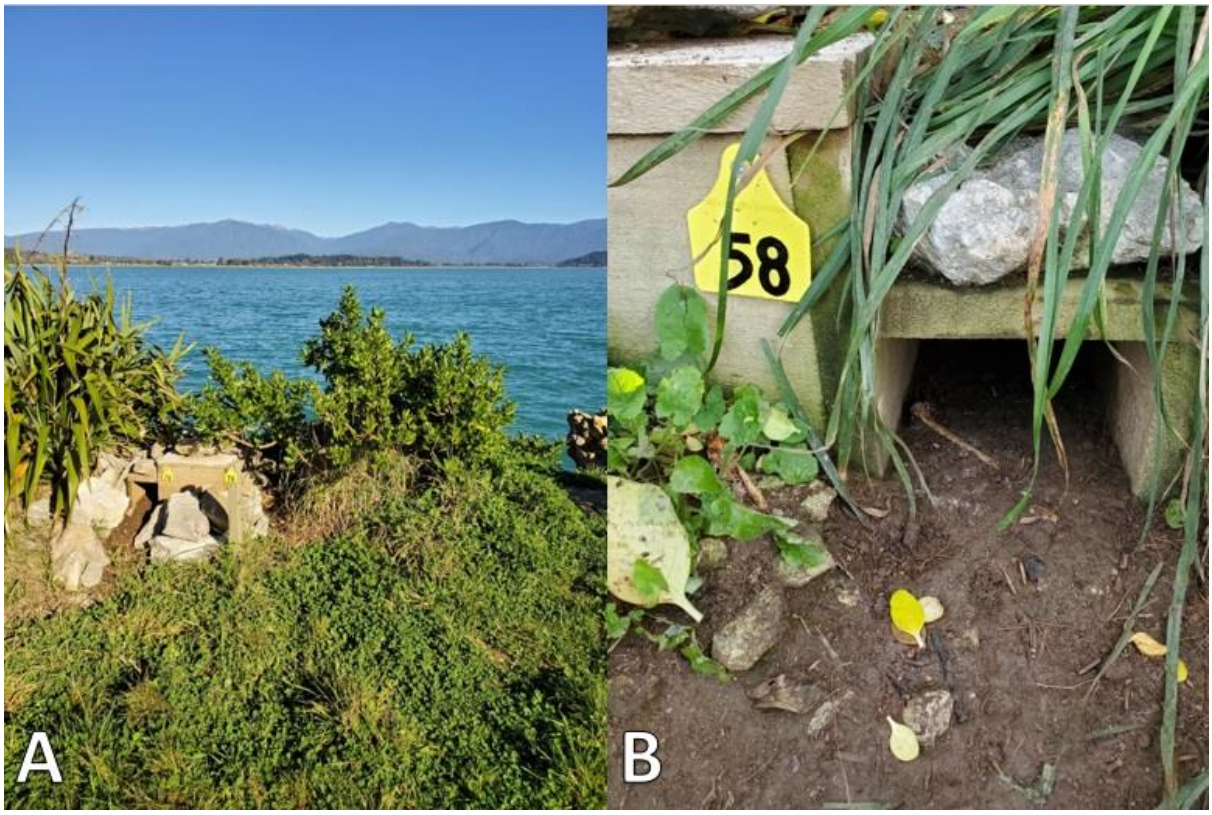


Fig. 2.3. Nestboxes at Port Tarakohe. A. Nestbox surrounded by natural vegetation and rocks, with entrance facing away from the sea. B. Tunnel entrance and nestbox number.

2.2.2 Data collection

The work was conducted under an approval from the Massey University Animal Ethics Committee (AEC 22/47) and a Department of Conservation Wildlife Act Authorisation (93253-FAU). Data collection for this study commenced on 7 April 2021 and ended on 30 July 2021. All 150 nestboxes were checked approximately every second day for the first two months and then twice a week for the next two months. If there were penguins in a nestbox they were scanned at the back of the neck with a Gallagher HR5 handheld EID tag reader to check for a microchip. The number of penguins in each nestbox was recorded, together with microchip numbers for penguins with microchips. Notes were also made of nesting material in nestboxes. Penguins that did not have microchips were weighed, microchipped and had their flipper length measured. Penguins were picked up from nestboxes through the removable top lids and placed into a lightweight cloth bag. Penguins were weighed in the bag to the nearest gram using a Pesola spring balance tared for the weight of the bag. One flipper was then carefully extended for the measurement of the length from the base of the flipper at the penguin's body to the tip of the flipper. Flipper length was measured to the nearest millimetre. Penguins were then microchipped with Trovan ID162VB/1.4 microchips (8 mm long and 1.4 mm diameter) inserted under the skin of the upper surface of the neck. The insertion site was prepared by spraying alcohol on the surface of the skin to reduce the risk of infection. Once all procedures were completed, the penguins were gently released back into the entrance to the tunnel into their nestbox. Observations of sea and weather conditions such as water clarity, waves, cloud cover, and rain, as well as the presence of birds, seals and fish were also noted on each day that nestboxes were checked.

For comparison with my data, the numbers of penguins present at Phillip Island were taken from Fig. 2. in Reilly and Cullen (1981). Phillip Island lies just off Australia's Southern

Coast, seventy kilometres from Melbourne, Victoria (Chiaradia and Kerry, 1999; Reilly and Cullen, 1981). Mean, standard error and sample size were taken from Johannesen *et al.* (2002b) to analyse penguins weights from Pilots Beach. Pilots Beach is located at Taiaora Head, Otago Peninsula, New Zealand (Johannesen *et al.*, 2002b). Penguin body weights from Matiu Somes Island were calculated from the data in Table 11 and Table 12 from Kinsky (1960). Matiu Somes Island is situated in the middle of the Wellington harbour in the North Island or New Zealand (Kinsky, 1960).

2.2.3 Method of distinguishing sex

Nestbox checks and microchipping of new penguins and of penguin chicks before fledging, has been continued at Port Tarakohe since the current study finished in 2021. The checks have been conducted by two volunteers, and information from the continued nestbox checks has been used for determining the sex of most penguins in the current study. Penguins were identified as male or female based on a combination of attributes such as body weight, flipper length, behaviour across multiple sightings, presence in a nestbox with another penguin to which sex had already been assigned (penguins that are consistently together in a nestbox are always a male and a female), and size and shape of the bill. Males tend to be more aggressive than females and have shorter, stouter beaks with a well-developed hook on the upper mandible, while females are generally quieter and have bills that are longer and thinner than males (Kinsky, 1960; O'Brien, 1940).

2.2.4 Lunar days

Lunar days were extracted from Calendar Australia (https://www.calendar-australia.com/lunar-calendar/) for each day from 1 April to 31 July 2021 to see if there was any correlation between the number of penguins in nestboxes during daytime checks and

lunar phase. A lunar day is the time it takes the earth to rotate in respect to the moon which takes approximately 24.84 solar hours. The synodical month, also known as the lunar cycle, is the time it takes the moon to revolve around the earth in relation to the sun. This takes approximately 29.5 days (https://tidesandcurrents.noaa.gov/glossary.html#synodicalmonth). Day 0 is a new moon and around day 15 is a full moon. The lunar cycle was divided into six separate groups of five lunar phases to get lunar day groups. The six groups were lunar days 1-5, 6-10, 11-15, 16-20, 21-25 and 26-30. The lunar cycle has four prominent phases; new moon (NM), first quarter (FQ), full moon (FM) and third quarter (TQ) (Chakraborty, 2020). I divided the lunar cycle into these four phases with first quarter being moon days 1-8, full moon being moon days 9-15, last quarter being moon days 16-23, and new moon being moon days 24-30.

2.2.5 Data analysis

All statistical analyses were conducted using GraphPad Prism 5.03 (GraphPad Software, Inc.). A one-way Kruskal-Wallis ANOVA was performed for lunar day groups and lunar phase groups to determine if there were significant differences in the number of penguins in nestboxes during day checks. A one-way Kruskal-Wallis ANOVA was performed for month groups to assess significant differences in body weight and condition index (calculated as body weight/flipper length cubed) for both male and female penguins. T-tests were performed to test for significant differences between male and female penguins in body weight, flipper length and condition index. Mann-Whitney tests were used to check for significant differences between the number of days male and female penguin spent at sea and on land. A T-test was performed to test for significant differences in breeding success between penguin pairs who stayed in the same nestbox and pairs who switched between multiple nestboxes.

To calculate peaks and troughs for colony attendance, extrapolated lines were drawn onto a printed copy of the graph showing numbers of penguins in nestboxes on each day of nestbox checks, with the x-axis having days instead of months for ease of calculation (see Fig. 2.4). The lines were drawn along the sides of the peaks, with the points where the lines intersected used as the peak and trough values. For example, Peak one (P1) is at the intersection of lines at day 36 while peak two (P2) is at the intersection of lines at day 62. The time from peak one and two is therefore 26 days.

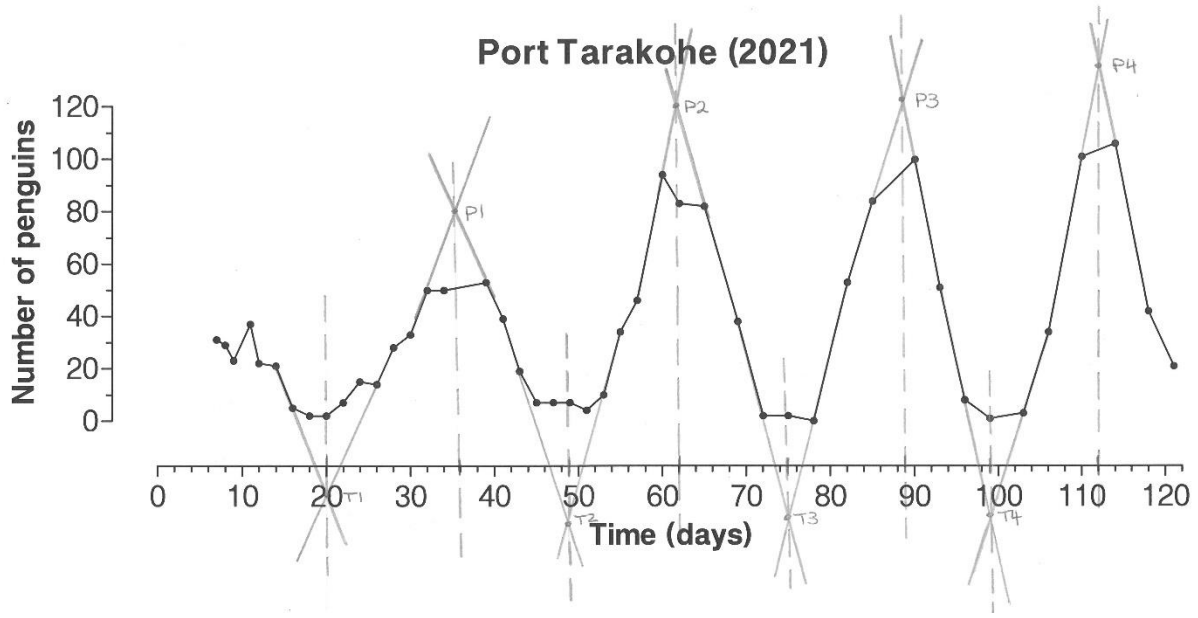


Fig. 2.4. Extrapolations and calculations of peaks and troughs from printed graph.

2.3 Results

2.3.1 Colony attendance patterns

The total number of penguins in nestboxes during daytime checks from April to July 2021 varied from 0 to 106 penguins per day (n = 45 nestbox checks, see Fig. 2.5). There was a clear cyclic pattern in the number of penguins present at the colony, with regular peaks and troughs. There were 53, 94, 100 and 106 penguins in nestboxes for the four peaks from early May to mid-July, with 4, 0 and 1 penguins in nestboxes for the three troughs between these peaks. The cycles in the number of penguins in nestboxes comprised approximately one week when numbers were increasing, one week with relatively high numbers, one week of declining numbers, and a trough of approximately one week.

Dates of peaks and troughs were estimated by manual extrapolation (see section 2.2.5 for details) to be 6 May, 1 June, 28 June and 21 July for peaks and 20 April, 19 May, 14 June and 8 July for troughs. The mean periods between peaks and troughs were 25.33 ± 0.98 days (n = 3) and 26.33 ± 1.19 days (n = 3) respectively, making the cycle of penguin attendance at the colony approximately three-and-a-half-weeks long.

The total number of male penguins in nestboxes during daytime checks was similar to that of female penguins (Fig. 2.6). There were 25, 48, 51 and 54 male penguins in nestboxes for the four peaks from early May to mid-July, with 1, 0 and 1 penguins in nestboxes for the troughs between these peaks. There were 27, 46, 49 and 55 female penguins in nestboxes for the four peaks from early May to mid-July, with 2, 0 and 0 penguins in nestboxes for the troughs between these peaks.

The total number of penguins on land during daytime checks on Phillip Island in 1969 ranged from 1 to 48 and 0 to 31 in 1970 respectively (n = 21 data points, see Fig. 2.9). There was a clear cyclic pattern with regular peaks and troughs in both years. In 1969 there were 12, 20, 12, 32, 21 and 48 penguins in nests for the six peaks across April to August, with 4, 3, 9, 4 and 8 penguins in nests for the five troughs between these peaks. In 1970 there were 13, 24, 19, 31, 28 and 24 penguins in nests for the six peaks across April to August, with 3, 4, 0, 0 and 9 penguins in nests for the five troughs between these peaks. The periods of the cycles of the number of penguins in nests were approximately three weeks each year.

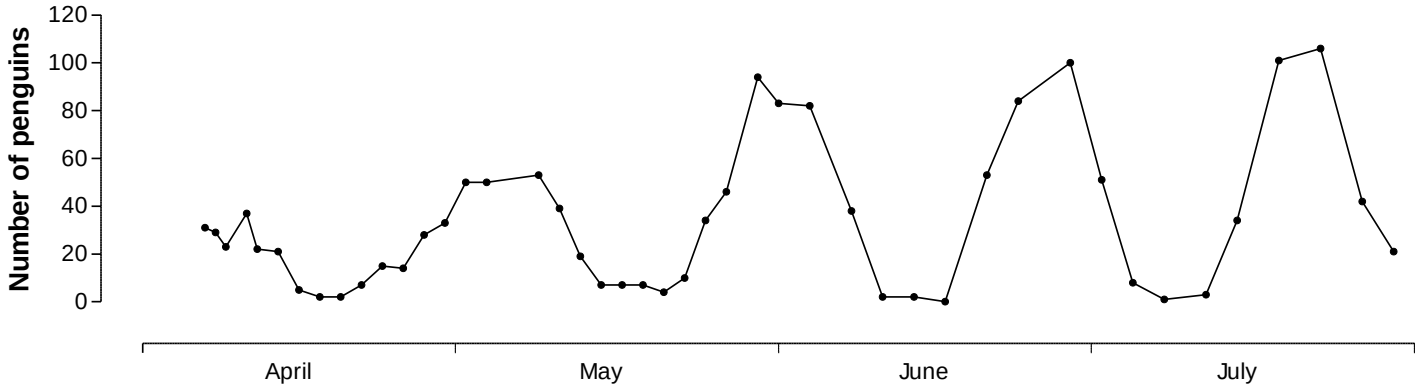


Fig. 2.5. Total number of penguins on land during daytime nestbox checks at Port Tarakohe from April to July 2021.

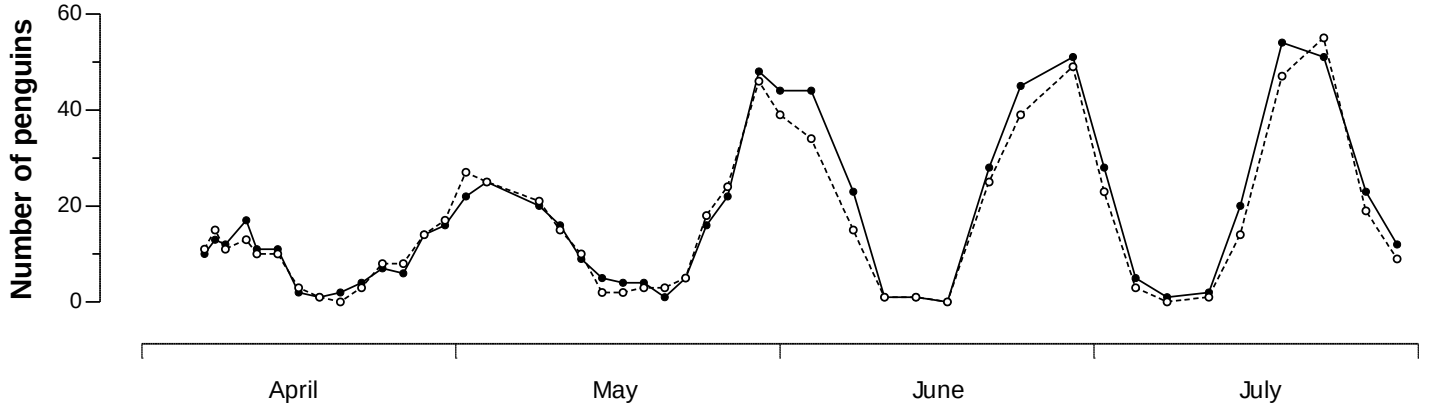


Fig. 2.6. Total number of male (–●–) and female (--○--) penguins on land during daytime nestbox checks at Port Tarakohe from April to July 2021.

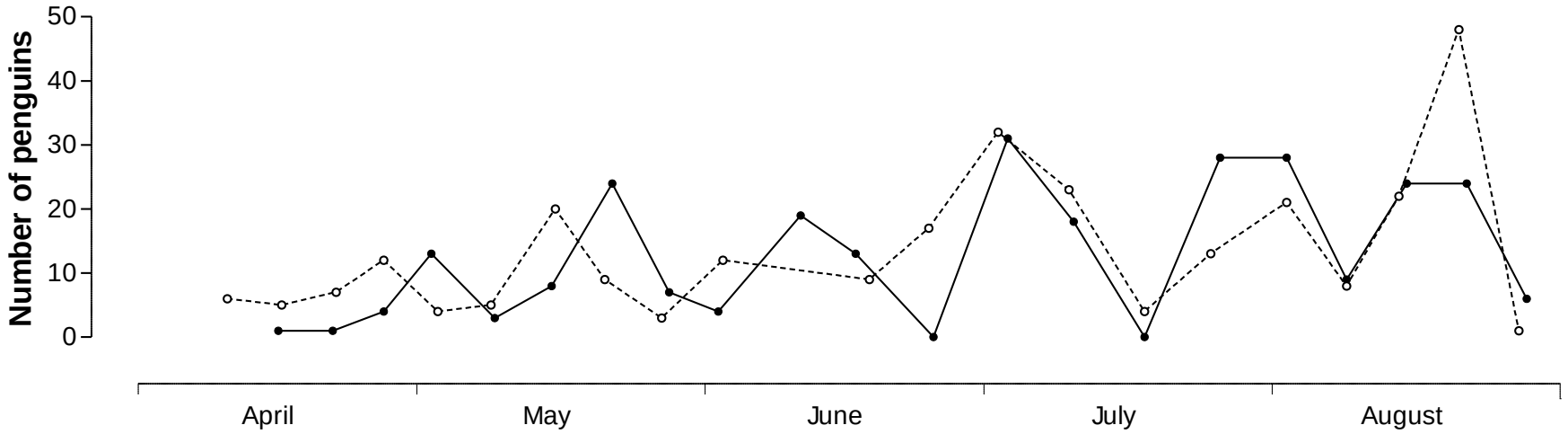


Fig. 2.7. Number of penguins present in nests checked weekly at Phillip Island in 1969 and 1970. Redrawn from (Reilly and Cullen, 1981) (--○--) and 1970 (⁻●⁻).

2.3.2 Lunar cycle

2.3.2.1 Port Tarakohe

The number of penguins present in nestboxes during daytime checks varied from 0 to 34 during the first nine lunar days (Fig. 2.8). From lunar day 10 onwards, there were from 1 to 106 penguins present in nestboxes at the colony.

There were four cycles of penguin attendance during my study (Fig. 2.9). Each month these cycles got earlier and earlier in relation to the lunar cycle, suggesting that lunar cycle does not influence colony attendance. The lunar cycle takes approximately 29.5 days. The mean periods between peaks and troughs were 25.33 ± 0.98 days (n = 3) and 26.33 ± 1.19 days (n = 3) respectively (see section 2.4.1). If the penguins were coming ashore and staying in their nestboxes during the day in relation to the lunar cycle, we would expect to see consistent peaks around the same time each month.

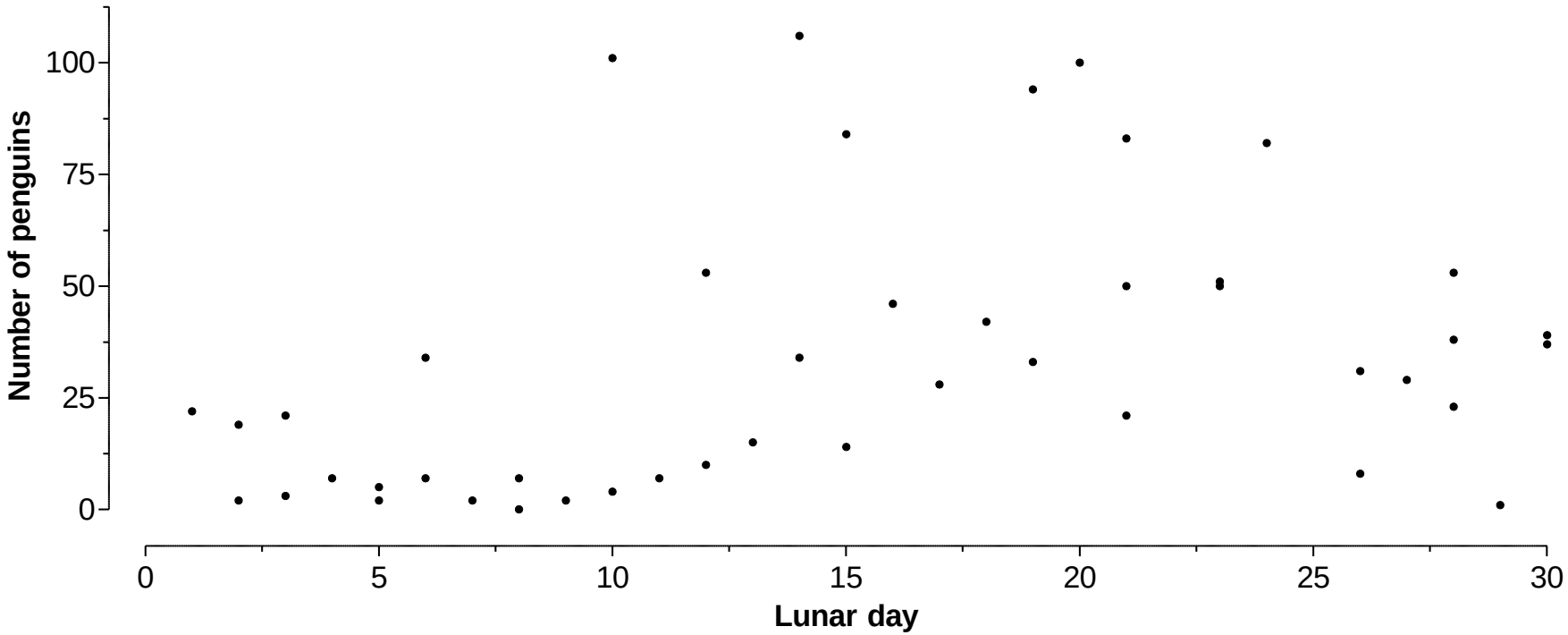


Fig. 2.8. Number of penguins home at each lunar day during April-July nestbox checks at Port Tarakohe in 2021. Lunar day 0 is a new moon and lunar day 15 is a full moon.

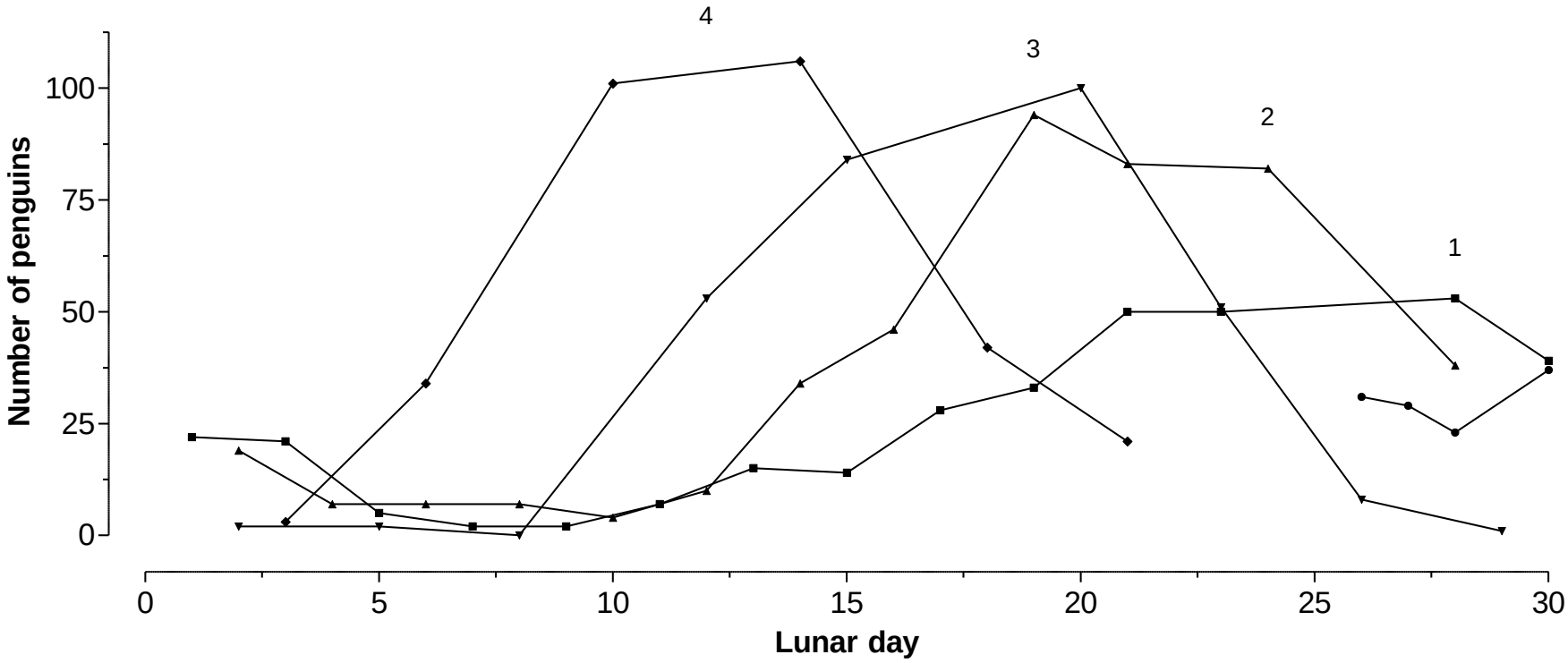


Fig. 2.9. Four different penguin attendance cycles from April to July 2021 daytime nestbox checks, in relation to the phase of the moon. Each attendance cycle was earlier in the lunar month than the previous cycle.

The minimum and maximum numbers of penguins home were 2 and 22 for lunar days 1 – 5, 0 and 101 for lunar days 6 - 10, 7 and 106 for days 11 - 15, 28 and 100 for lunar days 16-20, 21 and 83 for lunar days 21-25 and 1 and 53 for lunar days 26-30 (Fig. 2.10).

There were significant differences between lunar day groups in the number of penguins home in nestboxes during daytime checks ($K_5 = 17.76$, $p = 0.0033$; see Fig. 2.11). Mean numbers of penguins in nestboxes were greater for lunar days 16 - 20 than lunar days 1 - 5 (10.13 ± 3.15, 57.17 ± 12.89; $Z = 3.005$, $p < 0.05$).

The mean numbers of penguins home in nestboxes during daytime checks in relation to lunar day groups were 10.13 ± 3.15 for lunar days 1-5, 19.63 ± 12.25 for lunar days 6-10, 40.38 ± 13.22 for lunar days 11-15, 57.17 ± 12.89 for lunar days 16-20, 56.17 ± 9.53 for lunar days 21-25, and 28.78 ± 5.38 for lunar days 26-30.

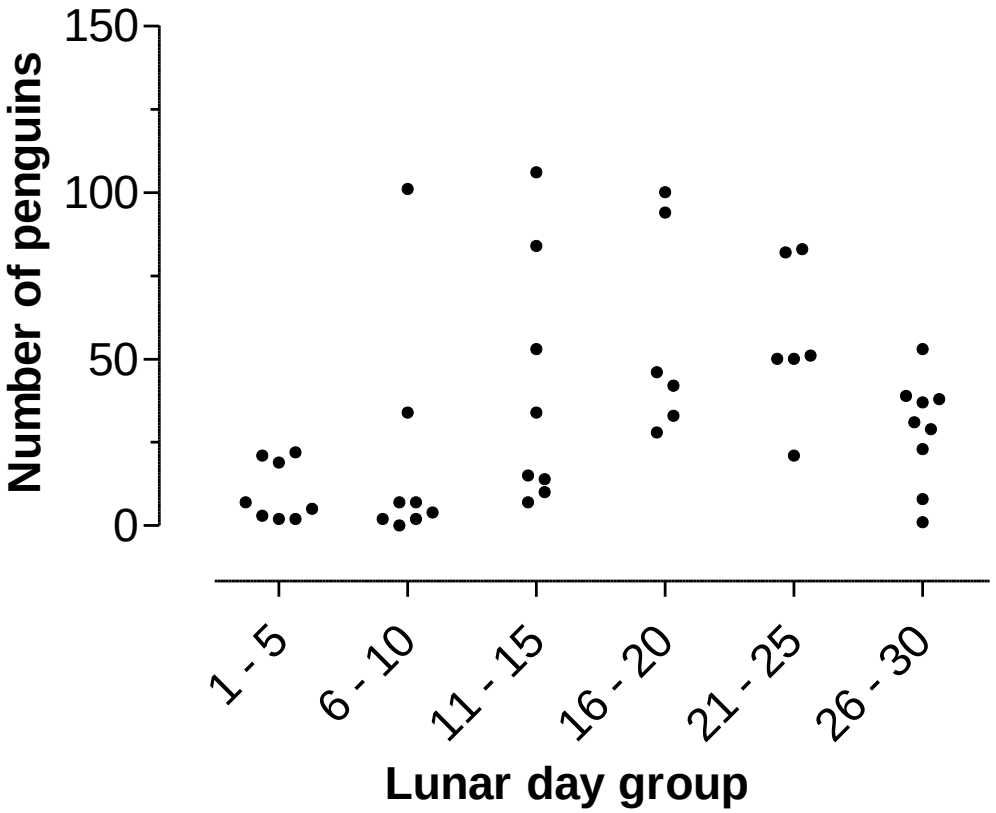


Fig. 2.10. Number of penguins present at the colony during daytime nestbox checks for each lunar day group from April to July 2021.

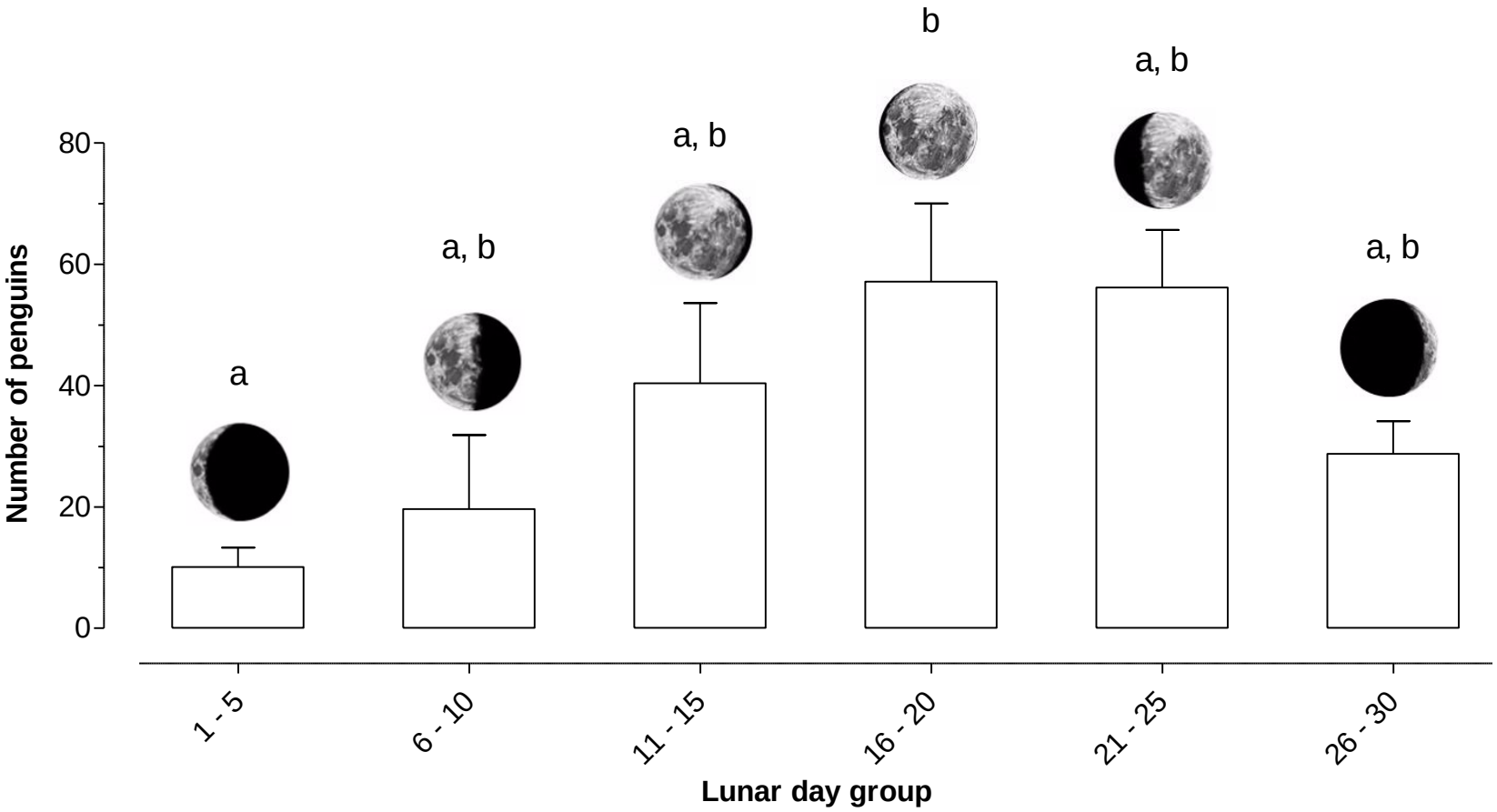


Fig. 2.11. Mean and standard error of the number of penguins present at the colony during daytime nestbox checks for each lunar day group from April-July 2021. Images represent the approximate phase of the moon halfway through each lunar day group. E.g. lunar phase in group 1-5 will be at day 2.5. Bars with different letters are significantly different from each other.

The minimum and maximum numbers of penguins home were 0 and 34 for the first quarter, 2 and 106 for the full moon, 21 and 100 for the last quarter and 1 and 82 for the new moon (Fig. 2.12).

There were significant differences between lunar phase groups in the number of penguins home in nestboxes during daytime checks ($K_3 = 15.77$, $p = 0.0013$; see Fig. 2.13). The mean number of penguins in nestboxes was greater in the last quarter than the first quarter (55.22 $\pm$ 9.84, 10.08 $\pm$ 2.90; $Z = 15.77$, $p < 0.0013$), and greater in the last quarter than the new moon (36.83 $\pm$ 6.21, 10.08 $\pm$ 2.90; $Z = 15.77$, $p < 0.0013$).

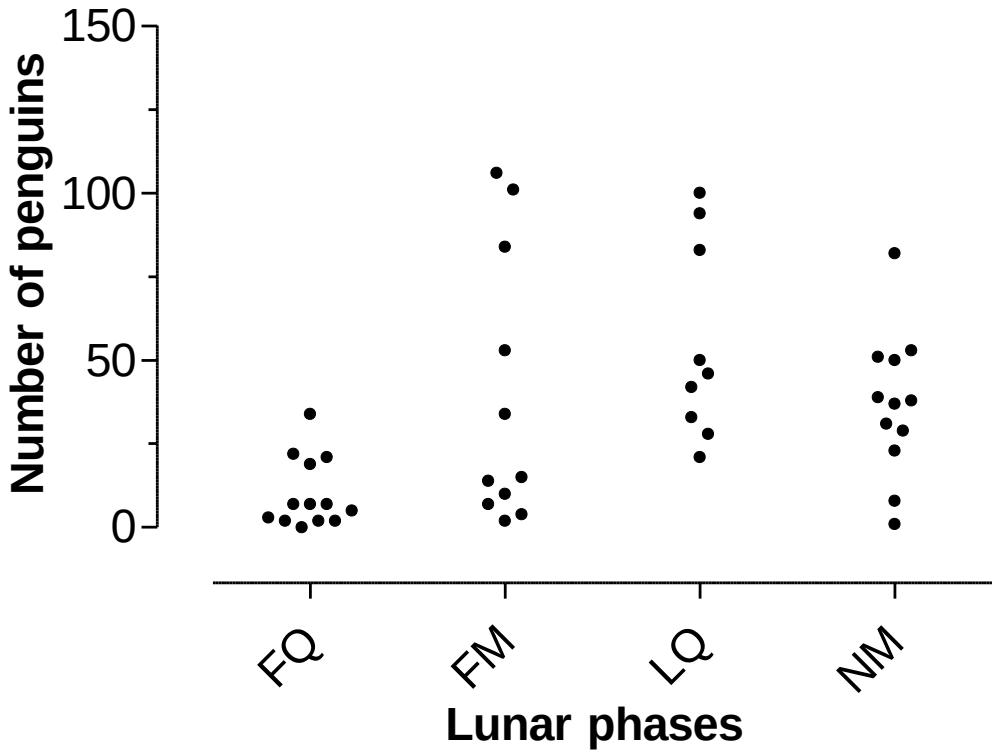


Fig. 2.12. Number of penguins home at each lunar phase during daytime nestbox checks at Port Tarakohe (April-July 2021). FQ=first quarter, FM=full moon, LQ=last quarter, NM=new moon.

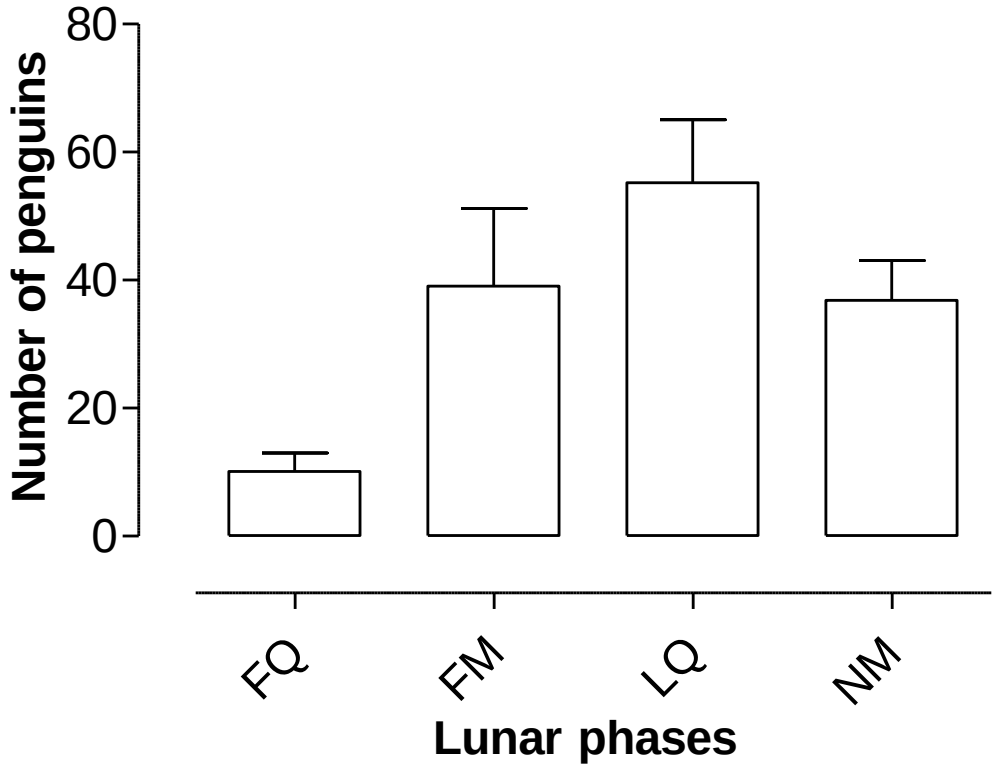


Fig. 2.13. Mean and standard error of the number of penguins home at each lunar phase during daytime nestbox checks at Port Tarakohe (April-July 2021).

2.3.2.2 Phillip Island

In 1969 the minimum and maximum number of penguins home were 4 and 22 for lunar days 1 - 5, 7 and 48 for lunar days 6 - 10, 3 and 17 for days 11 - 15, 1 and 32 for lunar days 16-20, 5 and 6 for lunar days 21-25 and 5 and 23 for lunar days 26-30 (Fig. 2.14).

There were no significant differences between lunar day groups in the number of penguins home in nestboxes during daytime checks ($K_5 = 1.655$, $p = 0.8945$).

The mean numbers of penguins home in nestboxes during daytime checks in 1969, in relation to lunar day groups, were 13.75 ± 4.33 for lunar days 1-5, 21.33 ± 13.35 for lunar days 6-10, 11.25 ± 2.96 for lunar days 11-15, 14.00 ± 5.68 for lunar days 16-20, 5.50 ± 0.50 for lunar days 21-25, and 12.00 ± 5.57 for lunar days 26-30.

In 1970 the minimum and maximum number of penguins home were 3 and 31 for lunar days 1 - 5, 9 and 19 for lunar days 6 - 10, 1 and 24 for days 11 - 15, 0 and 24 for lunar days 16-20, 0 and 28 for lunar days 21-25, and 4 and 13 for lunar days 26-30 (Fig. 2.15).

There were no significant differences between lunar day groups in the number of penguins home in nestboxes during daytime checks ($K_5 = 3.173$, $p = 0.6733$).

The mean numbers of penguins home in nestboxes during daytime checks in 1970, in relation to lunar day groups, were 20.67 ± 8.88 for lunar days 1-5, 15.33 ± 3.18 for lunar days 6-10, 11.50 ± 4.84 for lunar days 11-15, 8.33 ± 7.84 for lunar days 16-20, 12.60 ± 5.62 for lunar days 21-25, and 7.67 ± 2.73 for lunar days 26-30.

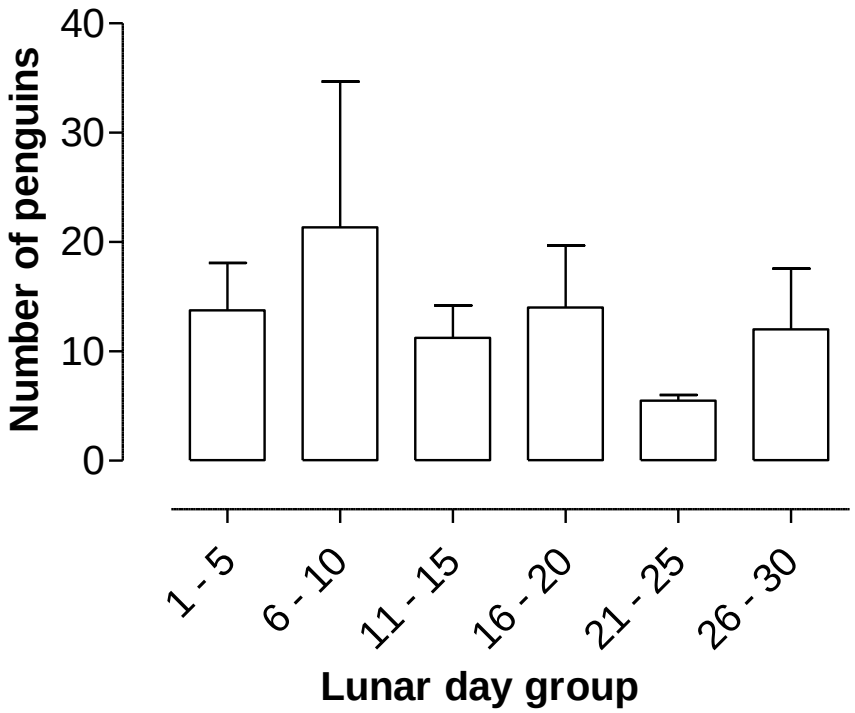


Fig. 2.14. Mean and standard error of the number of penguins present at Phillip Island during daytime nestbox checks for each lunar day group from April-August 1969.

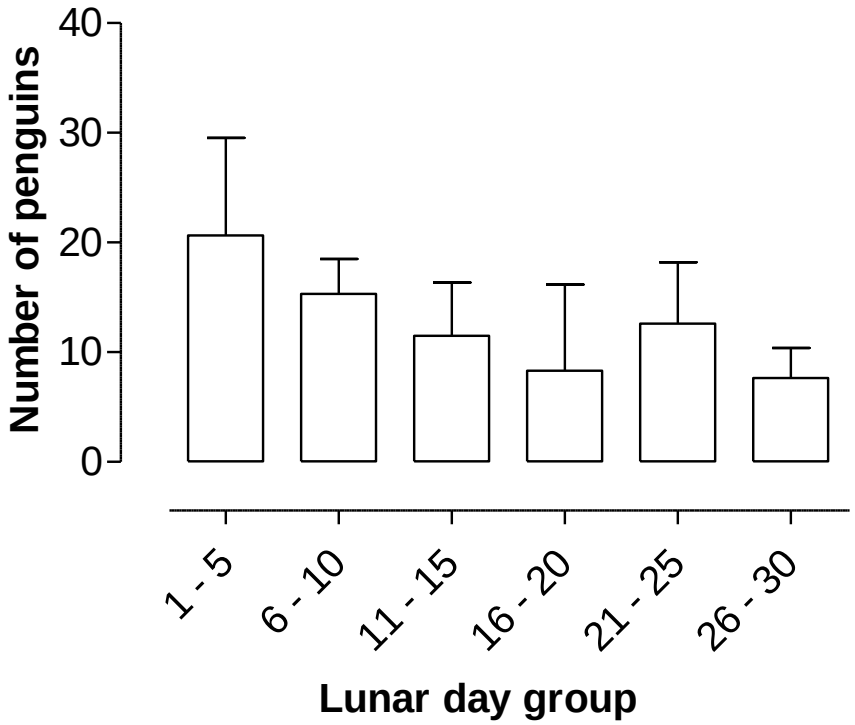


Fig. 2.15. Mean and standard error of the number of penguins present at Phillip Island during daytime nestbox checks for each lunar day group from April-August 1970.

2.3.3 Body weight, condition index and flipper length

2.3.3.1 Body variables in relation to month

I found no clear pattern of body weight increase in male or female penguins before the breeding season (see Figs. 2.16, 2.17, 2.20 and 2.21). The minimum and maximum body weights for male penguins were 1000 and 1420 g in April, 980 and 1450 g in May, 1100 and 1490 g in June, and 1120 and 1250 g in July (Fig. 2.18). The mean body weights of male penguins were 1216.7 ± 13.34 g in April, 1206 ± 26.71 g in May, 1217.5 ± 27.61 g in June, and 1166.7 ± 41.77 g in July. There was no significant difference in body weight between months for male penguins ($K_3 = 0.9076$, $p = 0.8236$; see Fig. 2.19).

The minimum and maximum body weights for female penguins were 840 and 1220 g in April, 880 and 1380 g in May, 920 and 1240 g in June, and 780 and 1320 g in July (Fig. 2.22). The mean body weights of female penguins were 1035.8 ± 14.18 g in April, 1110.5 ± 24.80 g in May, 1052.1 ± 23.61 g in June, and 1043.3 ± 59.61 g in July. There was no significant difference in body weight between months for female penguins ($K_3 = 6.515$, $p = 0.0891$; see Fig. 2.23).

Although there were no significant differences between months in penguin body weights leading up to the breeding season, there is a slight wave pattern which could be an indication of weight gain and loss depending on whether I weighed penguins just after arriving back from feeding at sea, in the middle of their stay on land, or just before they went back to sea to feed after being on land for a short while. During April and May, nestboxes were checked approximately every two days, so I can assume that penguins were weighed within two days of arriving on land after being at sea, while in June and July nestboxes were checked approximately every three to four days so penguins may have been on land for at least four

days since last being at sea. At the beginning of the study, all but nine penguins sighted at the colony were weighed and microchipped on day one. By day two of my study, all penguins sighted were weighed and microchipped.

There was no clear pattern of condition index increase in male or female penguins prior to the breeding season (see Figs. 2.24, 2.25, 2.28 and 2.29). The minimum and maximum condition indices for male penguins were 5.19 and 8.55 in April, 5.27 and 7.08 in May, 6.02 and 8.28 in June, and 5.47 and 7.06 in July (Fig. 2.26). Condition index units were body weight (g)/flipper length $(mm)^3$ x 10 000. The mean condition indices of male penguins were 6.57 ± 0.11 in April, 6.32 ± 0.12 in May, 7.02 ± 0.19 in June, and 6.02 ± 0.52 in July. There was a significant difference in condition index between months for male penguins ($K_3 = 8.191$, $p = 0.0422$). There was no apparent gradual increase in condition index from April to July, so no apparent increase from autumn towards the beginning of the breeding season (see Fig. 2.27).

The minimum and maximum condition indices for female penguins were 4.52 and 8.11 in April, 4.92 and 8.24 in May, 4.82 and 8.26 in June, and 5.23 and 7.83 in July (Fig. 2.30). The mean condition indices of female penguins were 6.38 ± 0.11 in April, 6.56 ± 0.16 in May, 6.7 ± 0.27 in June, and 6.63 ± 0.25 in July. There was no significant difference in condition index between months for female penguins ($K_3 = 3.010$, $p = 0.9901$; see Fig. 2.31).

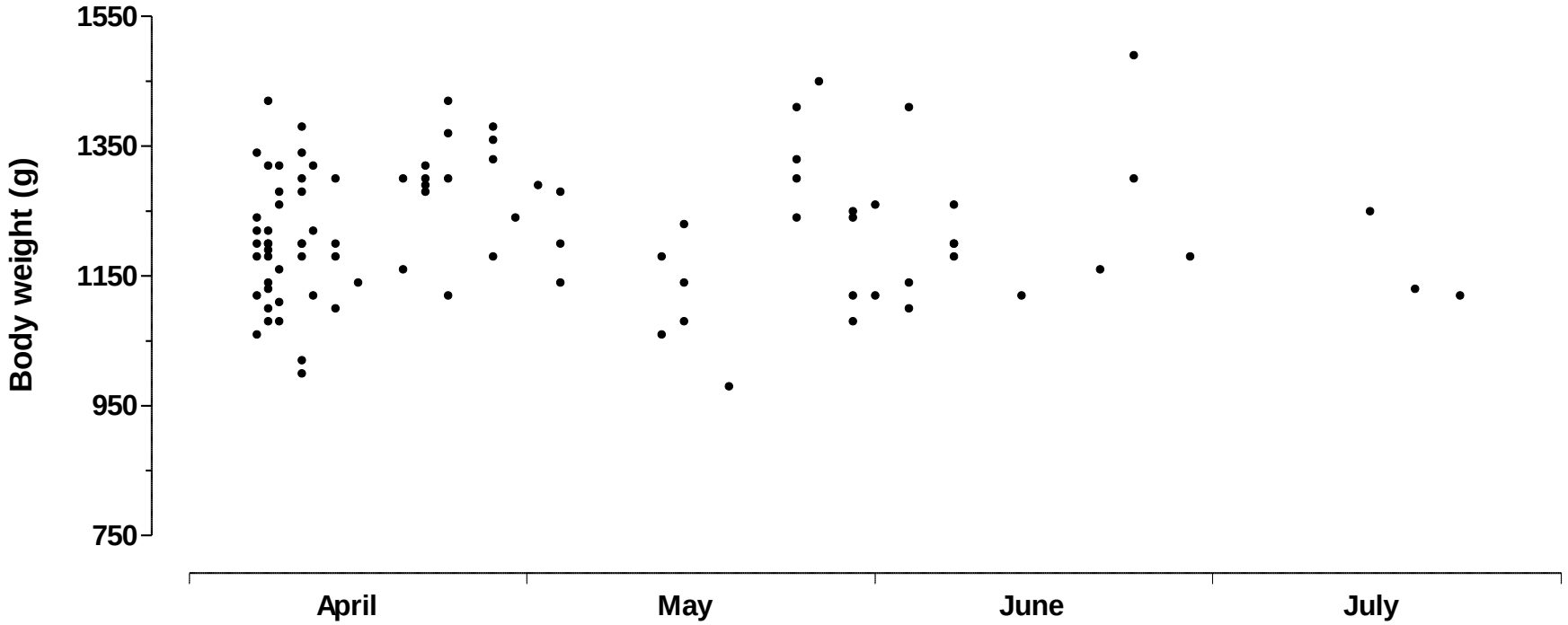


Fig. 2.16. Body weights of male penguins at the time they were first sighted and microchipped at the colony.

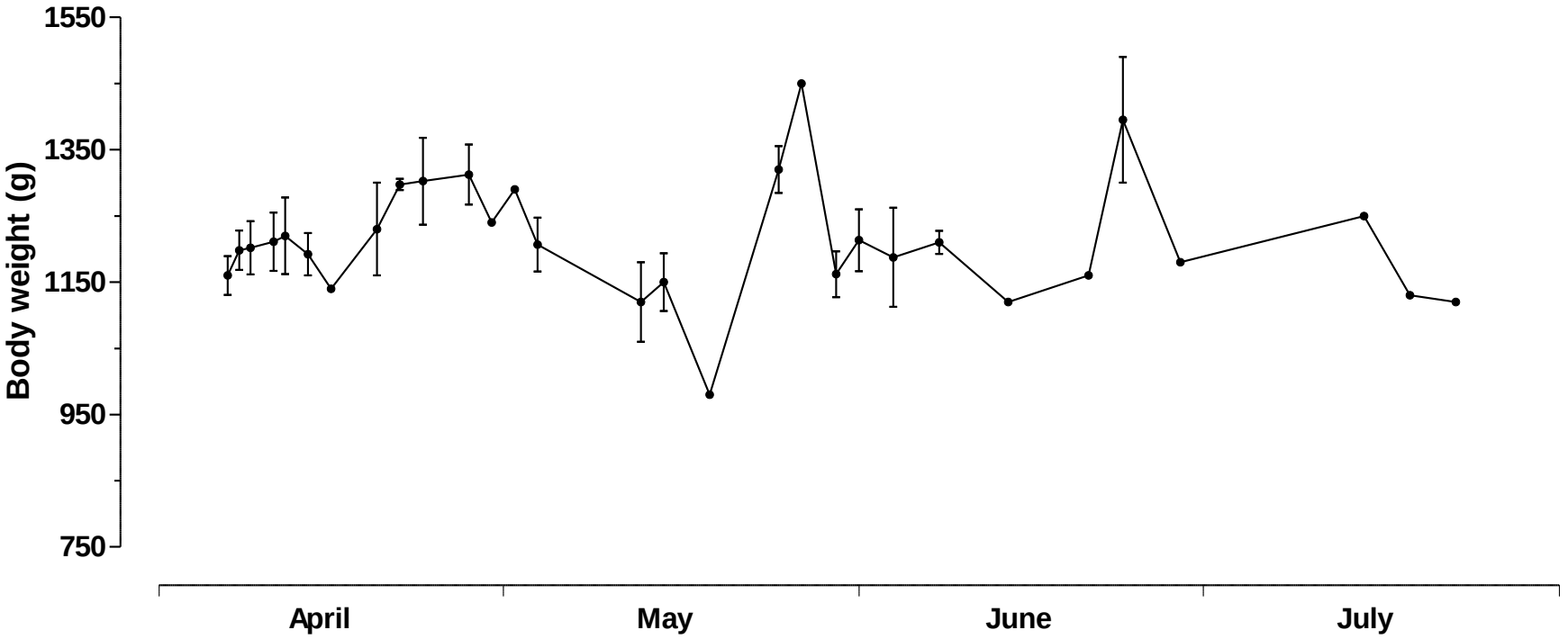


Fig. 2.17. Mean ± S.E. body weights of male penguins at the time they were first sighted and microchipped at the colony.

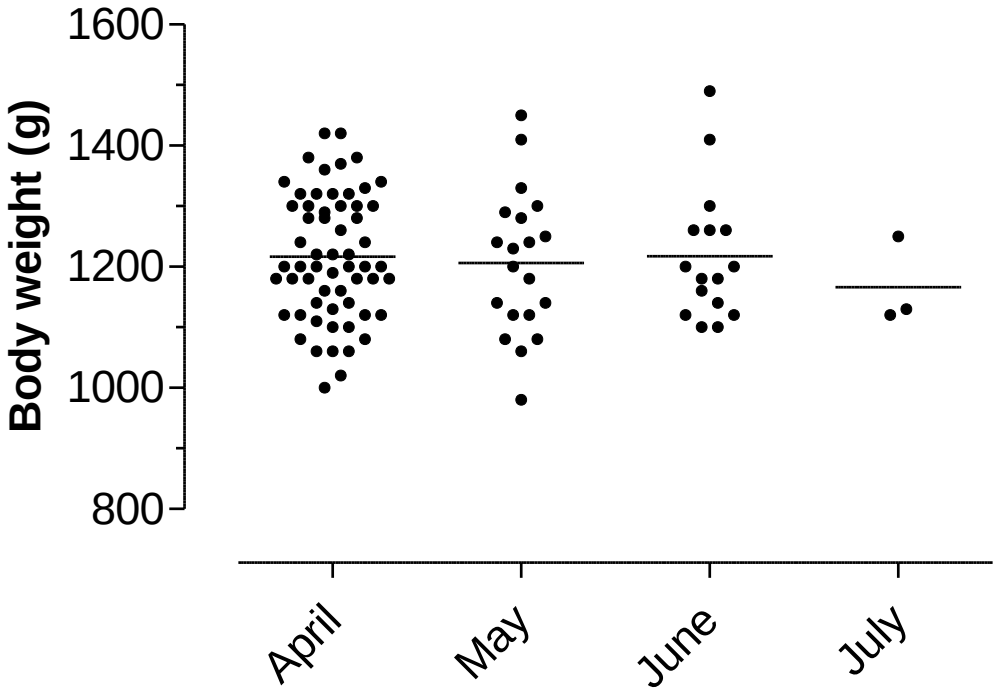


Fig. 2.18. Body weights of male penguins at the time of microchipping during each month of my study in 2021. Lines represent the mean body weights for each month.

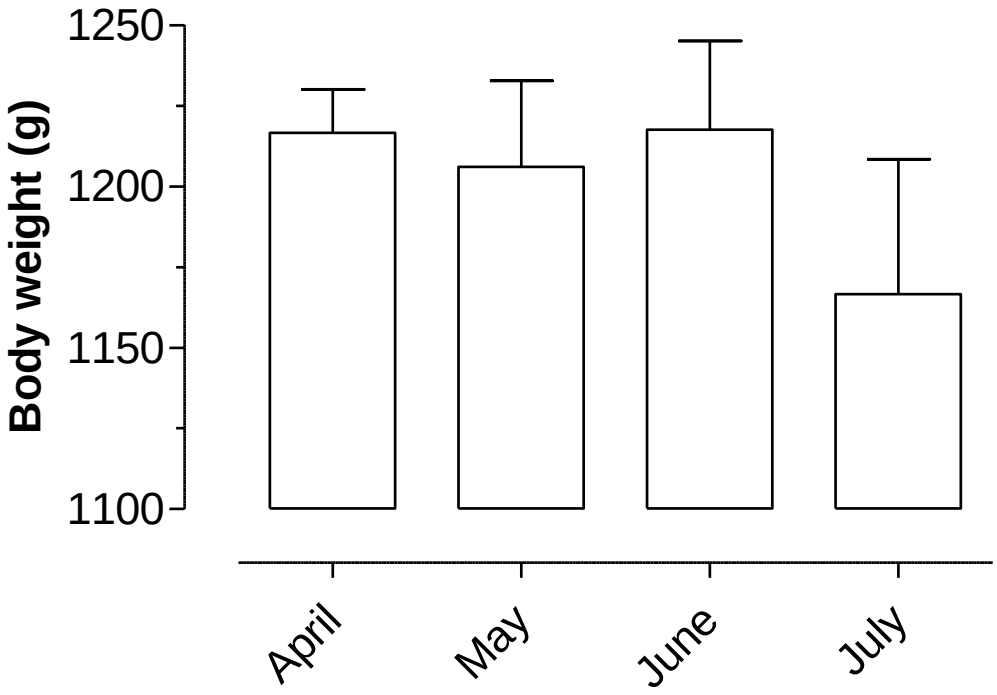


Fig. 2.19. Means and standard errors of male penguin body weights at the time of microchipping during each month of my study in 2021.

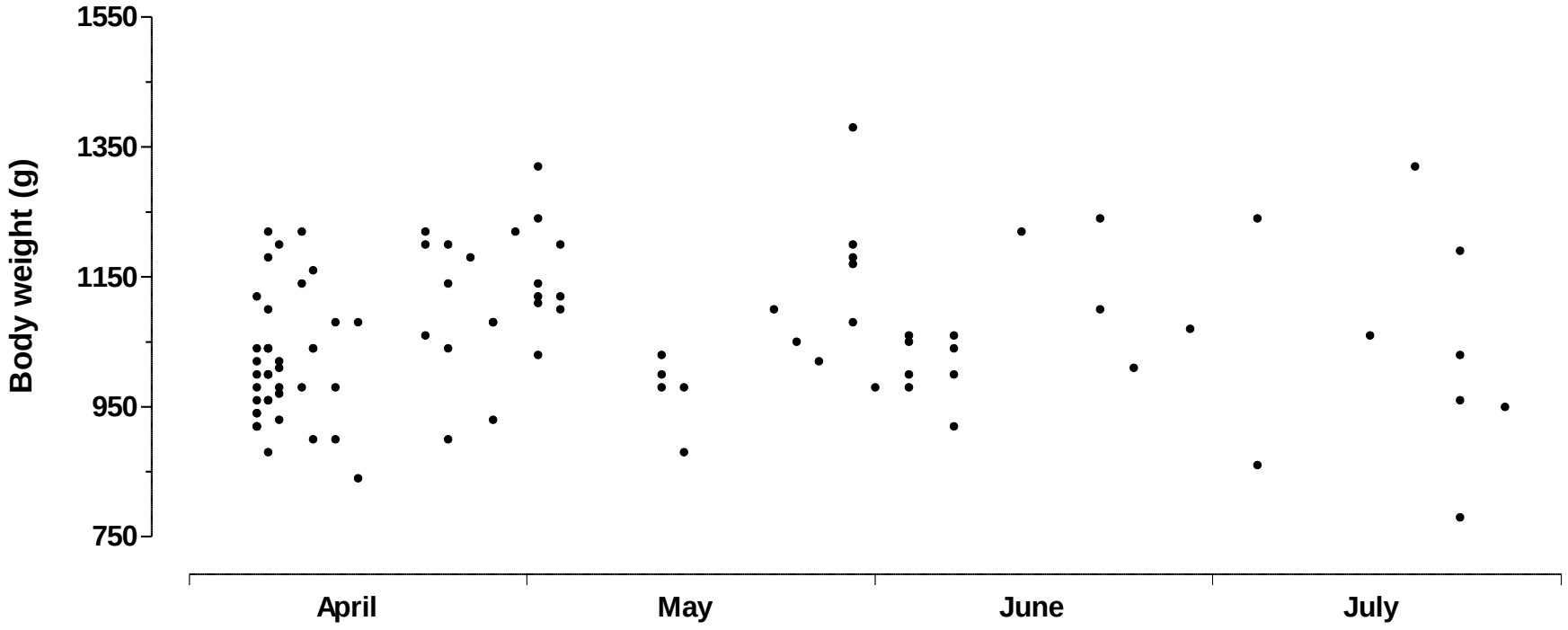


Fig. 2.20. Body weights of female penguins at the time they were first sighted and microchipped at the colony.

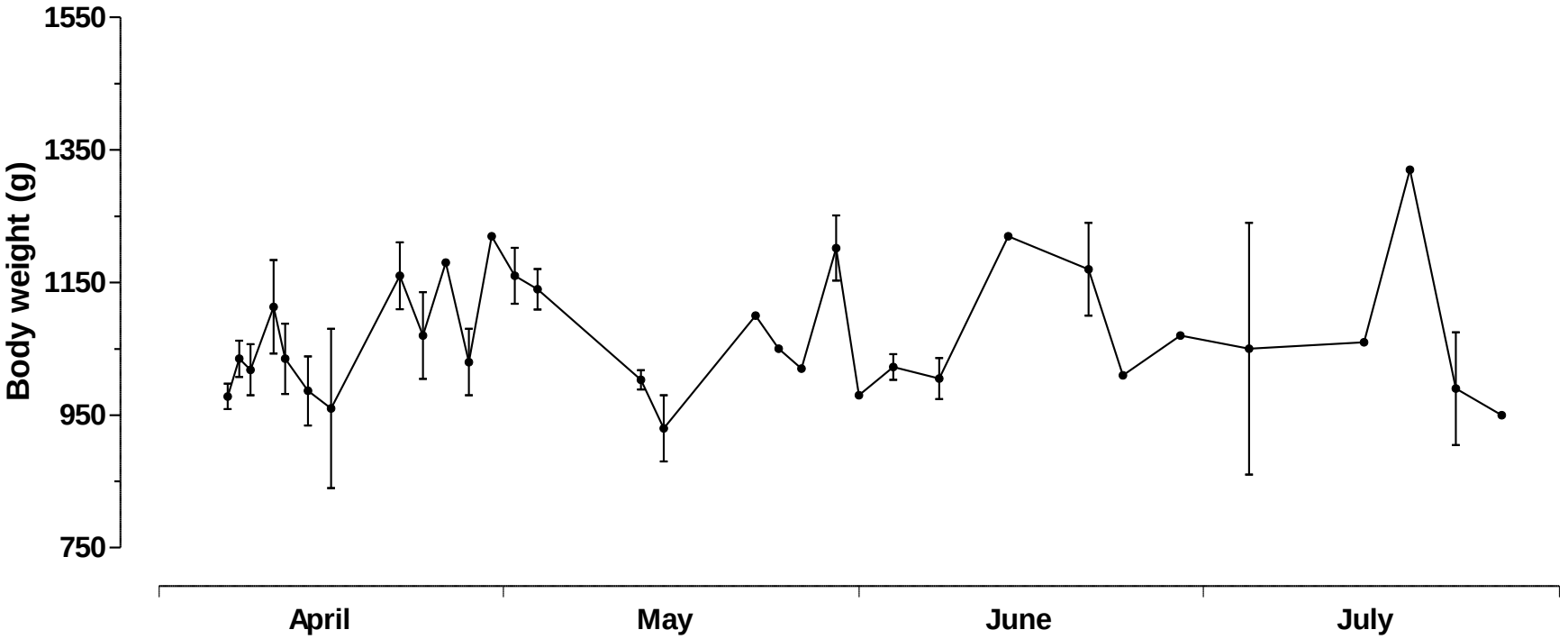


Fig. 2.21. Mean ± S.E. body weights of female penguins at the time they were first sighted and microchipped at the colony.

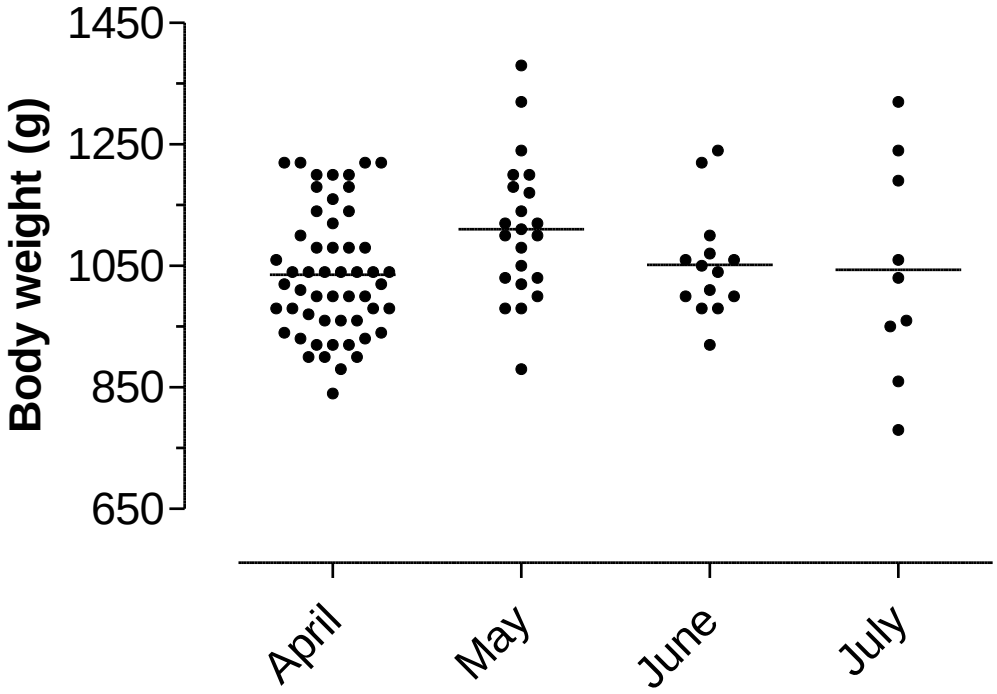


Fig. 2.22. Body weights of female penguins at the time of microchipping during each month of my study in 2021. Lines represent the mean body weights for each month.

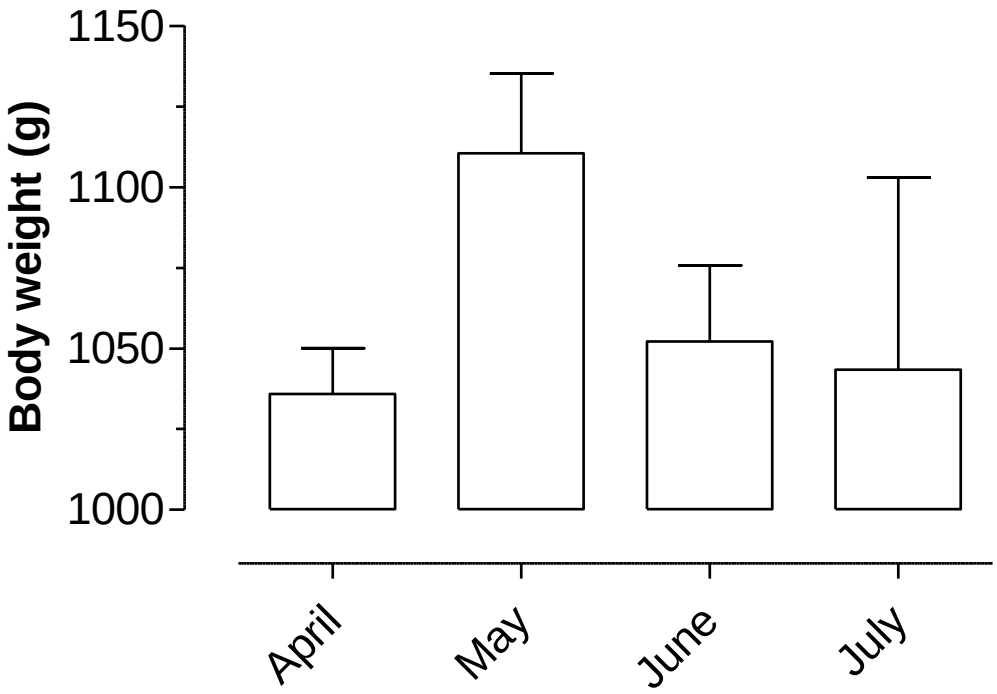


Fig. 2.23. Means and standard errors of female penguin body weights at the time of microchipping during each month of my study in 2021.

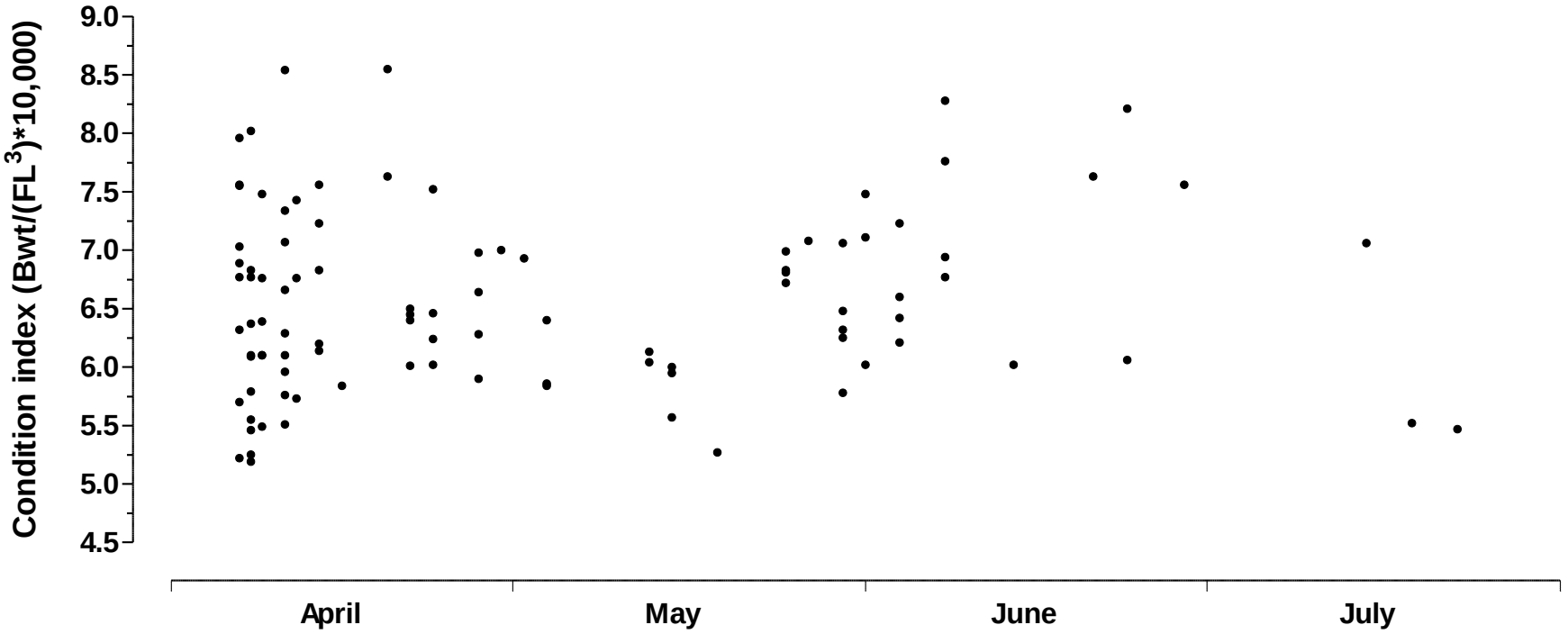


Fig. 2.24. Condition index of male penguins at the time they were first found and microchipped at the colony.

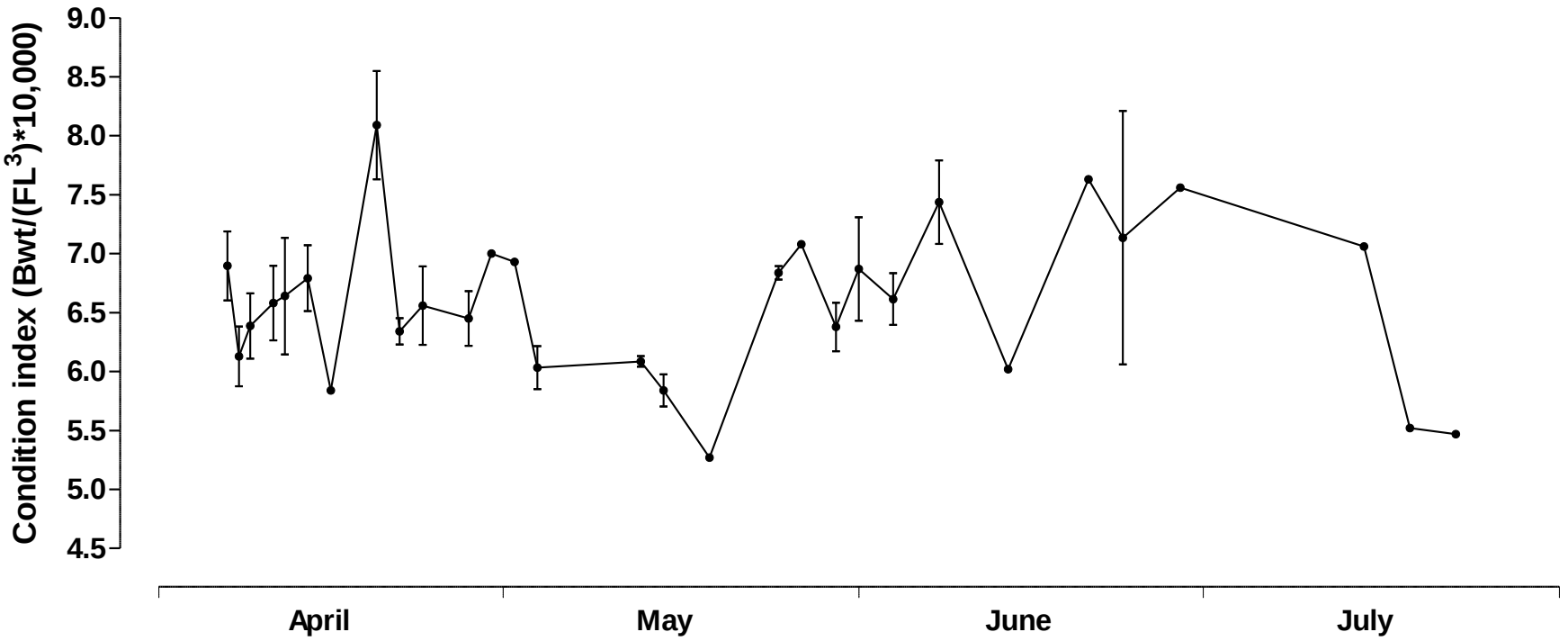


Fig. 2.25. Mean ± S.E. condition index of male penguins at the time they were first found and microchipped at the colony.

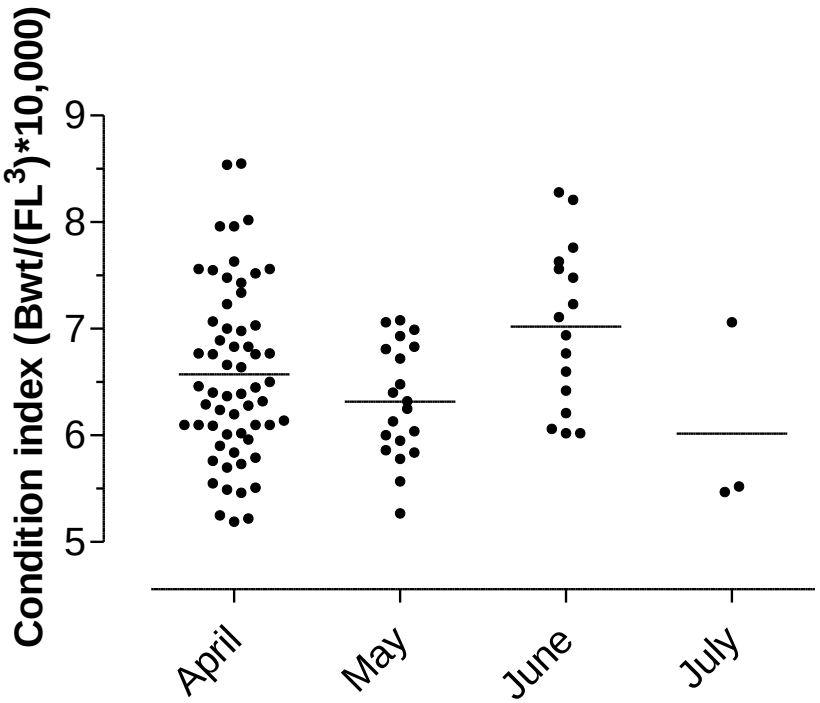


Fig. 2.26. Condition index of male penguins at the time of microchipping during each month of my study in 2021. Lines represent the mean body weights for each month.

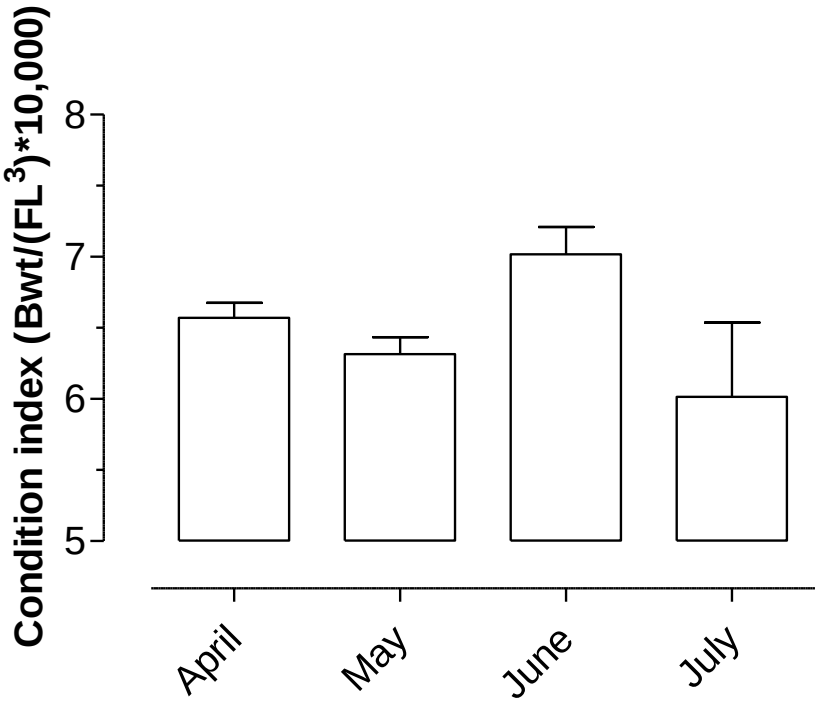


Fig. 2.27. Means and standard errors of male penguin condition index at the time of microchipping during each month of my study in 2021.

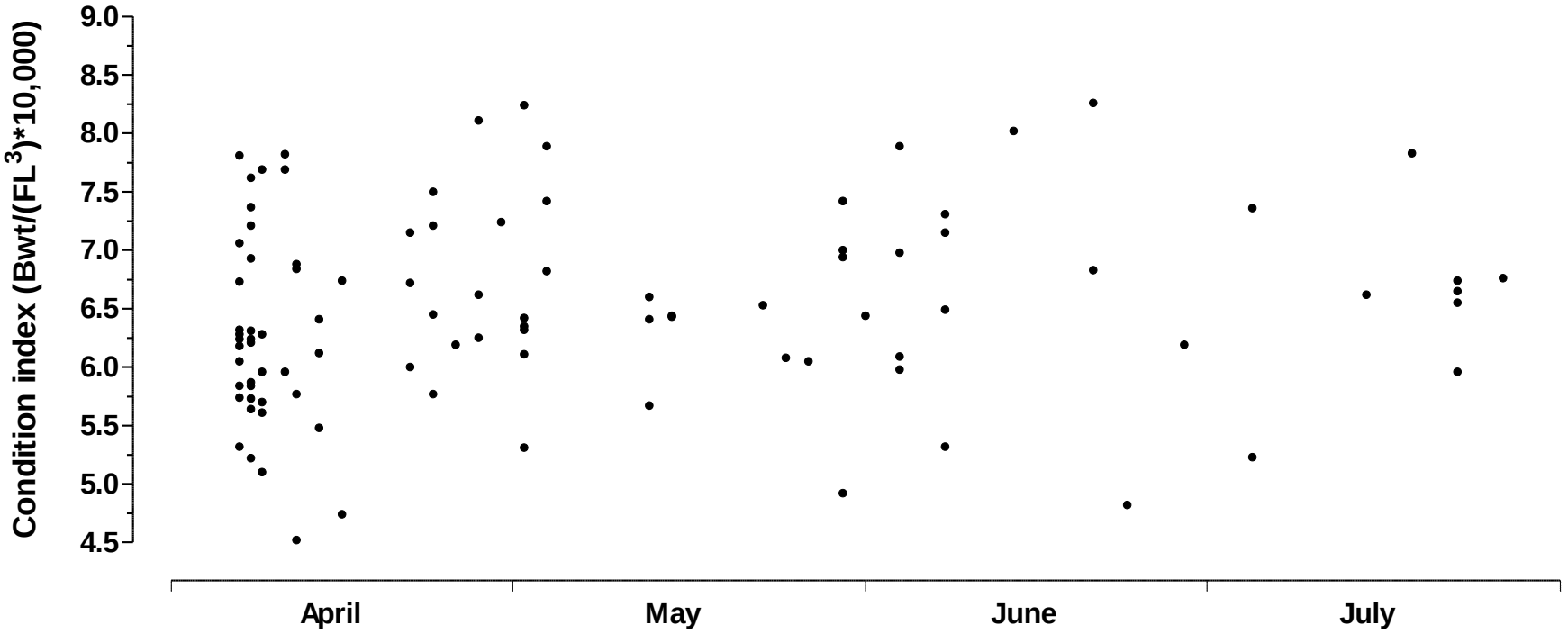


Fig. 2.28. Condition index of female penguins at the time they were first found and microchipped at the colony.

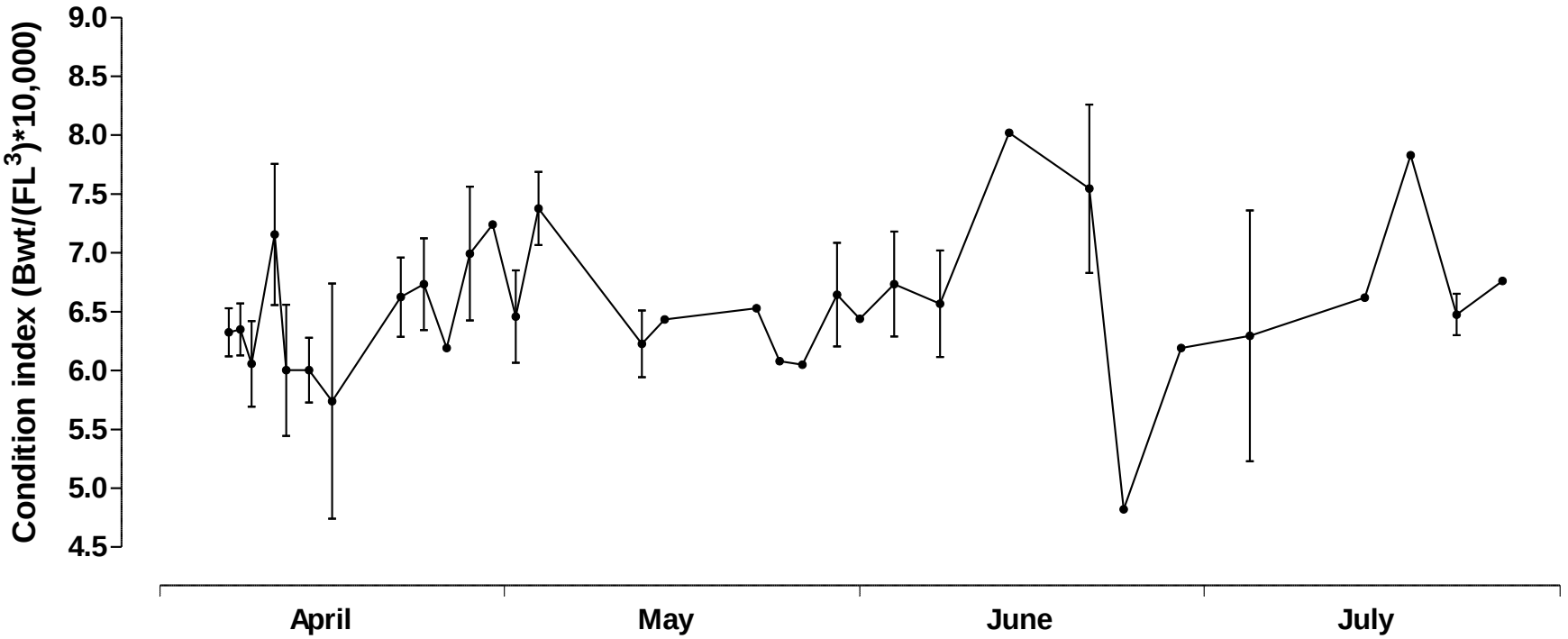


Fig. 2.29. Mean ± S.E. condition index of female penguins at the time they were first found and microchipped at the colony.

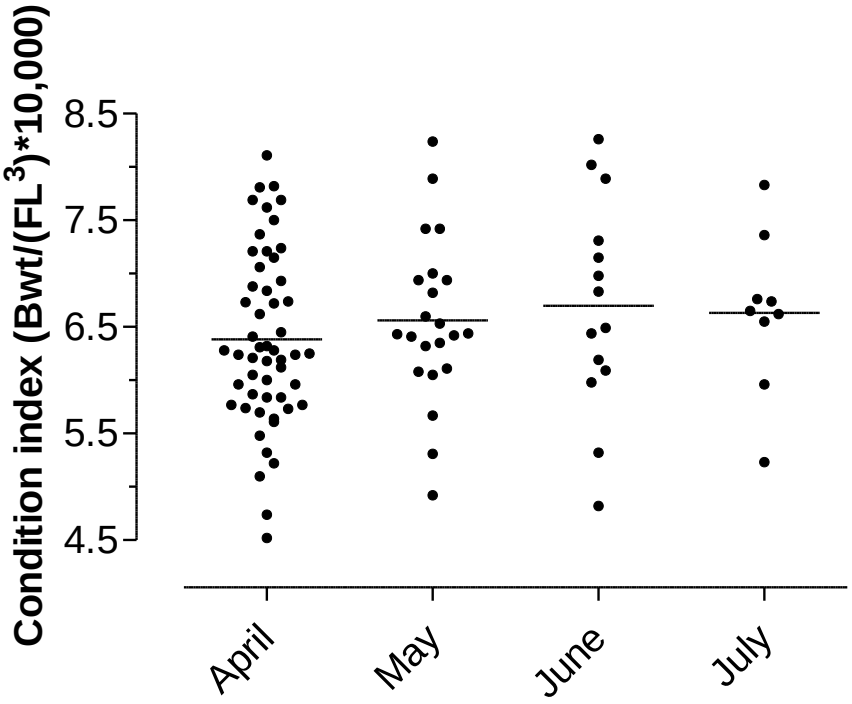


Fig. 2.30. Condition index of female penguins at the time of microchipping during each month of my study in 2021. Lines represent the mean body weights for each month.

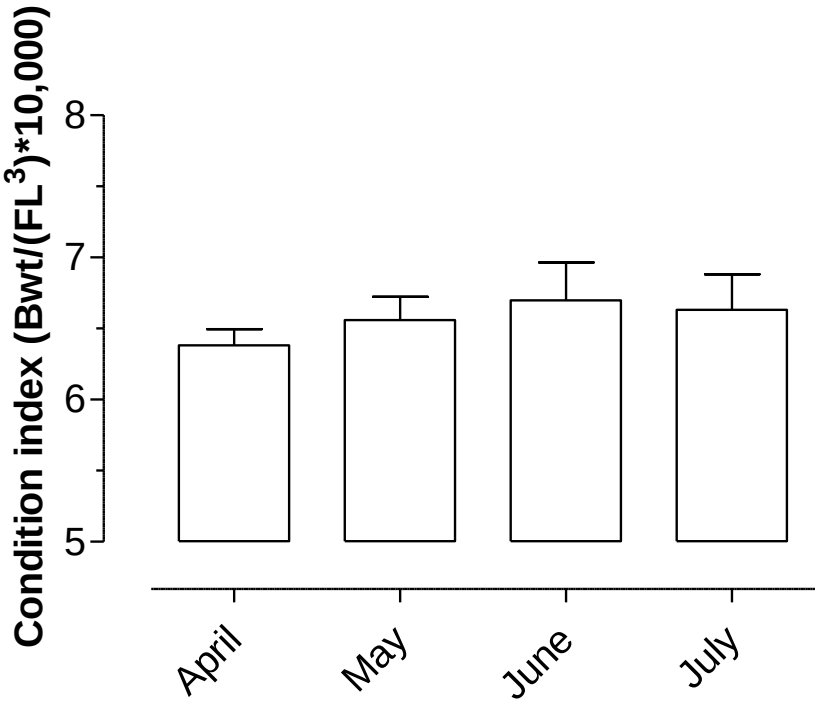


Fig. 2.31. Means and standard errors of female penguin condition index at the time of microchipping during each month of my study in 2021.

2.3.3.2 Body variables in relation to sex

There were significant differences between male and female penguins in mean body weight and flipper length ($t_{188} = 10.25$, $p < 0.0001$; $t_{190} = 7.62$, $p < 0.0001$; see Fig 2.32 and 2.33, and see Table 2.1).

There were no significant differences between male and female penguins in mean condition index ($t_{188} = 0.8351$, $p = 0.4047$; see Fig. 2.34 and Table 2.1).

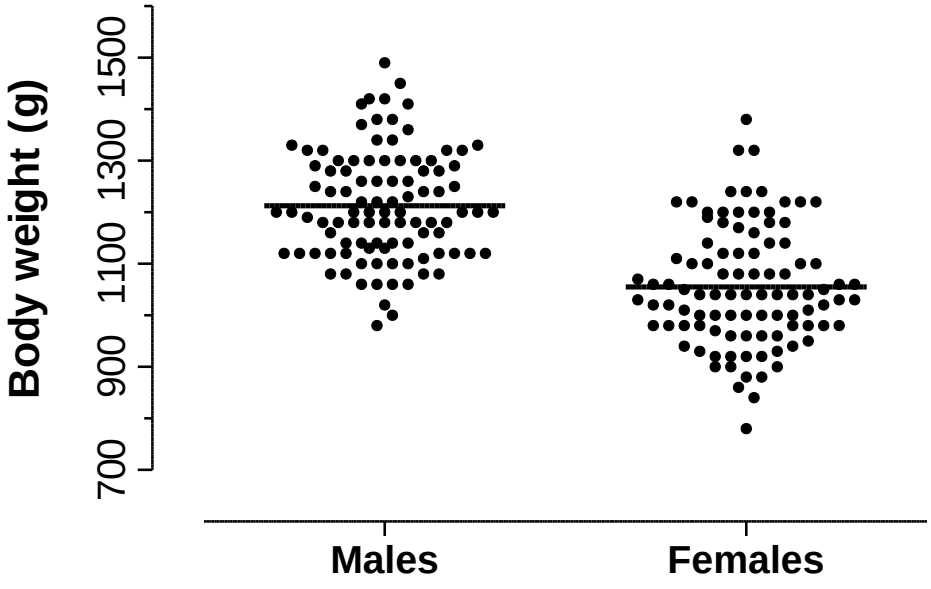


Fig. 2.32. Body weights of male and female penguins at Port Tarakohe from April to July 2021. The mean values are indicated by horizontal lines.

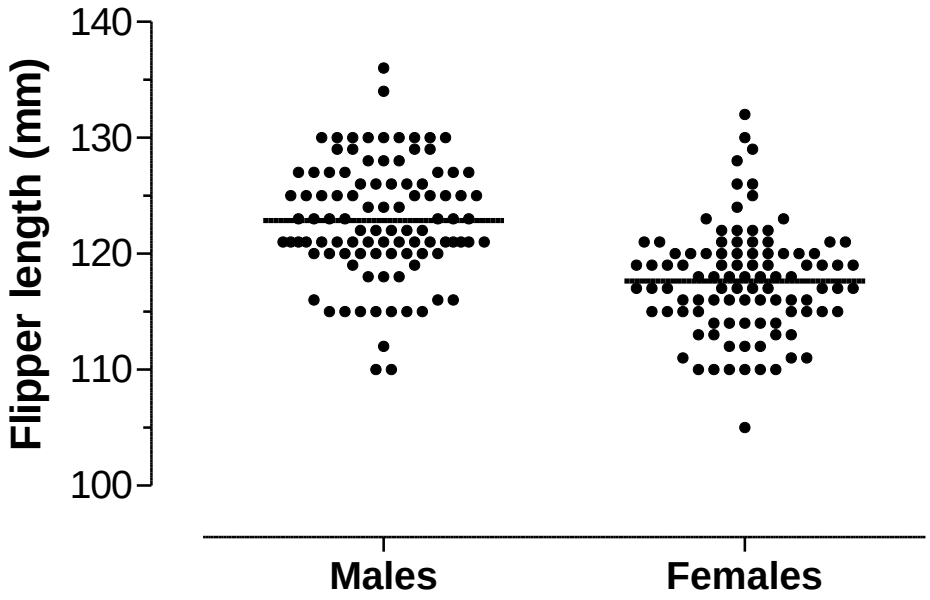


Fig. 2.33. Flipper lengths of male and female penguins at Port Tarakohe from April to July 2021. The mean values are indicated by horizontal lines.

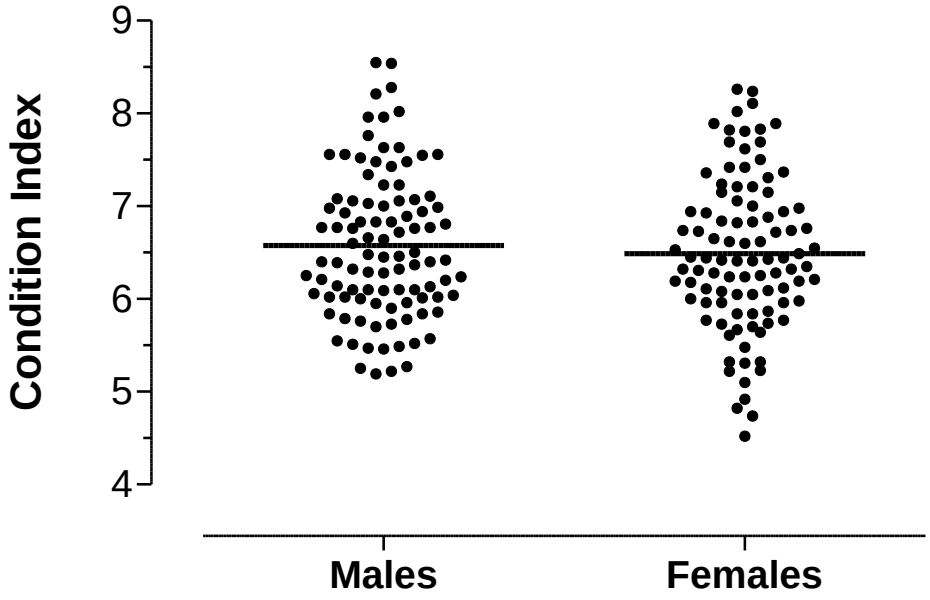


Fig. 2.34. Condition index (body weight/(flipper length^3) x 10 000) of male and female penguins at Port Tarakohe from April to July 2021. The mean values are indicated by horizontal lines.

Table 2.1. Body weight, flipper length and condition index data for male and female penguins at Port Tarakohe from April to July 2021.

	Mean	S.E.	Minimum	Maximum	Sample size
Body weight (g)					
Male	1213.1	10.7	980	1490	99
Female	1055.6	11.6	780	1380	98
Flipper length (mm)					
Male	122.9	0.5	110	136	99
Female	117.7	0.5	105	132	100
Condition index ($Bwt/(FL^3)*10,000$)					
Male	6.58	0.08	5.19	8.55	99
Female	6.49	0.08	4.52	8.26	98

There were no clear patterns of body weight increase during the autumn and winter months (April – July) for male and female penguins at Port Tarakohe (2021), Matiu Somes Island (1957), or Pilots Beach (2000) (see Table 2.2. and Fig. 2.35). Note that the sample size for Port Tarakohe penguins declined from April to July, not because there were less penguins present at the colony, but rather because weights were primarily measured when a penguin was first microchipped. As the study went on, fewer new penguins were sighted and therefore fewer were weighed.

Table 2.2. Body weights (g) of male and female little penguin at Port Tarakohe (2021), Matiu Somes Island (Kinsky, 1960) and Pilots Beach (Johannesen *et al.*, 2002b). Because data was extracted from publications, some values are missing from the table below.

		Port Tarakohe 2021				Matiu Somes Island 1957				Pilots Beach 2000			
		April	May	June	July	April	May	June	July	April	May	June	July
Male	Mean	1216.7	1206	1217.5	1166.7	1260.5	1243	1261	1273.8	1276	1302	1221	1333
	SE	13.34	26.71	27.61	41.77					61	44	31	37
	Min	1000	980	1100	1120	1063.1	1020.6	1077.3	1020.6				
	Max	1420	1450	1490	1250	1644.3	1445.8	1474.2	1615.9				
	N	60	20	16	3	121	65	75	118	13	13	17	15
Female	Mean	1035.8	1110.5	1052.1	1043.3	1073.8	1098.9	1089.8	1150	1145	1188	1154	1246
	SE	14.18	24.80	23.61	59.61					30	40	29	30
	Min	840	880	920	780	907.2	864.7	878.8	863.3				
	Max	1220	1380	1240	1320	1304.1	1261.6	1360.8	1587.6				
	N	53	22	14	9	74	63	52	92	20	16	21	22

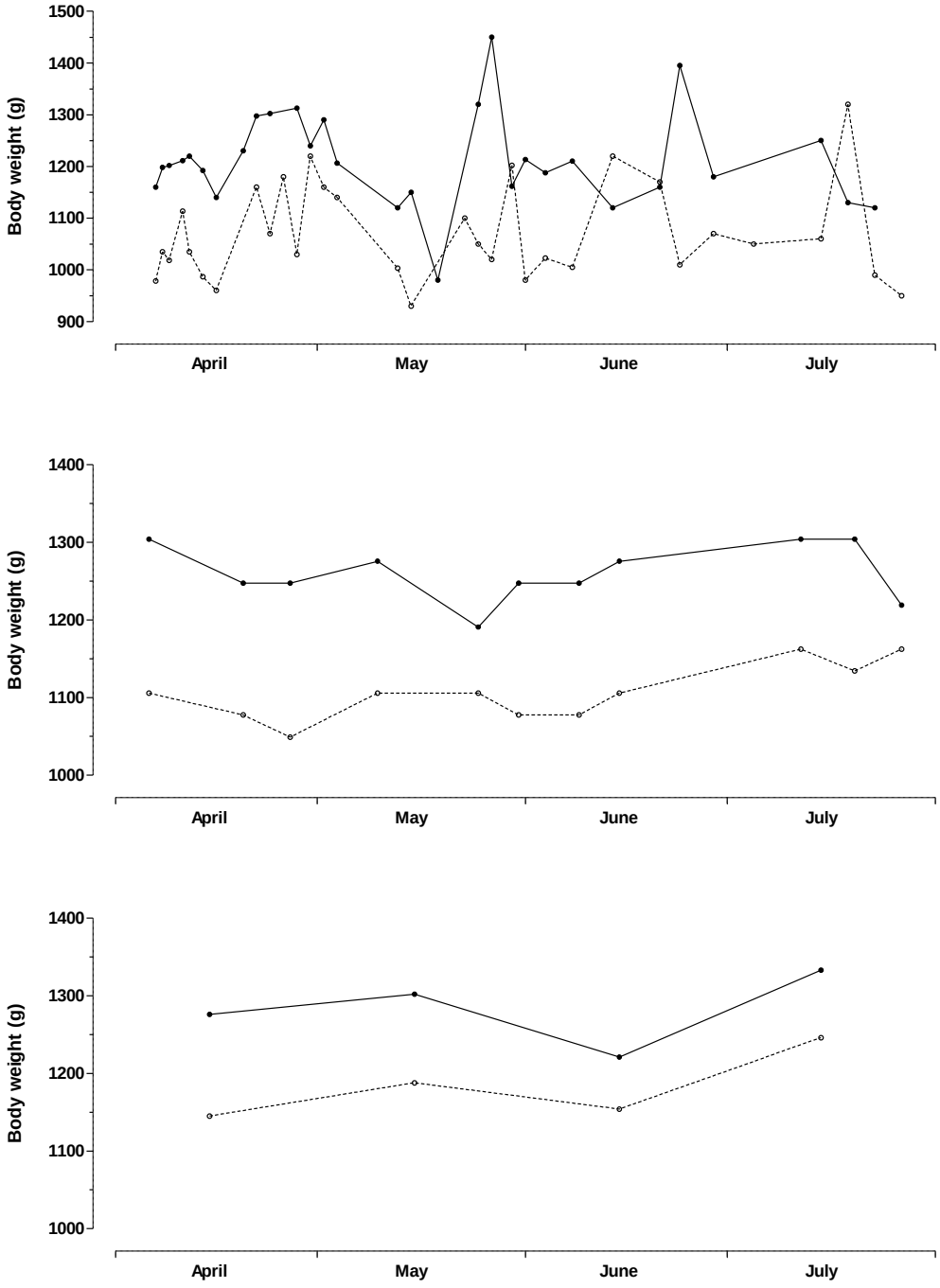


Fig. 2.35. Mean body weights of male (⁻●⁻) and female (--○--) penguins from Port Tarakohe 2021 (top), Matiu Somes Island 1957 (middle), and Pilots Beach 2000 (bottom) from April to July. Data extracted and re-drawn from Kinsky (1960), and (Johannesen *et al.*, 2002b). S.E. values were not available for all data sets, so S.E. values are not presented in the figure.

2.4 Discussion

There was a distinct cyclical pattern in the presence of penguins in nestboxes at Port Tarakohe during daytime checks from April to July 2021, with the number of penguins present alternating from relatively high numbers to relatively low numbers. The cycle was approximately three-and-a-half-weeks long (see section 2.2.5 and 2.3.1). The total number of penguins present during peaks in attendance increased from autumn towards the end of winter. A cyclic pattern of nest site attendance was also found in 1969 and 1970 for penguins on Phillip Island in the study of Reilly and Cullen (1981). In their study, they found that penguins were present at the colony all year round and that colony numbers increased leading up to the breeding season. They reported a three-week cyclic pattern of nest site attendance from April to August (see Fig. 2.7), which was similar to but different than the pattern found at Port Tarakohe. It is possible that penguins in their study may have also had a three-and-a-half-week colony attendance cycle but because their study site was only checked once a week, I cannot draw a definitive conclusion. The three-week cycle may be the real cycle duration, or it may be an artifact of their study design. Further studies with the same methodology are needed to investigate cyclic colony attendance patterns between these two locations.

There have been many reports of marine animals changing their behaviours in response to the lunar cycle (Yamamoto *et al.*, 2008), so relationships between penguin nestbox attendance and the lunar cycle were investigated in the current study. Changes in animal behaviour in relation to the lunar cycle may be due to changes in lunar illumination, lunar gravitational force, or the electromagnetic field (Chakraborty, 2020). The current results indicate that daily nestbox attendance of little penguins is not correlated with lunar cycle phase. While there was a cyclic pattern for penguin numbers in nestboxes that appeared to have a peak

around the full moon phase of the lunar cycle, the period of the cycle of attendance was shorter than the period of the lunar cycle, so the peak in numbers of penguins in nestboxes became earlier and earlier each month. If this autumn and winter study was to be repeated in another year, then the phase of the moon at the start of the study would be different from the current study, so different results would be obtained for the relationship between numbers of penguins and phase of the lunar cycle. The results in the current study, where more penguins were present during the full moon phase of the lunar cycle than during the new moon phase, are considered to be an artefact arising from the timing of the study in relation to the timing of the lunar cycle in 2021. Reilly and Cullen (1981) also found no correlation between lunar phase and penguin nest site attendance (see Fig. 2.14 and Fig. 2.15).

There are very clear cyclic patterns of nest site attendance in other seabird species such as Cory's shearwater (*Calonectris borealis*; (Granadeiro *et al.*, 2009), horned puffin (*Fratercula corniculate*; (Harding *et al.*, 2005) and common murres (*Uria aalge*; (Wilhelm and Storey, 2002). For seabirds, the regulatory mechanisms that underlie these cycles and their biological significance are virtually unknown (Granadeiro *et al.*, 2009). Since there was no clear relationship between the lunar cycle and the cycle of numbers of penguins at the colony in nestboxes, there would be value in future studies investigating other factors that could be related to the cycle.

Several hypotheses have been proposed to explain cyclical patterns in colony attendance of seabirds. These include pre-breeding cyclic nest site attendance increasing the time neighbouring birds and pairs spend together and therefore increases egg-laying synchrony and reducing predation risk (Wilhelm and Storey, 2002), journeying to rich food sources to support egg laying (Perrins, 1970), trade-offs between short trips and long trips to find food

resources (Weimerskirch, 1998), and facilitating social interactions at the colony (Granadeiro *et al.*, 2009). Future studies investigating whether any of these hypotheses relate to little penguin colony attendance cycles would help us to better understand why they have this cyclic pattern of colony attendance and may help to improve monitoring strategies. There would also be value in looking at little penguin nest site attendance for consecutive years to see if these three-and-a-half-week cycles occur every year and how they may influence reproductive success. If the cyclic colony attendance is related to improving foraging or decreasing predation risks, then I would expect penguins with strong autumn and winter colony attendance cycles to be more successful in the following breeding season.

There were no differences in colony attendance between male and female penguins at Port Tarakohe in the current study. Reilly and Cullen (1981) found that males were generally present more often at the colony from moult through autumn and winter until eggs were laid. They also found twice as many males than females at newly excavated nests and proposed that males may be primarily responsible for digging natural nest sites. The differences in nesting sites between Phillip Island and Port Tarakohe may explain why there was no difference between male and female nest attendance patterns at Port Tarakohe, where penguins were in artificial nestboxes, in comparison with observations reported by Reilly and Cullen (1981). In their study they had a combination of natural nest sites and artificial burrows. The artificial burrows were filled with sand after penguins had moulted, then penguins had to dig sand out of the artificial burrows before they reoccupied them.

It has been hypothesised for other seabirds that an increase in the formation of social bonds could be a driver for cyclic colony attendance (Granadeiro *et al.*, 2009). It would be worth examining this hypothesis in little penguins. I would expect to see successful penguin pairs

spending more time at the colony together in the autumn and winter months prior to breeding and this could explain why males and females had similar colony attendance rates in my study.

There was no evidence of an increase in body weights or condition index in male or female penguins during the months of April to July. This is consistent with observations of little penguins on Somes Island in 1957 and Pilots Beach in 2000 (Johannesen *et al.*, 2002b; Kinsky, 1960). It is interesting to see similar results from locations with different timings of the annual cycle as this may suggest that the lack of increase in body weight or condition is a consistent biological pattern, rather than a response to local conditions or timing.

During the winter months, little penguins have been found to have larger foraging ranges than in summer. It has been suggested that this could be due to reduced local prey abundance and the need for penguins to travel further away for food (McCutcheon *et al.*, 2011). It would be interesting to do further research in this area to see if little penguins use particular foraging strategies during this time of year. It may be that after moult they can find enough prey to regain their body condition, but during the winter they can only maintain body weight, rather than increase it prior to breeding. By attaching tracking devices and measuring body weight on the day little penguins arrive back on land to the colony, a better understanding of this could be obtained. There would also be value in extending this research from the end of moult period through autumn and winter to the start of egg laying. Another explanation for body weight increasing before moult but not in winter prior to breeding is that little penguins may be income breeders. Income breeders rely on nutrient supply consumed concurrently with offspring development rather than storing energy in advance of breeding (capitol

breeding) (Stephens *et al.*, 2014; Whiteman *et al.*, 2021). Further studies over consecutive years would be useful for exploring this idea.

It is important to note that, in my study sample sizes for body weight in June and July were smaller than in April and May, so definitive conclusions about body weight in June and July, in comparison with April and May, cannot be drawn. When my study began, no penguins at Port Tarakohe were individually identified with microchips, so when penguins were weighed at the time of microchipping it was not known how long they had been fasting on land before being weighed. This limitation usually applies to studies of body weight in little penguins and also applied to the study of Kinsky (1960). However, in the current study, once all penguins were microchipped, with nestbox checks every second day, all body weights were measured in penguins that had been on land for no more than two days during April and May. During June and July, nestbox checks were less frequent, so penguins may have been fasting on land for longer before being weighed than was the case for penguins weighed in April and May. In future studies of body weight in autumn and winter, the best results would be obtained when all penguins were microchipped and nestboxes were checked every day or every second day, so the maximum period of fasting at the time of weighing would be two days.

3. Individual penguin behaviours and nestbox occupancy in autumn and winter

3.1 Introduction

Artificial nestboxes provide shelter for little penguins, and their eggs and chicks, against harsh weather conditions as well as from predators (Clitheroe, 2021; Ropert-Coudert *et al.*, 2004). Nestboxes provide opportunities for detailed studies of individual penguins that cannot be conducted for penguins in natural nest sites (Ratz, 2019). Nestboxes are also an effective management tool for little penguin conservation and there can be a high uptake when nestboxes are provided (Sutherland *et al.*, 2014). Nestboxes also provide a location in which pairing and courtship can take place and are readily used for moult and for breeding (Clitheroe, 2021; Ratz, 2019).

Little penguins tend to return to their former breeding site, or to one nearby if their previous nest site is not available (Reilly and Cullen, 1981; Sutherland *et al.*, 2014). Little is known about individual little penguin use of nestboxes during autumn and winter, with no published information on how many nestboxes an individual penguin may visit, durations of nestbox occupancy during the day, and how many potential partners use a nestbox.

The only previous studies of individual penguin nest occupancy for some of the winter months are those of Chiaradia and Kerry (1999), and Reilly and Cullen (1981). Chiaradia and Kerry (1999) recorded nest attendance patterns of 53 little penguin pairs on Phillip Island from 28 June 1995 to 30 January 1996. They found that both male and female penguins made occasional visits to the colony during the winter months, but both male and female penguins of a future breeding pair were rarely in attendance at the colony at the same time during these months. Reilly and Cullen (1981) recorded nest attendance patterns of 15

penguin pairs in June and July 1978, and found that male and female penguins were present at their nest during this time. Penguins in their study had a general pattern of staying in their nest for a few days and then going to sea for longer periods. While they usually stayed in the same nest, if they did change nests, the male and female in the pair remained together. Penguin pairs showed some synchronisations of their arrival and departure times. Pairs in nests together usually left the colony on the same day, or within several days of each other.

Data from Reilly and Cullen (1981) suggested that pairs that arrived at the colony together may have been together at sea. Other penguin pairs appeared to synchronise their return to the colony even though they had previously left the colony at different times. There were many instances of short breaks where penguins left the colony and their mate for a night, as well as longer breaks of five days or more.

Individual little penguin behaviours in relation to how many nestboxes they visit or how many different penguins each is seen with during autumn and winter, and how long penguins spend on land and at sea, have not previously been studied. This chapter describes a study of individual penguin behaviours in relation to their nestboxes during the autumn and winter months at Port Tarakohe in 2021. Nestbox attendance patterns, how many different nestboxes each penguin was sighted in, how many penguins were sighted in each nestbox, how many different penguins each penguin was seen with, individual nestbox attendance patterns, paired penguin nestbox attendance patterns, and penguin durations on land in nestboxes compared to at sea, were investigated.

3.2 Materials and methods

Materials and methods are described in section 2.

3.3 Results

3.3.1 Penguin presence in nestboxes

A total of 205 penguins were microchipped in nestboxes during the study. Sexes were subsequently assigned (see section 2.3.3) to 199 penguins, with 99 male and 100 female penguins.

Penguins were seen during the study in 111 of the 150 nestboxes at Port Tarakohe. Graphs showing the number of penguins present at each nestbox check are shown for these nestboxes in Appendices 1 to 5. Nestboxes were assigned to one of five groups depending on the pattern of the number of penguins seen in the nestbox.

Penguins were present on one day of nestbox checks in 21 nestboxes (see example in Fig. 3.1 and graphs in Appendix 1). One penguin (of any identity) was seen in seven of these nestboxes and two penguins were seen in 14 of these nestboxes.

Penguins were present on two to five days of nestbox checks in 27 nestboxes (see example in Fig. 3.2 and graphs in Appendix 2). In some nestboxes, one or two penguins were present on days spread throughout the study period (see Fig. 3.2), and in other nestboxes penguins were present occasionally (e.g. nestbox 42, Appendix Fig. 6.4; nestbox 88, Appendix Fig. 6.5).

One nestbox had one penguin present on seven days and two penguins present on one day (see Fig. 3.3). This nestbox was considered to have regularly had one penguin present on days of nestbox checks.

Thirty-two nestboxes regularly had two penguins present on days of nestbox checks (see example in Fig. 3.4 and graphs in Appendix 4). The penguins in nestbox 12 (Fig. 3.4) were present in the nestbox for between eight and eleven days, and away from the nestbox for between nine and twelve days, from late April until early July. There were four recurrences of the penguins being in the nestbox for consecutive days and then away for consecutive days. These periods corresponded with the four peaks in the total numbers of penguins in nestboxes (see Fig.2.5).

Other nestboxes regularly had one or two penguins present on days of nestbox checks (see example in Fig. 3.5 and graphs in Appendix 5). Thirty nestboxes were identified with this pattern of occupancy by penguins.

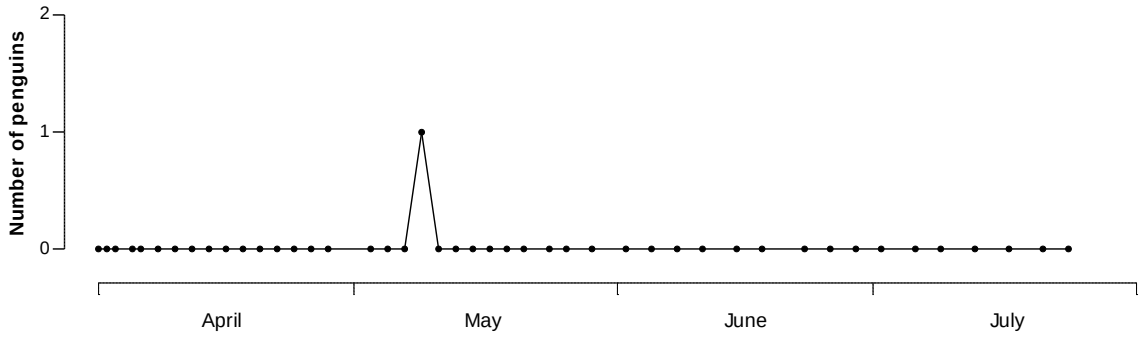


Fig. 3.1. Number of penguins in nestbox 30 when the nestbox was checked on 45 days from 7 April to 30 July 2021. A penguin was present in the nestbox on one day.

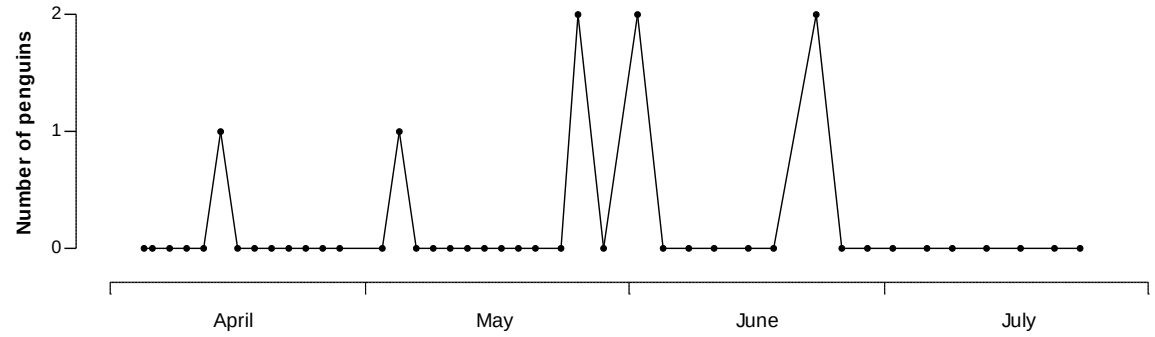


Fig. 3.2. Number of penguins in nestbox 129 when the nestbox was checked on 45 days from 7 April to 30 July 2021. One or two penguins were present in the nestbox on five days.

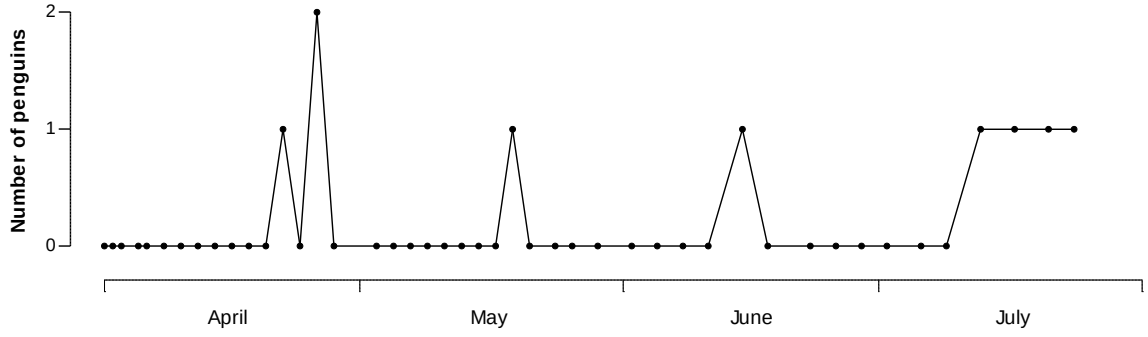


Fig. 3.3. Number of penguins in nestbox 22 when the nestbox was checked on 45 days from 7 April to 30 July 2021. One penguin was present in the nestbox on seven days, and two penguins were present on one day.

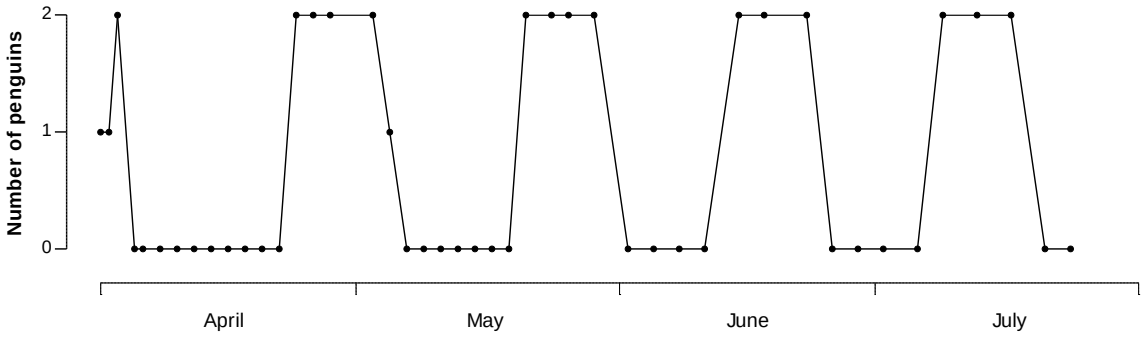


Fig. 3.4. Number of penguins in nestbox 12 when the nestbox was checked on 45 days from 7 April to 30 July 2021. There were four periods when penguins were present in the nestbox for periods of eight to thirteen consecutive days. Note that nestboxes were checked less frequently in June and July than in April and May, so penguins could have been present in June and July for longer than the recorded periods of consecutive days.

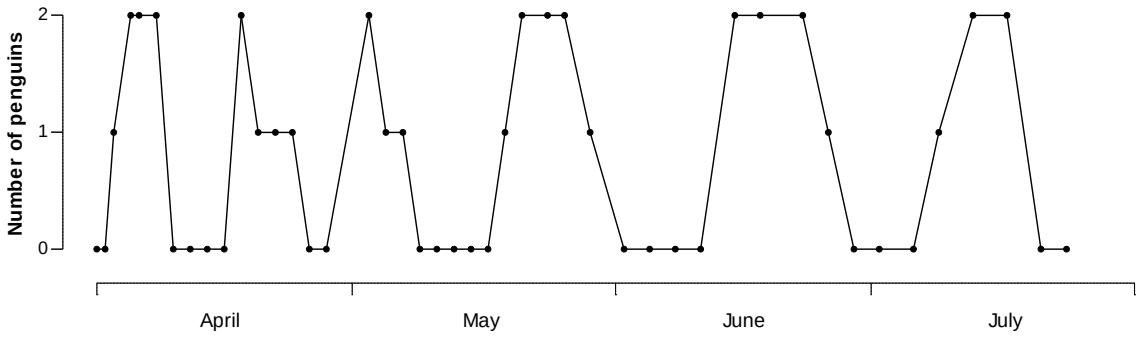


Fig. 3.5. Number of penguins in nestbox 71 when the nestbox was checked on 45 days from 7 April to 30 July 2021. One or two penguins were regularly present in the nestbox on consecutive days and then absent for consecutive days.

3.3.1.1 Numbers of nestboxes in which penguins were recorded

While a majority of penguins (123) were in the same nestbox on every day when they were seen, 47 penguins were seen in two different nestboxes, 23 penguins were seen in three different nestboxes, 9 penguins were seen in four different nestboxes, 2 penguins were seen in five different nestboxes and 1 penguin was seen in seven different nestboxes (see Fig. 3.6). The percentages of penguins seen in one or more different nestboxes were 60%, 22.9%, 11.2%, 4.4%, 1% and 0.5% respectively.

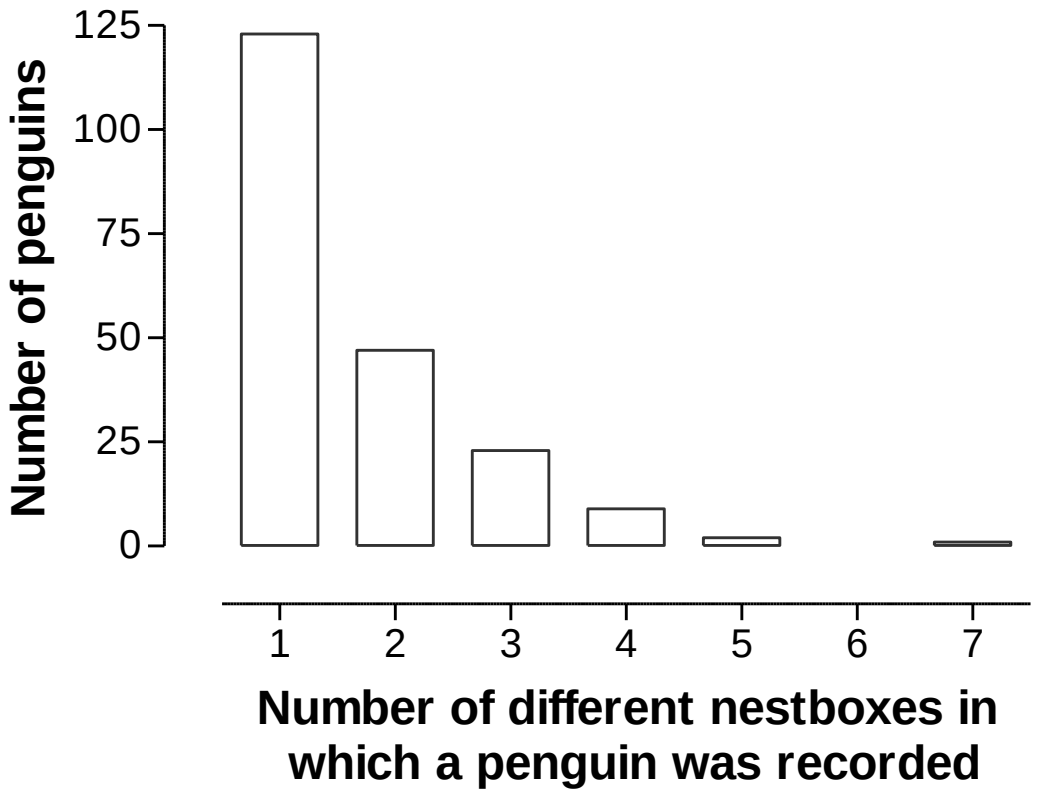


Fig. 3.6. Number of penguins recorded in different numbers of nestboxes.

The penguin (microchip number 13359879) seen in seven different nestboxes was a male that was twice seen in nestbox 90 and seen once in six other nestboxes (see Table. 3.1). The penguin was seen by himself on six of the eight occasions and with a female penguin (microchip number 13360479) on two occasions. He attempted to breed in nestbox 9 later in the year but both chicks died. In 2022 he successfully fledged two chicks in nestbox 87 with penguin number 13400472. Nestbox 87 was not one of the seven nestboxes he was originally sighted in during this study (see Table. 3.1).

It is important to note that nestboxes 8, 9 and 11 were across the path from nestboxes 88, 90, 91 and 92. There was only a few meters between each nestbox both across the path from one another and along the length of the port arm. The greatest distance between the nestboxes used by penguin 13359879 was approximately nine meters, from nestbox 8 to nestbox 11.

The two penguins seen in five different nestboxes were females. They were both seen with three other penguins (see Tables 3.2 and 3.3). The sex of one penguin (microchip number 13365552) was unknown, however the other five penguins were all males.

Table. 3.1. Records of the presence of a male penguin (microchip number 13359879) that was seen in seven different nestboxes.

Date	Nestbox number	Microchip number of a second penguin in the nestbox
11.4.21	91	13360479
12.4.21	90	
14.4.21	90	
4.5.21	92	
11.5.21	11	13360479
8.6.21	8	
29.6.21	88	
27.7.21	9	

Table. 3.2. Records of the presence of a female penguin (microchip number 13363547) that was seen in five different nestboxes.

Date	Nestbox number	Microchip number of a second penguin in the nestbox
28.4.21	61	13359816
23.5.21	62	13359816
1.6.21	55	13373608
21.6.21	69	13359816
23.7.21	72	13363487

Table. 3.3. Records of the presence of a female penguin (microchip number 13388899) that was seen in five different nestboxes.

Date	Nestbox number	Microchip number of a second penguin in the nestbox
7.4.21	9	13358553
2.5.21	90	13365552
9.5.21	17	
30.5.21	82	13359556
4.6.21	9	13359556
19.7.21	88	13359556
23.7.21	9	13359556

As with the previous example (see Table 3.1), it is important to note that nestbox 9 is across the path from nestboxes 82, 88 and 90. There was only a few meters between each nestbox both across the path from one another and along the length of the port arm. Nestbox 17 was a bit further up the port arm. The greatest distance between the nestboxes used by penguin 13363547 was approximately 32 meters, from nestbox 55 to nestbox 72). The greatest distance between the nestboxes used by penguin 13388899 was approximately 27 meters, from nestbox 9 to nestbox 28).

The proportions of male and female penguins seen in one to four different nestboxes were similar (see Fig. 3.7.).

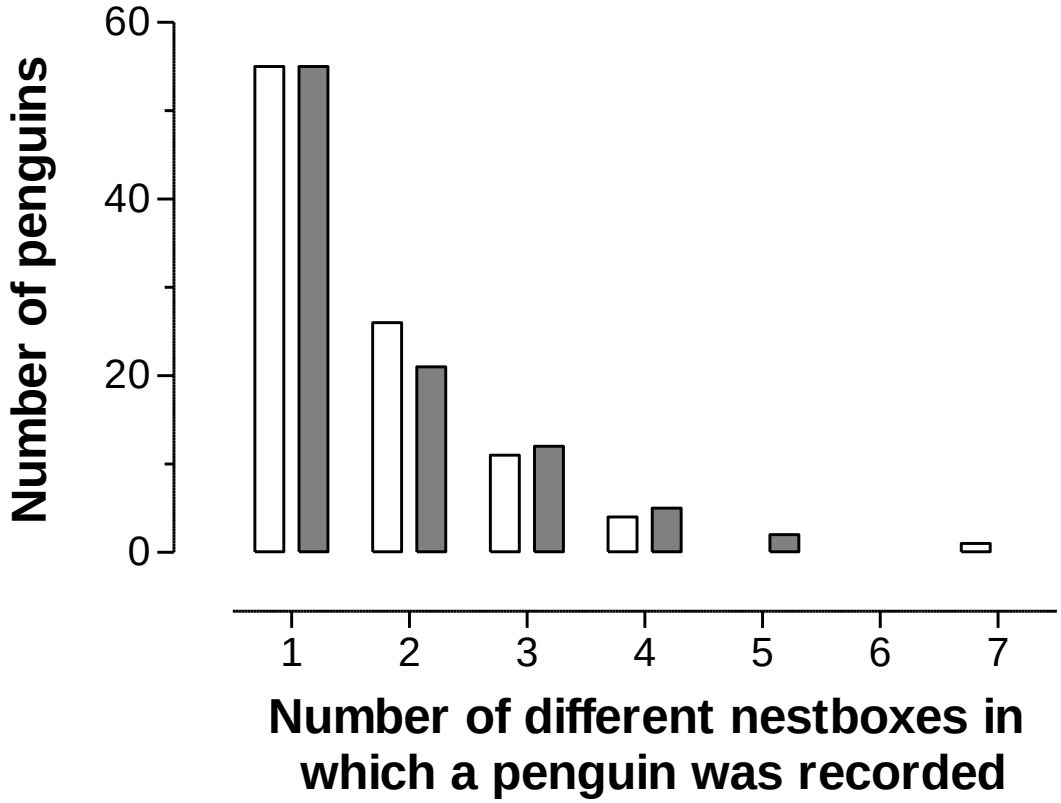


Fig. 3.7. Numbers of male and female penguins recorded in different numbers of nestboxes. Numbers of males are shown by white bars and number of females are shown by shaded bars.

3.3.1.2 Number of penguins per nestbox

There were 45 nestboxes in which two different penguins were seen in during my study. There were 7 nestboxes in which only one penguin was seen in, 23 nestboxes had three different penguins seen in them, 21 nestboxes had four different penguins seen in them, 7 nestboxes had five different penguins seen in them, 6 nestboxes had six different penguins seen in them, 1 nestbox (number 55, see Fig. 3.9) had nine different penguins seen in it and 1 nestbox (number 130, Fig. 3.10) had ten different penguins seen in it (see Fig. 3.8). The percentages of nestboxes in which from one to ten different penguins were seen were 6.3%, 40.5%, 20.7%, 18.2%, 6.3%, 5.4%, 0.9% and 0.9% respectively.

During April and May, nestbox 55 had five single penguin visits from four different penguins (two teal, one pink, one orange and one yellow dot) and two paired penguin visits from four different penguins (one green, one red, one grey and one blue dot). During June and July there were three paired penguin visits and one single penguin visit. All three paired penguin visits were from penguin 13354590 (yellow dots) and 13357491 (purple dots) (see Fig. 3.9).

Nestbox 55 was located on the outer side of the western breakwater near the end and may have been situated near one of the main pathways penguins use when they return from sea. Nestbox 55 was successfully used to fledge two chicks in both the 2021 and 2022 breeding season by male penguin 13354590 (yellow dot) and female penguin 13357491 (purple dot).

Nestbox 130 had eight single penguin visits by four different penguins (four green, one yellow, two red and one grey dot) and ten paired penguin visits by nine different known penguins (one pink, one blue, one orange, one yellow, three red, six green, one purple, one brown and one teal dot) and four unknown penguins (four black dots) (see Fig. 3.10).

Nestbox 130 was located near the middle of the port arm that extends into the harbour (see Fig 2.2). There was a flattened dirt track next to nestbox 130, indicating that it was next to a main path for penguins when they return from sea. It is possible that many penguins took refuge in this nestbox to rest or hide after returning to land. Nestbox 130 was decommissioned on October 5 due to it being continuously wet and muddy. Female penguin 13396991 (red dot) and male penguin 13389355 (green dot) were regularly seen in this nestbox up until it was decommissioned and may have attempted to breed here.

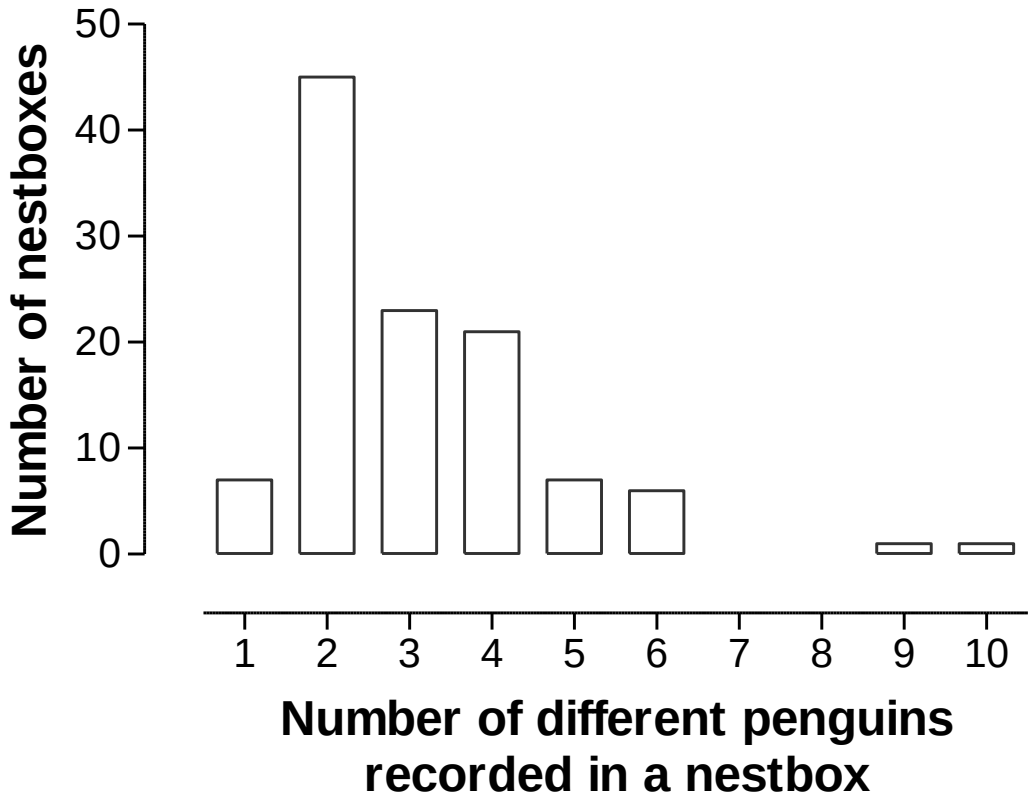


Fig. 3.8. Number of nestboxes in which different numbers of penguins were recorded.

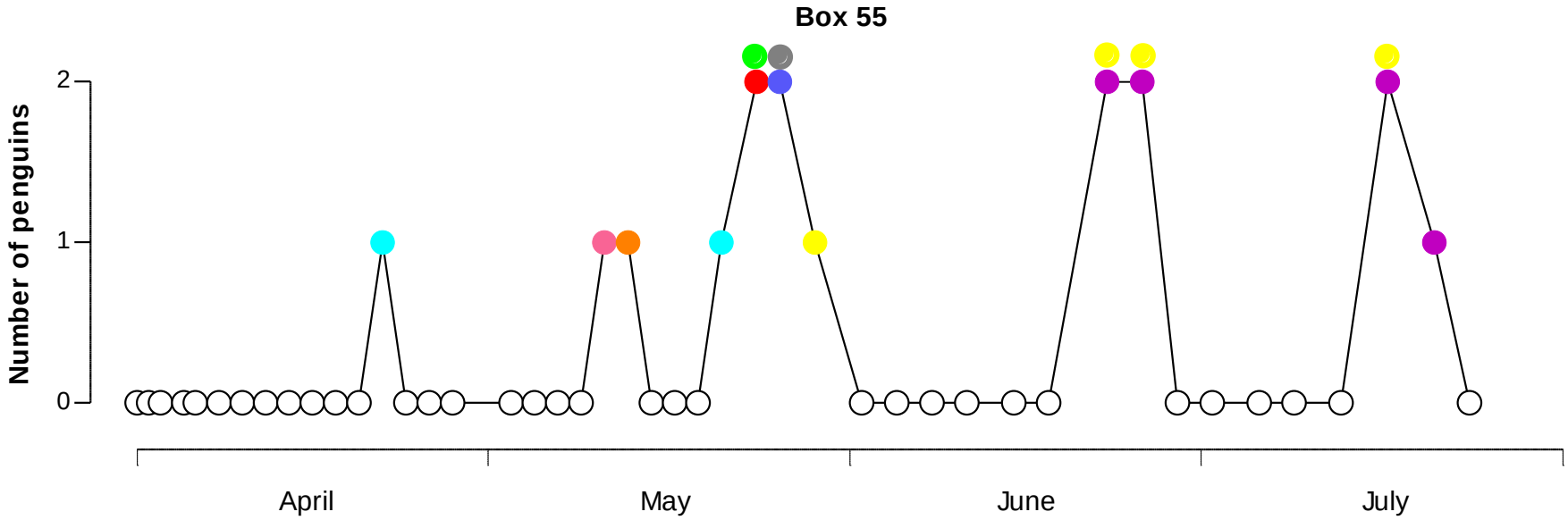


Fig. 3.9. Number of penguins in nestbox 55 when the nestbox was checked on 45 occasions from 7 April to 30 July 2021. Nine different penguins were recorded in this nestbox. The different penguins are shown by different coloured dots.

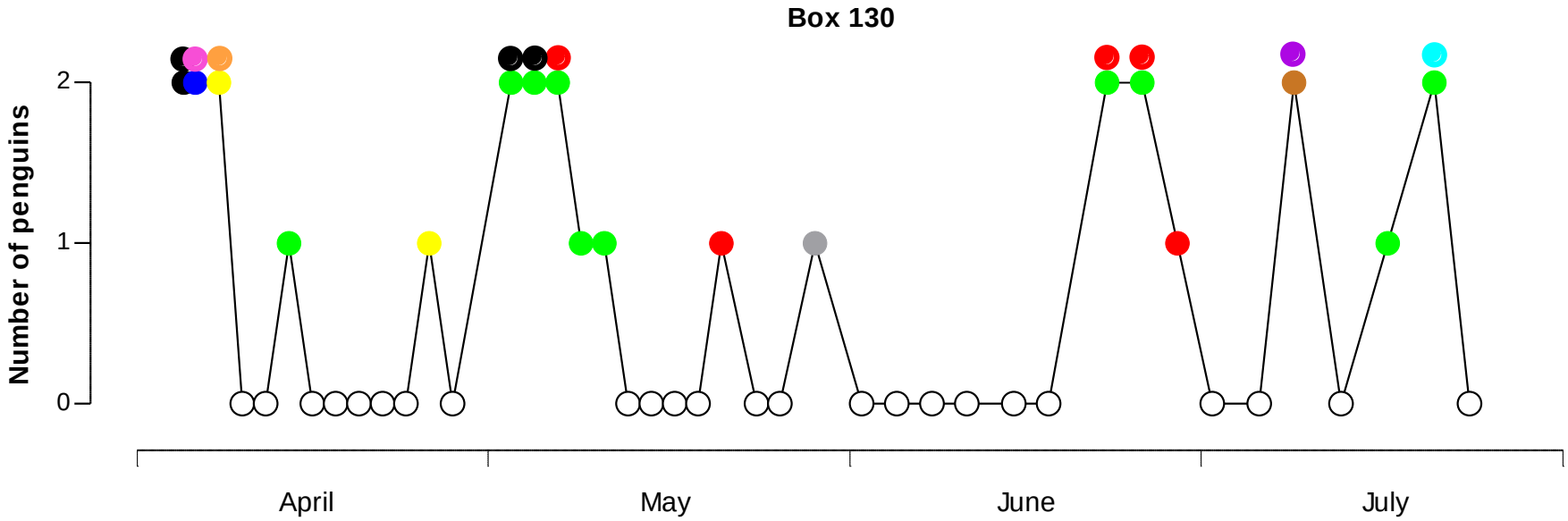


Fig. 3.10. Number of penguins in nestbox 130 when the nestbox was checked on 45 occasions from 7 April to 30 July 2021. Ten different penguins were individually identified from their microchips. The different penguins are shown by different coloured dots. Penguins that did not have microchips and hence could not be identified are represented by black dots. It is likely that two penguins without microchips on one occasion in early April, and one penguin without a microchip in early May, were microchipped one or two days later and hence are included in the total of ten individually identified penguins in nestbox 130.

3.3.2 Number of other penguins each penguin was seen with

Ten penguins (4.9%) were only seen by themselves and were never seen with another penguin. One hundred and fifty-five penguins (75.6%) were with the same penguin on all occasions when they were seen with another penguin. Thirty-two penguins (15.6%) were seen with two different penguins, seven (3.4%) with three different penguins, and one (0.5%) with four different penguins (see Fig. 3.11). The proportions of male and female penguins seen by themselves or with from one to three different penguins were similar (see Fig. 3.12). Penguins seen with other penguins may also have been seen by themselves at least once.

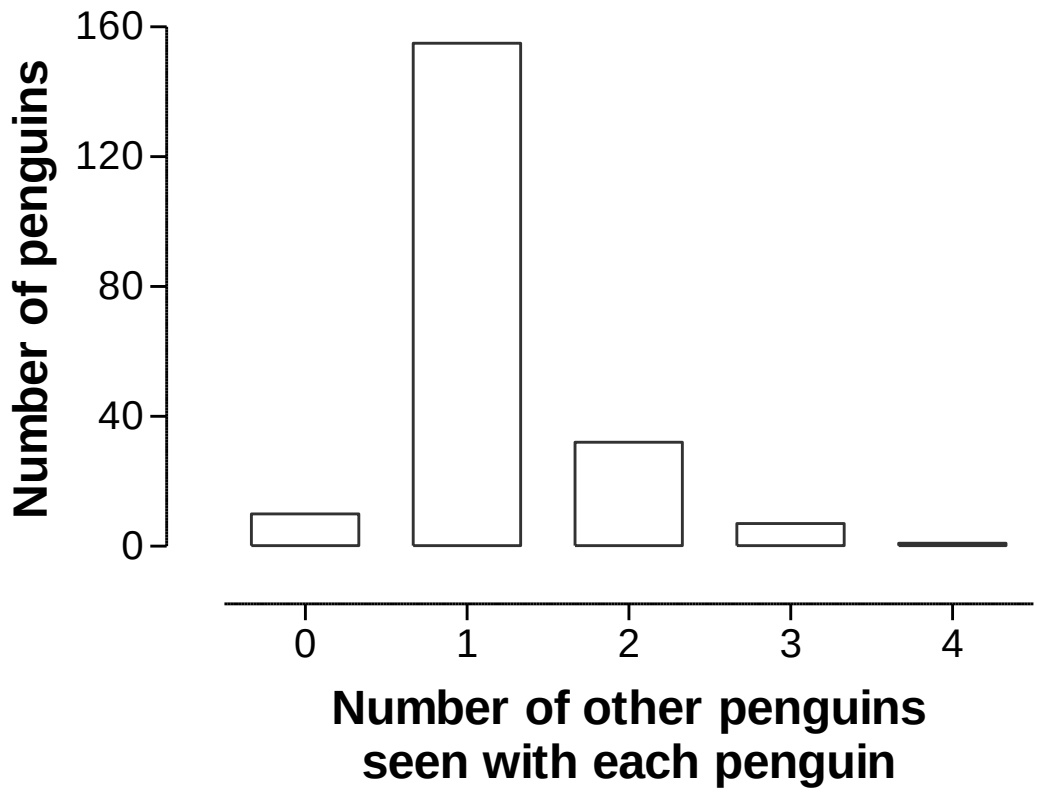


Fig. 3.11. Numbers of penguins recorded with different numbers of other penguins.

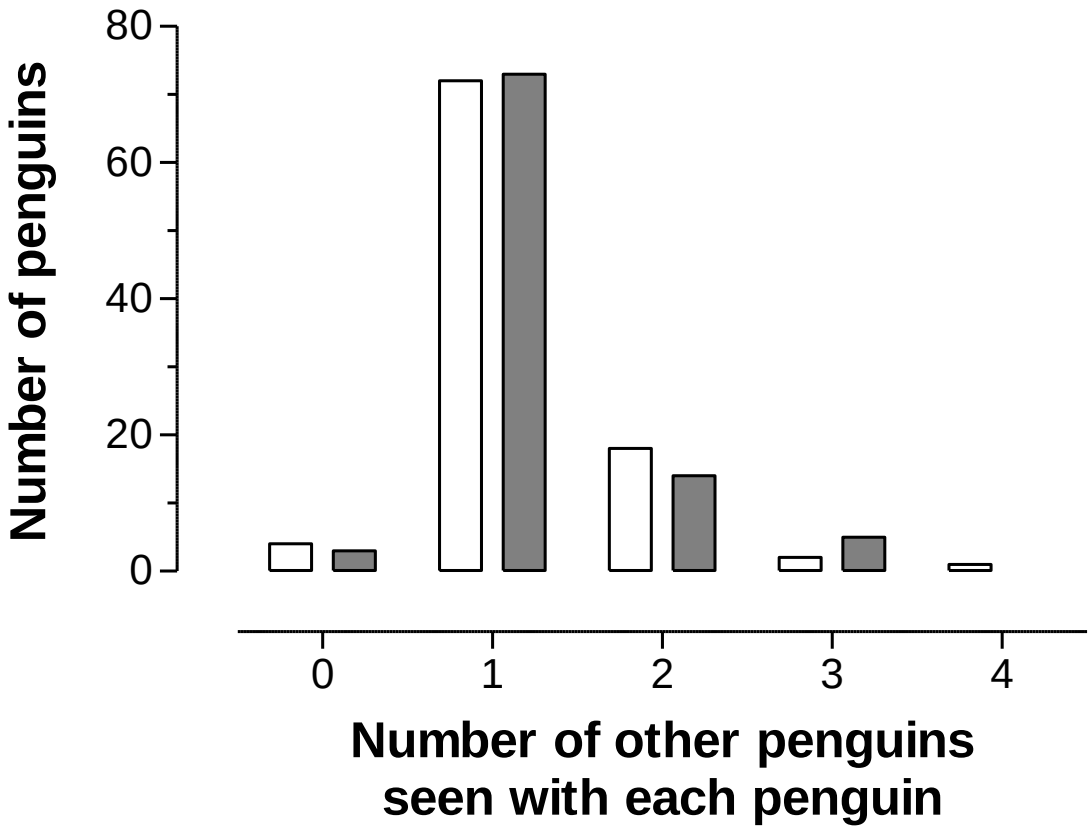


Fig. 3.12. Number of penguins recorded with different numbers of other penguins. Numbers of males shown by white bars and number of females are shown by shaded bars.

3.3.3 Individuals and paired penguin patterns

Nestboxes were checked less frequently in June and July than in April and May, so the records of penguin presence were less comprehensive for the latter two months of the study.

3.3.3.1 Attendance patterns of 30 penguins

Thirty penguins were selected for analysis of attendance patterns. Records for individual penguins were sorted by microchip number then the first 30 penguins with more than five sightings were used for analysis.

Days when penguins were present in nestboxes during checks from April to July 2021 are shown for 30 penguins in Fig. 3.13. The presence of a penguin in a nestbox could only be recorded on days when nestboxes were checked, so the absence of a record of penguin presence on a particular day does not indicate that the penguin was not present at the colony on that day.

There were differences between penguins in their patterns of presence in nestboxes. Some penguins, such as 13354053, 12202389 and 12189316 were mostly seen in April and May but not seen regularly or at all in June and July. Other penguins, such as 13355867, 13354784 and 12196454 were seen more regularly in June and July but not seen as regularly at the start of the study.

Many of the penguins shown in Fig. 3.13 (such as penguins 12202029, 12202015 and 12125143) have clear patterns of presence and absence from the colony which correspond to the peaks and troughs of colony attendance shown in Fig. 2.5. When looking at Fig. 3.13, I

can see clear ‘groups’ of times when penguins were sighted in their nestboxes and times when they weren’t.

Penguins were seen in nestboxes either by themselves or with one other penguin. Twenty of the penguins in Fig. 3.13 were always seen with the same penguin when they were with another penguin. The other ten penguins were seen with at least two different penguins when they were in a nestbox with one other penguin. The maximum number of penguins seen in a nestbox was two.

Eight of the 30 penguins were seen only in one nestbox while the other 22 were seen in more than one nestbox. Five of the 30 penguins were seen in only one nestbox with only one other penguin (like those in Fig. 3.14). Attendance patterns of two of the 30 penguins (12196736 and 13350759) are included in Fig. 3.14, and attendance patterns of four of the 30 penguins (13355867, 12202411, 12196454 and 12196300) are included in Fig. 3.15.

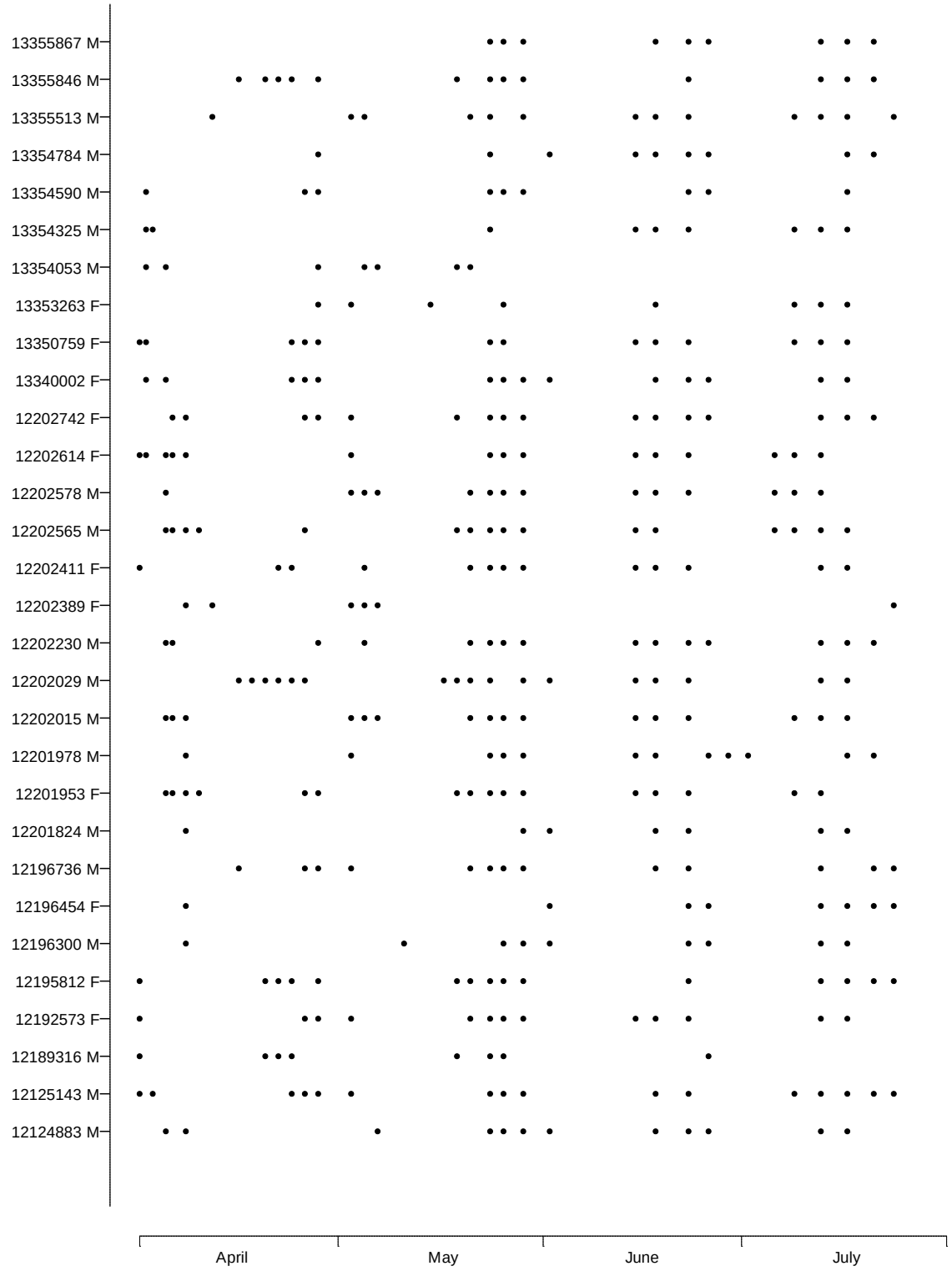


Fig. 3.13. Presence of penguins in a nestbox during daytime checks from April to July. Dots represent days when penguins were present and letters represent sex (M=male, F=female). Nestboxes were checked less frequently in June and July than in April and May.

3.3.3.2 Penguins seen in just one nestbox and only with their mate

Some pairs of penguins were recorded in just one nestbox, where they were seen either by themselves or with their mate, and were never seen with another penguin. Attendances of eight of these pairs are shown in Fig. 3.14. As seen in Fig. 3.13, there were times when all the penguins were present in nestboxes and, other periods when they were away at sea.

Four of the penguin pairs were almost always sighted together. Penguins in pairs H and pair D were seen together on all but one occasion, and penguins in pairs F and pair G were seen together on all but two occasions. It appears that these penguin pairs synchronised their departure and return to the colony, as they frequently were together in their nestbox on the same day after time away at sea and departed for the sea on the same day. Penguin pairs A, B, C, and E were sometimes seen in nestboxes with their mate and sometimes by themselves. These penguin pairs appear to have a less synchronised nestbox attendance pattern, spending more time alone in their nestbox before or after their mate arrived/left.

Pair A successfully fledged two chicks in nestbox 60 in 2021 and 2022. Penguin 12196736 is also pictured in Fig. 3.13.

Pair B successfully fledged two chicks in nestbox 43 in 2021 and 2022. Penguin 13350759 is also pictured in Fig. 3.13.

Pair C has no breeding record for the 2021 season but did successfully fledge two chicks in nestbox 52 in 2022. They were in attendance together at the colony during the April and May months of the study but were not sighted towards the end of the study. It is possible that they found an alternative natural nest site in the rocks of the breakwater.

Pair D, E and F all successfully fledged two chicks in both the 2021 and 2022 breeding season in nestbox 49, 45 and 24 (respectively).

Pair G successfully fledged two chicks in nestbox 12 in 2021 and again in nestbox 11 in 2022.

Pair H were unsuccessful in their 2021 breeding attempt with one egg failing and one chick dying in nestbox 3. They successfully fledged two chicks in nestbox 4 the following year (2022).

Of the four pairs of penguins that were almost always sighted together, all four pairs attempted to breed in 2021, the year of the study, and three pairs were successful. Of the other four pairs of penguins, three pairs were successful, and pair C was unknown but could have bred successfully in a natural nest site.

There was no significant difference in breeding success (defined as the number of chicks successfully fledged) between penguin pairs that stayed in the same nestbox and penguin pairs that switched between multiple nestboxes during the four months of the study (April to July; $t_{14.33} = 1.370$, $p = 0.1918$; see Fig. 3.14 and Fig. 3.15).

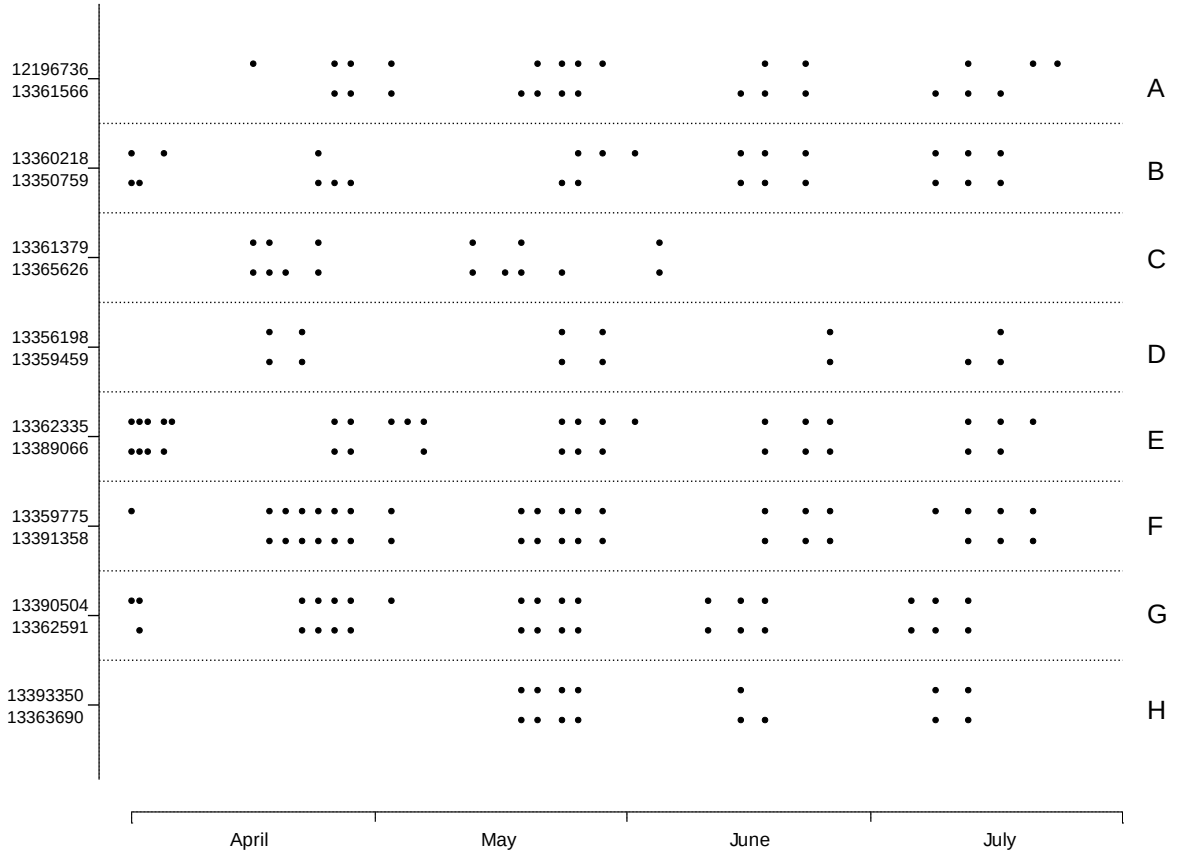


Fig. 3.14. Attendance of individual penguins (pairs) in nestboxes during April-July nestbox checks at Port Tarakohe 2021. These eight pairs were only ever sighted in one nestbox together. Males listed first (top) in each pair.

3.3.3.3 Penguins seen in more than one nestbox and only with their mate

Some pairs of penguins were recorded in more than one nestbox, where they were seen either by themselves or with their mate, and were never seen with another penguin. Attendances of 11 of these pairs are shown in Fig. 3.15. As seen in Fig. 3.13, there were times when all the penguins were present in nestboxes and, other periods when they were away at sea. Five penguin pairs (E, F, H, I and J) were seen together at least 84% of the time. The six other pairs were together less often, with the lowest proportion of time being together being 45%. Some penguin pairs showed high levels of synchronisation, such as pairs E, F, and H that were almost always present together in their nestbox. Other pairs, such as pair A and C, showed less synchronisation, with penguins often sighted without their mate.

Pair A were unsuccessful in their 2021 breeding attempt with both chicks dying. There is no record of a breeding attempt in the 2022 season. Initially penguin 13363010 was first sighted in nestbox 2 but was subsequently seen in nestbox 118 for the remainder of my study.

Pair B successfully fledged one chick from a one egg clutch in the 2021 breeding season and successfully fledged two chicks in the 2022 breeding season. Both penguins were seen in nestbox 63, 64 and 68 while penguin 13361762 was also seen in nestbox 42 during my study. Ultimately, they chose nestbox 63 for both breeding seasons.

Pair C successfully fledged two chicks in nestbox 35 in the 2021 breeding season. Penguin 13361695 was seen once in nestbox 36 in the middle of the study while penguin 13365468 was only ever sighted in nestbox 35. Pair C also successfully fledged two chicks in the 2022 breeding season in nestbox 54.

Pair D were sighted in multiple different nestboxes leading up to the 2021 breeding season Penguin 12196300 was seen in nestbox 142, 143, 145 and 147 while penguin 12196454 was seen in nestbox 138, 139, 142 and 143. These two penguins did not end up breeding together. Penguin 12196300 successfully fledged one chick from a one egg clutch with another penguin (13365122) in nestbox 145 in the 2021 breeding season and successfully fledged two chicks with the same penguin in nestbox 145 in the 2022 breeding season. There was no record of penguin 12196454 breeding in 2021, but she successfully fledged one of two eggs in the 2022 breeding season with penguin 13362981. Both penguins from pair D are also shown in Fig. 3.13.

Pair E were seen switching between nestbox 108 and 109 during the April to July months of 2021. During the 2021 breeding season they abandoned a two-egg clutch in nestbox 108 and in 2022 they successfully fledged two chicks in nestbox 109.

Pair F were initially sighted in nestbox eight on two occasions before moving to nestbox 96 (across the path) for the remainder of the study. They successfully fledged two chicks in nestbox 96 in the 2021 breeding season and successfully fledged one chick from a two-egg clutch in the same nestbox the following year. Penguin 13355867 is also pictured in Fig. 3.13.

Pair G were seen switching from nestboxes 13 and 14 during the April and May months before settling into nestbox 89 for the remainder of the study. They successfully fledged two chicks in nestbox 89 in the 2021 breeding season and successfully fledged one chick from a two-egg clutch in the same nestbox the following year. Penguin 12202411 is also pictured in Fig. 3.13.

Pair H were both seen switching between nestbox 11, 14, 85 and 87 before settling into nestbox 85 for the breeding season. They successfully fledged two chicks in this nestbox in both the 2021 and 2022 breeding seasons.

Pair I successfully fledged two chicks in nestbox 48 in the 2021 breeding season and again in nestbox 47 in the 2022 breeding season. Penguin 13363118 was sighted in three different nestboxes in 2021 (37, 42 and 48) while penguin 13365272 was seen in two different nestboxes (37 and 48).

Pair J were both sighted in nestbox nine on ten occasions before switching into nestbox 10 where they successfully fledged one chick from a two-egg clutch in 2021. In 2022 they successfully fledged two chicks in nestbox 93 which is across the path from nestbox 10.

Pair K were initially sighted in nestbox 107 on one occasion but subsequently sighted in nestbox 1 for the remainder of this study. In 2021 they abandoned their first clutch and laid a second clutch of one egg that successfully fledged. In 2022 they moved to nestbox 2 and abandoned their first clutch, re-clutched, then abandoned their re-clutch as well.

Of the five pairs of penguins that were sighted together at least 85% of the time, three pairs successfully fledged two chicks, one pair successfully fledged one chick from a two-egg clutch and one pair had a failed breeding attempt and abandoned their two eggs. Of the other six pairs of penguins sighted together at least 85% of the time, two pairs successfully fledged two chicks, one pair successfully fledged one chick from a one egg clutch, one pair abandoned their first clutch but successfully fledged one chick from their second one egg

clutch, one pair failed their two egg clutch and one pair swapped mates so did not attempt to breed together.

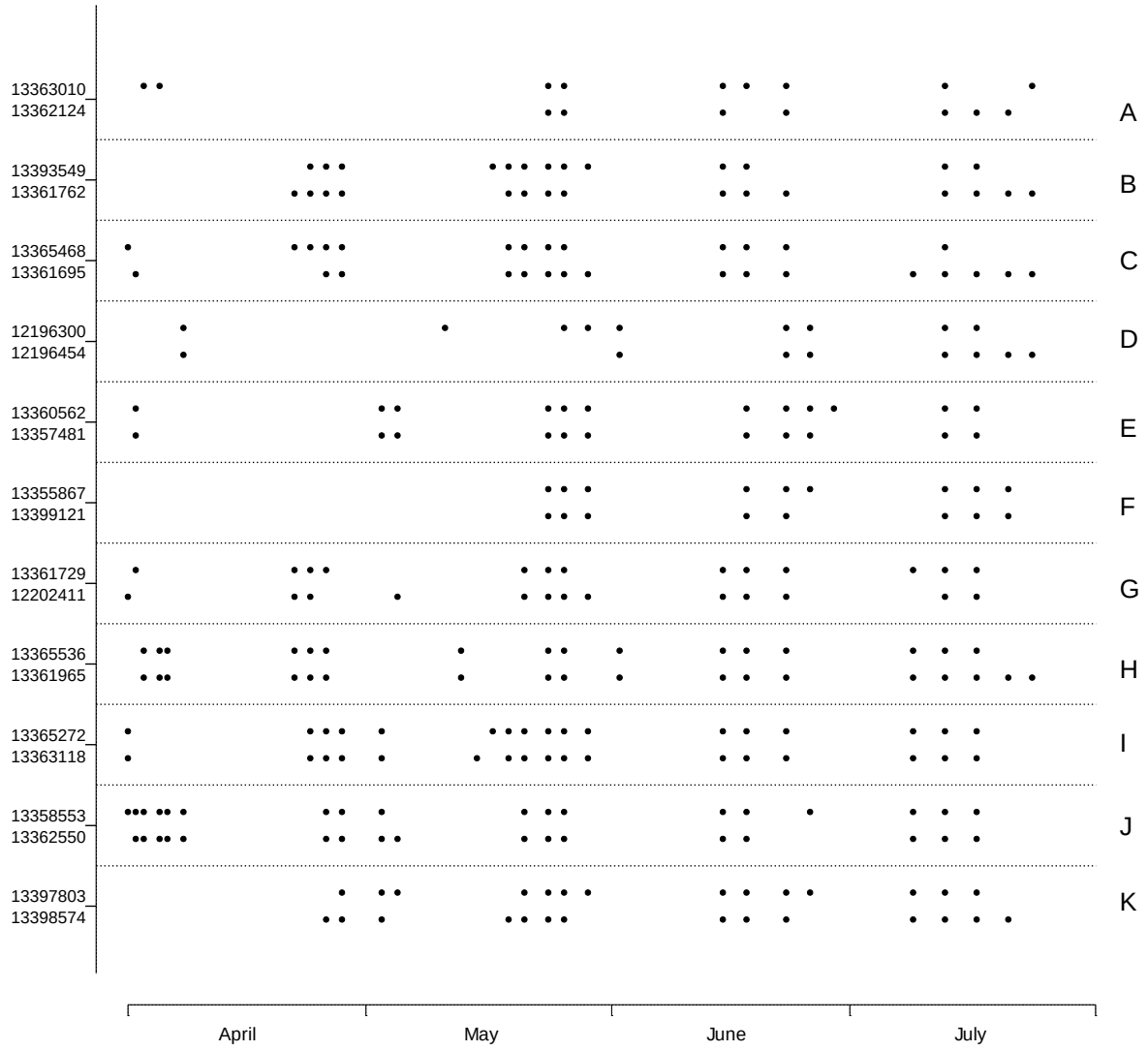


Fig. 3.15. Attendance of individual penguins (pairs) in nestboxes during April-July nestbox checks at Port Tarakohe 2021. These 11 pairs were sighted across multiple nestboxes together. Males listed first (top) in each pair.

3.3.4 Durations of nestbox occupancy and time at sea

Durations of nestbox occupancy and time at sea were determined from results of nestbox checks. The first day of nestbox occupancy was the first day when a penguin was in a nestbox after the penguin had not been present on previous checks. This day was also taken as the day when the penguin had returned from sea. The day when nestbox occupancy had ended was the first day when a penguin was not in a nestbox after the penguin had been present on previous checks. This day was also taken as the first day when the penguin was at sea. Table 3.4 shows dates and data for durations of nestbox occupancy and time at sea for two penguins.

It is important to note that the calculated durations of nestbox occupancy and time at sea are dependent on the frequency of nestbox checks and are estimated rather than actual durations. Nestbox checks were mostly every two days in April and May then twice weekly in June and July, so the accuracy of the estimates was lower for durations in June and July compared with April and May. Some penguins were not seen in nestboxes for periods of one month or more. These penguins were likely to have been at sea for long periods rather than following the cycle of time in nestboxes and time at sea shown by most penguins at the colony. Durations of nestbox occupancy and time at sea were calculated for penguins that were not seen in nestboxes for up to 76 days during the study period from 7 April to 30 July 2021.

Table 3.4 Examples for two penguins of dates when penguins were present or absent from nestboxes, and durations of nestbox occupancy and time at sea[1] derived from these dates.

First day of nestbox occupancy	Day when penguin absent from nestbox	First day at sea	Day when penguin returned from sea	Duration of nestbox occupancy (days)	Time at sea (days)
Penguin microchip number 12124883					
11/4/2021	12/4/2021	12/4/2021	14/4/2021	1	2
14/4/2021	16/4/2021	16/4/2021	13/5/2021	2	27
13/5/2021	15/5/2021	15/5/2021	30/5/2021	2	15
30/5/2021	11/6/2021	11/6/2021	24/6/2021	12	13
24/6/2021	5/7/2021	5/7/2021	19/7/2021	11	14
19/7/2021	27/7/2021			8	
Penguin microchip number 12125143					
7/4/2021	8/4/2021	8/4/2021	9/4/2021	1	1
9/4/2021	11/4/2021	11/4/2021	30/4/2021	2	19
30/4/2021	11/5/2021	11/5/2021	30/5/2021	11	19
30/5/2021	8/6/2021	8/6/2021	24/6/2021	9	16
24/6/2021	2/7/2021	2/7/2021	15/7/2021	8	13

[1]Time at sea = the duration of time a penguin was not in the nestbox during daytime checks. It is possible, but unlikely, that a penguin could have been on land in a natural site when it was not in one of the study nestboxes.

Penguins were present in nestboxes for periods of 1 to 15 days and were at sea for 1 to 76 days (see Fig. 3.16 and Table 3.5), with mean durations of nestbox occupancy and time at sea of approximately one and two weeks respectively for both males and females (see Table 3.5).

Table 3.5. Statistics for 19 male and 11 female penguins and how many days they were observed to spend at home in nestboxes compared to away at sea[1].

	Male		Female	
	Nestbox	Sea	Nestbox	Sea
Mean (days)	6.72	14.88	7.36	16.53
S.E. (days)	0.40	0.98	0.55	0.98
N	96	81	50	47
Minimum (days)	1	1	1	2
Maximum (days)	15	49	14	76

[1]Data are for penguins that were away at sea for up to 76 days during the study period from 7 April to 30 July 2021.

There were significant differences between mean durations of nestbox occupancy and time at sea for both male and female penguins ($U = 1369$, $p < 0.0001$; $U = 320.5$, $p < 0.0001$ respectively).

There were no significant differences between male and female penguins in mean durations of nestbox occupancy or the time at sea ($U = 2168$, $p = 0.3378$; $U = 1788$, $p = 0.5669$ respectively).

Some penguins regularly visited their nestbox for only short durations such as males 3 and 13 and females 3 and 5 who never visited for more than six days. Other penguins tended to stay longer in their nestboxes such as males 9 and 19 or females 1 and 4 who always stayed for a minimum of seven days or more.

Some penguins spent a minimum of approximately two weeks at sea (males 4, 6, 11, 14, 15, and 19 or females 1, 3, 4, and 10), while others had a combination of short and long durations at sea (males 13, 17, and 18 or females 7 and 9).

Of the 96 data points for male penguins home in nestboxes, 75% were stays of ten days or less. Of the 50 data points for female penguins home in nestboxes, 68% were stays of ten days or less.

Of the 81 data points for males at sea, 75.3% were durations of more than ten days away. Of the 47 data points for females at sea, 80.9% were durations of more than ten days away.

Mean durations of nestbox occupancy by individual penguins varied from 3.20 $\pm$ 0.92 to 10.33 $\pm$ 0.67 days for male penguins, and from 3.33 $\pm$ 1.33 to 10.00 $\pm$ 0.91 days for female penguins (see Fig. 3.17).

Mean durations of times at sea of individual penguins varied from 9.00 $\pm$ 4.73 to 27.33 $\pm$ 11.02 days for male penguins, and from 12.00 $\pm$ 2.30 to 32.33 $\pm$ 22.39 days for female penguins (see Fig. 3.17).

There were significant differences between individual penguins in mean durations of nestbox occupancy and mean durations of times at sea for male penguins and for female penguins (mixed effects models; males at home $F_{6, 107} = 7445$, $p < 0.0001$; males at sea $F_{5, 57} = 21.83$, $p < 0.0001$; females at home $F_{5, 34} = 57.68$, $p < 0.0001$; females at sea $F_{4, 322} = 5.05$, $p < 0.0029$).

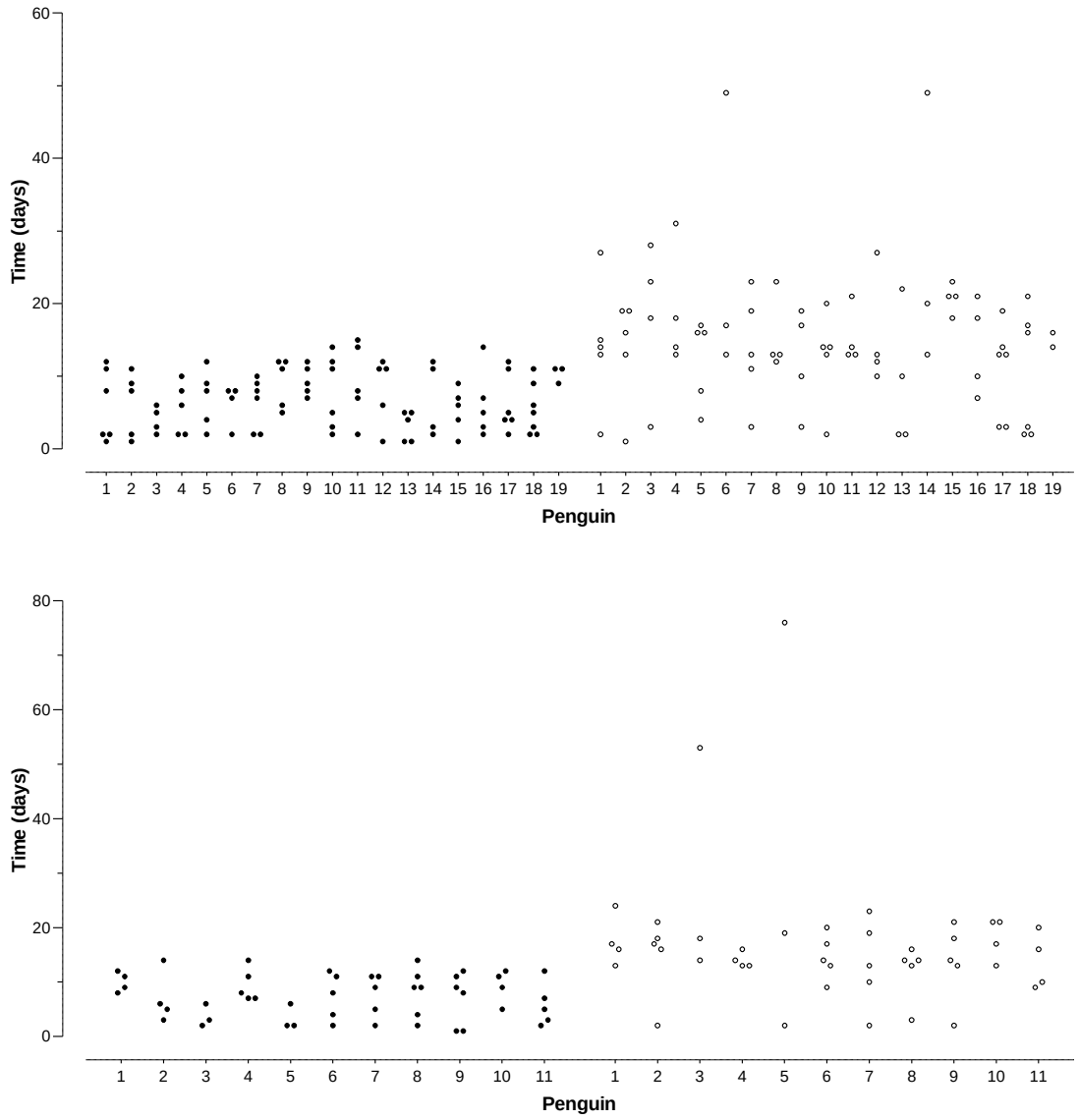


Fig. 3.16. Durations of nestbox occupancy (●) and time at sea (○) for 19 male (top) and 11 female (bottom) penguins.

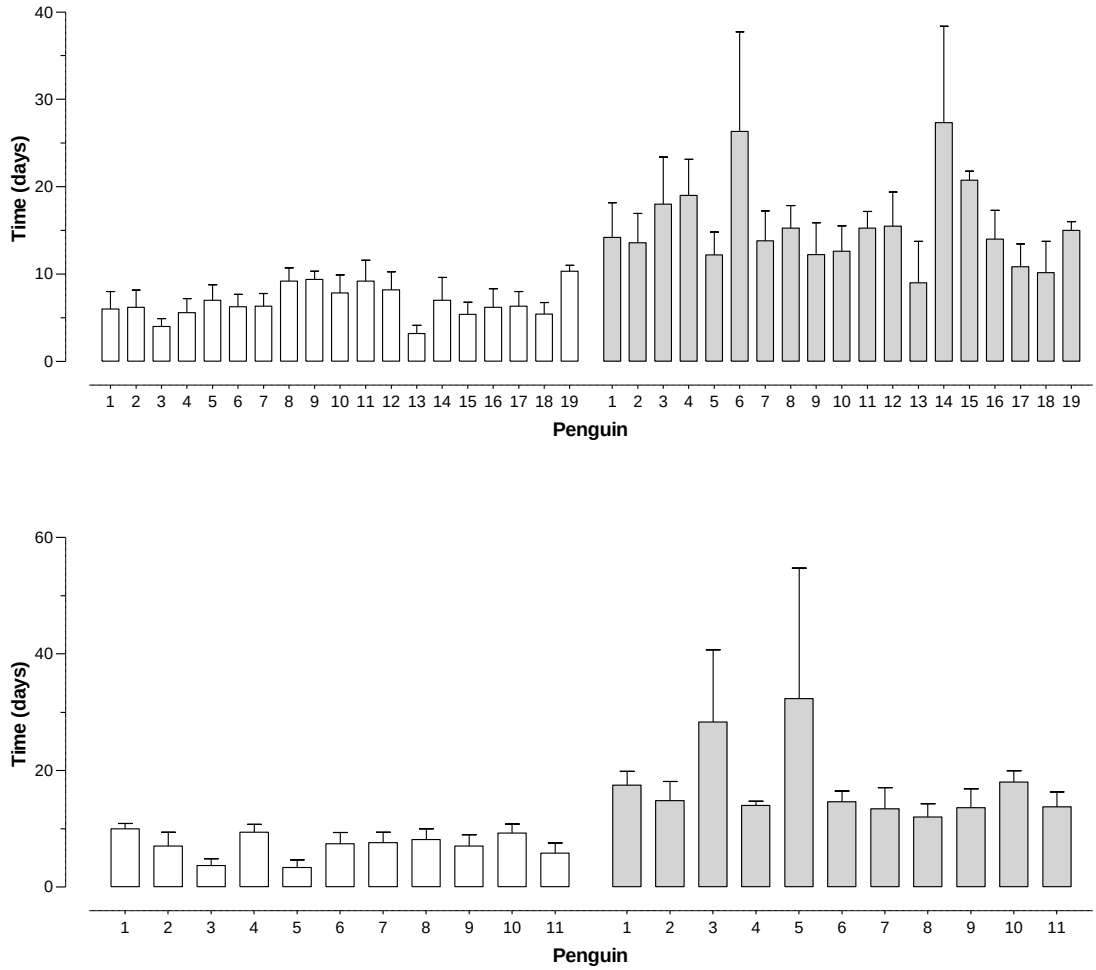


Fig. 3.17. Mean ± S.E. durations of nestbox occupancy (white bars) and time at sea (shaded bars) for 19 male (top) and 11 female (bottom) penguins.

3.4 Discussion

This is the first study of individual penguin behaviours in relation to nestbox use and individual nestbox attendance patterns in autumn and winter months of the year.

Of the 150 nestboxes available at Port Tarakohe, 74% were occupied by a penguin at least once during the study. Some nestboxes were occupied frequently and had regular peaks and troughs of occupancy (see Fig. 3.4), while other boxes were only occupied occasionally (see Fig. 3.1 and Fig. 3.2). While nestbox use in the autumn and winter has not previously been reported, features of the environment around nestboxes that may affect the use of nestboxes was considered by Ratz (2019), who found that shaded boxes with bare ground were preferred over unshaded boxes with surrounding ground vegetation. She also found that boxes on flat ground with flat entrances were preferred over boxes on sloped ground with sloped entrances. Half of the boxes used by penguins for breeding in her study were within 61 to 90 m of where penguins came ashore. Sutherland *et al.* (2014) studied little penguins on Phillip Island for 25 years and found that 92% of penguins in their study used nestboxes that had been installed for over seven years. The studies of Ratz (2019) and Sutherland *et al.* (2014) were conducted over the breeding season. Future studies in autumn and winter could be conducted to determine if nestbox visitations and subsequent selection of nestboxes during the autumn and winter months are related to the environmental features identified in previous studies during the breeding season. Further studies at Port Tarakohe would provide information to determine if the proportion of nestboxes that is used by penguins increases with time.

High temperatures can affect adult survival and breeding success (Ganendran *et al.*, 2016; Klomp *et al.*, 1991; Ratz, 2019; Ropert-Coudert *et al.*, 2004), so it would be interesting to

consider whether little penguins choose nestboxes in autumn and winter that will not be subjected to relatively high temperatures in spring and early summer. Additional data on long-term nestbox visitations, temperature variations, nest site parameters and future breeding and moult success are clearly needed to understand the importance for breeding success of nestbox selection in autumn and winter.

Sixty percent of penguins were recorded in just one nestbox in the current study, with no differences between males and females. There are many studies that show that little penguins have high site fidelity from year to year, and tend to return to their previous nest site (Bull, 2000; Johannesen *et al.*, 2002a; Rogers and Knight, 2006). Rogers and Knight (2006) found that over 70% of male and female little penguin returned to breed at the same nest site for multiple years in a row, and Johannesen *et al.* (2002a) found that little penguins were more likely to return to the same nestbox if breeding had been successful during the previous breeding season.

For the little penguins that were seen in more than one nestbox during the current study, they may have occasionally stopped at a nestbox that was on the route to the nestbox that they usually occupied. Nestbox 55 (Fig. 3.9) and 130 (Fig. 3.10) are examples of nestboxes that appeared to be stopover locations for penguins that regularly used a different nestbox. Some nestboxes that were occupied by relatively high numbers of different penguins may have been on routes used by many returning penguins. For example, there was a track leading to nestbox 130 on the Port arm, the nestbox was in the middle of the Port arm group of nestboxes, the box was occupied by a relatively high number of different penguins, and the nestbox was not used for breeding in the subsequent breeding season.

For some of the penguins that were sighted in multiple nestboxes, the nestboxes were within several metres of each other. This is consistent with the findings of Sutherland *et al.* (2014) and Reilly and Cullen (1981) who found that penguins tended to return to their previous nest site or to a site nearby.

The current nestbox colony at Port Tarakohe had been established in 2020 when new nestboxes were installed to replace old nestboxes, and additional new nestboxes were installed. Some of the penguins that used nestboxes in autumn and winter in the present study may not have previously been in any of the nestboxes, so penguins found in multiple nestboxes may have been exploring potential nest sites. Alternatively, they may have been penguins that bred in a nestbox in the previous year then returned to their previous nestbox after visiting other nestboxes. The age of first breeding for little penguins is two years of age, although most commonly breeding starts when penguins are three years of age (Nisbet and Dann, 2009; Reilly and Cullen, 1981). When penguins that fledged from nestboxes at Port Tarakohe return to breed at the colony, it would be worthwhile to examine patterns of nestbox use to determine if penguins were more likely to use different nestboxes if they were first breeders rather than experienced breeders. It would be of interest to study movements of penguins between nestboxes now that almost all penguins at the colony have been microchipped. It would be possible to determine if penguins visiting multiple nestboxes are juveniles returning for their first breeding season, returning adults that are moving between nestboxes before returning to their nestbox from the previous year, or returning adults that are switching nestboxes.

Most penguins (75.6%) in the current study were only ever sighted with one other penguin, with no differences between males and females. Rogers and Knight (2006) found a

significant relationship between breeding success in one year and mate fidelity the next, so it is likely the penguins in the current study that were only ever sighted with one other penguin had bred successfully in the previous year. Johannesen *et al.* (2002a) found that penguins breeding with the same partner as in the previous year were also more likely to be in their previous nestbox than in a different nestbox. It is interesting to see high mate and nestbox fidelity in autumn and winter, well before the breeding season.

It is possible that some pairs, most likely those that are consistently successful, are together throughout the year, both on land and at seas. It is also possible that members of a pair could forage separately at sea yet somehow synchronise their return to the colony, although how this could happen is unclear. Reilly and Cullen (1981) speculated that penguins in their study might be able to synchronise their return to the colony, even if they had been at sea separately. Berlincourt and Arnould (2014) conducted a tracking study of little penguins and found that 87.5% of penguins with tracking devices associated with other penguins while foraging. Association was defined as being within 0.5 km of another penguin while foraging. Sixty-nine percent of 84 recorded tracks were classified as including time when a penguin was associating while foraging or during the outward and inward swimming journeys to foraging areas. Members of pairs were not tracked simultaneously in the study of Berlincourt and Arnould (2014), so although it was found that little penguins forage in groups, foraging of individual pair members remained unknown.

While the consistent presence together on land of members of a pair has been found in the current study, there is no information on the movements of pairs of little penguins at sea. Tracking studies of both members of a pair after moult, in autumn and in winter are needed to investigate movements of pairs at sea. It would also be valuable to use trail cameras at

nestboxes to record the time of return of members of a pair. If they spent time together at sea before returning to the colony, it could be assumed they would return to the nestbox within a short time of each other.

Male and female penguins in the current study spent approximately one week on land in nestboxes and then two weeks at sea. Some penguins regularly made short visits to the colony and others regularly stayed longer, with equivalent patterns of time at sea. Some penguins stayed at sea for a minimum of two weeks, while others had short and long sea trips. It would be interesting to investigate these patterns in more detail, with daily nestbox checks. Penguins that had varying short and long trips to sea might be showing trade-offs between short and long foraging trips, as suggested by Weimerskirch (1998) for sooty shearwaters (*Ardenna grisea*). Also, penguins that spent a minimum of two weeks at sea might have been foraging in areas that took several days of swimming to reach but had rich food sources to subsequently support egg laying by females, as suggested by Perrins (1970) in a review of the timing of breeding in birds.

While patterns of regular nest attendance and evidence for synchronization between penguin pairs in autumn and winter were found by the Reilly and Cullen (1981) and were found in the current study, the results of Chiaradia and Kerry (1999) differed. They found that penguins only made occasional visits to the colony during the winter months, and that both male and female penguins of a future breeding pair were rarely seen at the colony together during winter. Approximately one quarter of their studied breeding pairs visited the colony in winter (28 June – 31 Aug). Courtship began approximately one month before egg laying and during this time, penguins were present at the colony regularly. The first egg laid in the study of Chiaradia and Kerry (1999) was laid in early October, whereas in the current study the first

egg was laid in late June, and in the study of Reilly and Cullen (1981), first eggs were laid in August in 1969 and July in 1970. It is possible that Chiaradia and Kerry (1999) did not observe the same patterns of colony attendance in winter because penguins in their study laid their first eggs much later.

The studies of Reilly and Cullen (1981) and Chiaradia and Kerry (1999) were conducted at the same penguin colony, and it is interesting that colony attendance patterns differed between the studies. Penguins in the Chiaradia and Kerry (1999) study were not regularly attending the colony during the day in the three months before egg laying began, in contrast to results from the current study and from Reilly and Cullen (1981). The current study and the Chiaradia and Kerry (1999) study were conducted in single years and the study of Reilly and Cullen (1981) was conducted over two years. Similar studies covering several years at one colony, and studies at other colonies around New Zealand and Australia, are needed to determine the extent to which autumn and winter colony attendance patterns vary between years at a colony, and whether there are consistent differences between colonies.

In the study of Chiaradia and Kerry (1999), it is interesting to see that penguin pair 22 had 3 penguins present in the nest over the duration of their study. Two males and one female were present, but both males were never seen in the nest at the same time as each other. This behaviour was not seen in the current study.

Colony attendance patterns were considered in detail for 30 individual penguins in the current study. While some of these penguins were seen regularly in April and May but not in June and July, others had the opposite pattern. Many of the 30 penguins had periods of presence and absence that correlated to the peaks and troughs of the total colony attendance, with some

individual attendances that differed from the overall colony pattern. When penguins were absent during the day, it was presumed that they were at sea. Observations from a little penguin colony at Napier Port have shown that some penguins are consistently at sea during the day and in nestboxes at night, at times when other penguin are in nestboxes during the day (J.F. Cockrem pers. comm.). These penguins follow the same cycle as other penguins of presence at the colony for a week or more then away for two weeks or more at the colony, except they go to sea each day. Observations of penguins at Port Tarakohe conducted by volunteers at the colony in 2022 and 2023 also indicate that the absence of a penguin from a nestbox during the day does not mean that the penguin is not visiting the colony at night before returning to sea before dawn. To monitor this, volunteers put sticks in front of the nestbox entrances. If on a subsequent check of the nestbox the stick was found to have been knocked down in the morning, then it was assumed that a penguin had visited that nestbox, even if there was no penguin in the nestbox during the day check. If the stick was still standing up, then they assumed no penguin visited that nestbox overnight. This approach, with daily nestbox checks, combined with some night time nestbox checks, would provide information on how many penguins visit the colony during the night, and how many stay during the day. Reilly and Cullen (1981) noted that during night checks, a quarter of the future breeding population was present at the colony during winter months, while during day checks, only an eighth of the future breeding population was present at the colony. Approximately one quarter of the penguins Chiaradia and Kerry (1999) studied were present at the colony during day time checks from 28 June to 31 August. Daily and nightly monitoring, or microchip readers at the entrance of each nestbox, would provide information to improve understanding of little penguin nestbox attendance during the day and during the night.

There was no significant difference in breeding success between penguin pairs who were only ever sighted together and in the same nestbox (Fig. 3.14) and penguin pairs who were only ever sighted together but across multiple nestboxes (Fig. 3.15). The sample size was small, and a definitive conclusion cannot be drawn about whether nestbox swapping in autumn and winter truly is related to future breeding success. Further studies with greater sample sizes would be worthwhile to identify whether strong site and mate fidelity in autumn and winter impacts is related to future breeding success.

4. General discussion

This study focused on little penguin colony attendance behaviours at Port Tarakohe, New Zealand during autumn and winter months (April to July) in 2021. To my knowledge, the studies of Reilly and Cullen (1981), Kinsky (1960), and Chiaradia and Kerry (1999) are the only other studies of little penguin colony attendance during these months. The current study is the first to examine individual little penguin behaviours in autumn and winter.

4.1 Major conclusions

The aim of this study was to find out more about the colony attendance behaviours of little penguins at Port Tarakohe during the less studied autumn and winter months of the year. The major conclusions of my study are:

1. Little penguin at Port Tarakohe have a three-and-a-half-week cyclical pattern of colony attendance in the autumn and winter months. The numbers of penguins present during the peak of each cycle gradually increased from April to July. The number of penguins at the colony varied from 0 to 106 over the duration of my study.
2. There was no correlation between the three-and-a-half-week colony attendance pattern and lunar phase. The lunar cycle takes approximately 29.5 days while the period of the penguin colony attendance cycle was approximately 25 days.
3. Little penguin body weight and condition index did not increase in the autumn and winter months prior to egg laying.
4. Sixty percent of penguins were always seen in the same nestbox and not seen in other nestboxes over the duration of the study, while 40% of penguins were seen in two to seven different nestboxes.
5. A majority of penguins (75.6%) were seen with only one other penguin while the other 24.4% were either seen by themselves or with two, three or four other penguins.

6. Individual penguin presence at the colony during daytime nestbox check varied greatly between individuals. However, most penguins showed the three-and-a-half-week cycle of colony attendance.
7. There was no significant difference in breeding success between penguin pairs who were only seen with their mate and in one nestbox during autumn and winter and penguin pairs who were only seen with their mate but were present in more than one nestbox in autumn and winter.
8. There were significant differences between durations of time on land in nestboxes and durations of time away at sea for both male and female penguins. Penguins spent approximately one week in nestboxes and approximately two weeks at sea.
9. The approximately three-and-a-half-week cycle of colony attendance at Port Tarakohe was similar but not identical to the three-week cycle on Phillip Island. This could be a real difference between colonies or an artifact of differences between study designs. The absence of an increase in penguin body weight before egg laying is similar to findings on Matiu Somes Island and Pilots Beach.

4.2 Future studies

Little penguins appear to have an approximately three-and-a-half-week cyclic pattern of colony attendance, with increasing numbers of penguins at the colony from autumn into winter, as the onset of egg-laying approaches. The mechanisms that underlie this attendance pattern are unknown. Future studies in this area are needed to investigate potential hypotheses that may explain this behaviour. Hypotheses proposed for other seabirds would be worthwhile to investigate. These hypotheses include cyclic colony attendance increasing the time neighbouring penguins spend together and therefore reducing predation risk, and cyclic colony attendance facilitating social interactions at the colony.

It would be valuable to study autumn and winter colony attendance of little penguins across consecutive years to determine if colony attendance patterns and individual attendance behaviours are consistent between years. It can be predicted that little penguins at Port Tarakohe would show similar attendance patterns across successive years.

To better understand why little penguins did not increase their body weight prior to the breeding season, we need to better understand their autumn and winter strategies. Future studies to investigate whether little penguins are income breeders would be of benefit, as well as more detailed studies on their body condition and weight. In a future study of changes in body weight in autumn and winter, daily nestbox checks would allow body weight measurements to be made on the day after penguins returned to their nestbox from the sea, rather than measurements being made when penguins had been back on land and fasting for different periods of time. It would be worthwhile to weigh individual penguins when they returned from the sea throughout autumn and winter, so individual patterns of changes in body weight and body condition could be determined.

Sixty percent of penguins were always seen in the same nestbox and not seen in other nestboxes over the duration of the study. In the current study, characteristics of nestboxes such as temperature inside the nestbox, vegetation cover around the nestbox and ground slope were not investigated in relation to nestboxes consistently used by one pair of penguins compared with nestboxes used by pairs of penguins that were found in two or more different nestboxes. Nestbox choice could also be investigated in relation to characteristics of nestboxes used by pairs that bred successfully the previous year in comparison with nestboxes used by pairs that did not breed successfully. For the penguins that used more than one nestbox, it would be valuable to investigate whether they were chicks returning for

their first breeding season, adults using a nestbox as temporary refuge, adults swapping nestboxes as they were unsuccessful the previous year, or adults swapping because their nestbox had another penguin take up residence in their nestbox.

While penguins in the current study were present on land at nestboxes during the day in autumn and winter, penguins in the study of Chiaradia and Kerry (1999) were not. Future studies across multiple years and multiple colonies would be useful to investigate whether presence at nestboxes in autumn and winter is a common behaviour for little penguins. It would also be fascinating to investigate further the patterns of nestbox attendance by penguin pairs that indicate the ability to synchronise their return to the colony. There are some studies that show penguins do associate at sea (Berlincourt and Arnould, 2014). Tracking of both members of pairs when they were at sea would provide insight into whether some penguin pairs leave nestboxes together and are at sea together before returning to land.

5. References

Banks, J., Mitchell, A., Waas, J. R. and Paterson, A. M. (2002). An unexpected pattern of molecular divergence within the blue penguin (*Eudyptula minor*) complex. Notornis, 49: 29-38.

Banks, J. C., Cruickshank, R. H., Drayton, G. M. and Paterson, A. M. (2008). Few genetic differences between Victorian and Western Australian blue penguins, *Eudyptula minor*. New Zealand Journal of Zoology, 35(3): 265-270.

Berlincourt, M. and Arnould, J. P. (2014). At-sea associations in foraging little penguins. PLoS One 9(8): e105065.

Bull, L. (2000). Fidelity and breeding success of the blue penguin *Eudyptula minor* on Matiu-Somes Island, Wellington, New Zealand. New Zealand Journal of Zoology, 27(4): 291-298.

Cannell, B. L., Campbell, K., Fitzgerald, L., Lewis, J. A., Baran, I. J. and Stephens, N. S. (2016). Anthropogenic trauma is the most prevalent cause of mortality in Little Penguins, *Eudyptula minor*, in Perth, Western Australia. Emu - Austral Ornithology, 116(1): 52-61.

Cargill, C. P., Judkins, A. G. and Weir, J. S. (2022). Distribution of little penguins (*Eudyptula minor*) along the greater Kaikōura coastline, New Zealand. New Zealand Journal of Marine and Freshwater Research, 56(1): 43-58.

Chakraborty, U. (2020). Effects of different phases of the lunar month on living organisms. Biological Rhythm Research, 51(2): 254-282.

Chiaradia, A., Costalunga, A. and Kerry, K. (2003). The diet of Little Penguins (*Eudyptula minor*) at Phillip Island, Victoria, in the absence of a major prey–Pilchard (*Sardinops sagax*). Emu, 103(1): 43-48.

Chiaradia, A., McBride, J., Murray, T. and Dann, P. (2007). Effect of fog on the arrival time of little penguins *Eudyptula minor*: a clue for visual orientation? Journal of Ornithology, 148(2): 229-233.

Chiaradia, A. F. and Kerry, K. R. (1999). Daily nest attendance and breeding performance in the little penguin *Eudyptula minor* at Phillip Island, Australia. Marine Ornithology, 27: 13-20.

Chiaradia, C. S. A. (2022). Age-related breeding success in little penguins: a result of selection and ontogenetic changes in foraging and phenology. Ecological Monographs, 92(1), e01495.

Clitheroe, E. (2021). Can artificial habitat mitigate impacts of climate change? Quantifying nesting habitat microclimate and use by little penguins (*Eudyptula minor*). Doctoral dissertation, Murdoch University).

Colombelli-Négrel, D. (2023). Estimating Little Penguin population sizes using automated acoustic monitoring and citizen science. Ibis, 165(4): 1423-1431.

Costello, E. C. and Colombelli-Négrel, D. (2023). Human activities at night negatively impact Little Penguin (*Eudyptula minor*) numbers and behaviours. Ibis, 165(4): 1378-1396.

Cullen, J. M., Montague, T. L. and Hull, C. (1991). Food of Little Penguins *Eudyptula minor* in Victoria: Comparison of Three Localities between 1985 and 1988. Emu-Austral Ornithology, 91(5): 318-341.

Dann, P., Carron, M., Chambers, B., Chambers, L., Dornom, T., Mclaughlin, A., Sharp, B., Talmage, M. E., Thoday, R. and Unthank, S. (2005). Longevity in little penguins *Eudyptula minor*. Marine Ornithology, 33: 71-71.

Dann, P. and Chambers, L. (2013). Ecological effects of climate change on little penguins *Eudyptula minor* and the potential economic impact on tourism. Climate Research, 58(1): 67-79.

Dann, P., Norman, F. I., Cullen, J. M., Neira, F. J. and Chiaradia, A. (2000). Mortality and breeding failure of little penguins, *Eudyptula minor*, in Victoria, 1995–96, following a widespread mortality of pilchard, *Sardinops sagax*. Marine and Freshwater Research, 51(4): 355-362.

Davis, L. S. and Renner, M. (2003). Penguins. T & A D Poyser, United States.

Fowler, G. S. and Fowler, M. E. (2001). Order Sphenisciformes (penguins). pp. 51-64. Biology, medicine, and surgery of South American animals. Iowa State University Press, South State Avenue, Ames, Iowa.

Gales, R. and Green, B. (1990). The annual energetics cycle of little penguins (*Eudyptula minor*). Ecology, 71(6): 2297-2312.

Ganendran, L. B., Sidhu, L. A., Catchpole, E. A., Chambers, L. E. and Dann, P. (2016). Effects of ambient air temperature, humidity and rainfall on annual survival of adult little penguins *Eudyptula minor* in southeastern Australia. International Journal of Biometeorology, 60(8): 1237-45.

Granadeiro, J. P., Alonso, H., Almada, V., Menezes, D., Phillips, R. A. and Catry, P. (2009). Mysterious attendance cycles in Cory's shearwater, *Calonectris diomedea*: an exploration of patterns and hypotheses. Animal Behaviour, 78(6): 1455-1462.

Groscolas, R. and Robin, J. P. (2001). Long-term fasting and re-feeding in penguins. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 128(3): 643-653.

Grosser, S., Scofield, R. P. and Waters, J. M. (2017). Multivariate skeletal analyses support a taxonomic distinction between New Zealand and Australian *Eudyptula* penguins (Sphenisciformes: Spheniscidae). Emu - Austral Ornithology, 117(3): 276-283.

Gwatkin, G. S. M. (2025). Interactions between kororā/little penguins (*Eudyptula minor*) and their terrestrial environment at Pōhatu/Flea Bay, Banks Peninsula. Master's thesis, University of Canterbury.

Hadden, P. W., Gerneke, D. A., Mcghee, C. N. and Zhang, J. (2020). Micro-computed tomography orbital anatomy of the little blue or fairy penguin, *Eudyptula minor*. Clinical & Experimental Ophthalmology, 48(1).

Harding, A. M. A., Piatt, J. F., Byrd, G. V., Hatch, S. A., Konyukhov, N. B., Golubova, E. U. and Williams, J. C. (2005). Variability in colony attendance of crevice-nesting Horned Puffins: implications for population monitoring. The Journal of wildlife management, 69(3): 1279-1296.

Harrigan, K. E. (1991). Causes of mortality of little penguins *Eudyptula minor* in Victoria. Emu-Austral Ornithology, 91(5): 273-277.

Heber, S., Wilson, K. J. and Molles, L. (2008). Breeding biology and breeding success of the blue penguin (*Eudyptula minor*) on the West Coast of New Zealand's South Island. New Zealand Journal of Zoology, 35(1): 63-71.

Johannesen, E., Perriman, L. and Steen, H. (2002a). The effect of breeding success on nest and colony fidelity in the Little Penguin (*Eudyptula minor*) in Otago, New Zealand. Emu, 102(3): 241-247.

Johannesen, E., Steen, H. and Perriman, L. (2002b). Seasonal variation in survival, weights, and population counts of blue penguins (*Eudyptula minor*) in Otago, New Zealand. New Zealand Journal of Zoology, 29(3): 213-219.

Joly, N., Chiaradia, A., Georges, J. Y. and Saraux, C. (2023). Unpacking the lifelong secrets of little penguins: individual quality, energy allocation, and stochasticity in defining fitness. Evolution, 77(9): 2056-2067.

Kemp, A. and Dann, P. (2001). Egg size, incubation periods and hatching success of Little Penguins, *Eudyptula minor*. Emu, 101(3): 249-253.

Kinsky, F. C. (1960). The yearly cycle of the northern blue penguin (*Eudyptula minor novaehollandiae*) in the Wellington harbour area. Dominion Museum, Wellington, New Zealand. 3: 145-218.

Klomp, N. I., Meathrel, C. E., Wienecke, B. C. and Wooller, R. D. (1991). Surface Nesting by Little Penguins on Penguin Island, Western Australia. Emu-Austral Ornithology, 91(3): 190-193.

Klomp, N. I. and Wooller, R. D. (1988). Diet of little penguins, *Eudyptula minor*, from Penguin Island, western Australia. Australian Journal of Marine and Freshwater Research, 39(5): 633-639.

Klomp, N. I. and Wooller, R. D. (1991). Patterns of arrival and departure by breeding little penguins at Penguin Island, Western Australia. Emu-Austral Ornithology, 91(1): 32-35.

Kooyman, G. L. and Lynch, W. (2013). Penguins: the animal answer guide. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Ksepka, D. T. and Ando, T. (2011). Penguins past, present, and future: trends in the evolution of the Sphenisciformes. Living dinosaurs, 155-186.

Marker, P. F., Wind, A. B. and Woehler, E. J. (2024). Guidelines for works in, and management of, Little Penguin habitat.

McCutcheon, C., Dann, P., Salton, M., Renwick, L., Hoskins, A. J., Gormley, A. M. and Arnould, J. P. Y. (2011). The foraging range of Little Penguins (*Eudyptula minor*) during winter. Emu-Austral Ornithology, 111(4): 321-329.

Nisbet, I. C. T. and Dann, P. (2009). Reproductive performance of little penguins *Eudyptula minor* in relation to year, age, pair-bond duration, breeding date and individual quality. Journal of Avian Biology, 40(3): 296-308.

O'Brien, P. J. (1940). Some Observations on the Breeding Habits and General Characteristics of the White Flippered Penguin:(*Eudyptula Albosignata Finsch*). The Press.

Perriman, L. and Steen, H. (2000). Blue penguin (*Eudyptula minor*) nest distribution and breeding success on Otago Peninsula, 1992 to 1998. New Zealand Journal of Zoology, 27(2): 269-275.

Perrins, C. M. (1970). The timing of birds 'breeding seasons. Ibis, 112(2): 242-255.

Peucker, A. J., Dann, P. and Burridge, C. P. (2009). Range-wide Phylogeography of the Little Penguin (*Eudyptula minor*): Evidence of Long-distance Dispersal. The Auk, 126(2): 397-408.

Priddel, D., Carlile, N. and Wheeler, R. (2008). Population size, breeding success and provenance of a mainland colony of Little Penguins (*Eudyptula minor*). Emu-Austral Ornithology, 108(1): 35-41.

Ratz, H. (2019). Parameters influencing selection of nest boxes by little penguins (*Eudyptula minor*). Notornis, 66(3): 129-138.

Reilly, P. N. and Cullen, J. M. (1979). The little penguin *Eudyptula minor* in Victoria. I: Mortality of adults. Emu-Austral Ornithology, 79(3): 97-102.

Reilly, P. N. and Cullen, J. M. (1981). The little penguin *Eudyptula minor* in Victoria, II: Breeding. Emu-Austral Ornithology, 81(1): 1-19.

Robinson, S., Chiaradia, A. and Hindell, M. A. (2005). The effect of body condition on the timing and success of breeding in Little Penguins *Eudyptula minor*. Ibis, 147(3), 483-489.

Rodriguez, A., Chiaradia, A., Wasiak, P., Renwick, L. and Dann, P. (2016). Waddling on the Dark Side: Ambient Light Affects Attendance Behavior of Little Penguins. Journal of Biological Rhythms, 31(2): 194-204.

Rodriguez, A., Holmberg, R., Dann, P. and Chiaradia, A. (2018). Penguin colony attendance under artificial lights for ecotourism. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology, 329(8-9): 457-464.

Rogers, T. and Knight, C. (2006). Burrow and mate fidelity in the little penguin *Eudyptula minor* at Lion Island, New South Wales, Australia. Ibis, 148(4): 801-806.

Ropert-Coudert, Y., Cannell, B. and Kato, A. (2004). Temperature inside nest boxes of little penguins. Wildlife Society Bulletin, 32(1): 177-182.

Ropert-Coudert, Y., Kato, A., Wilson, R. P. and Cannell, B. (2006). Foraging strategies and prey encounter rate of free-ranging Little Penguins. Marine Biology, 149(2): 139-148.

Rowe, L. K., Weir, J. S. and Judkins, A. G. (2020). Breeding of little penguins (*Eudyptula minor*), including multiple brooding, at South Bay, Kaikōura, New Zealand, 2006–2017. Notornis, 67(2): 451-458.

Salton, M., Saraux, C., Dann, P. and Chiaradia, A. (2015). Carry-over body mass effect from winter to breeding in a resident seabird, the little penguin. Royal Society Open Science, 2(1): 140390.

Saraux, C., Robinson-Laverick, S. M., Le Maho, Y., Ropert-Coudert, Y. and Chiaradia, A. (2011). Plasticity in foraging strategies of inshore birds: how little penguins maintain body reserves while feeding offspring. Ecology, 92(10): 1909-1916.

Sijbranda, D. C., Hunter, S., Howe, L., Lenting, B., Argilla, L. and Gartrell, B. D. (2017). Cases of mortality in little penguins (*Eudyptula minor*) in New Zealand associated with avian malaria. New Zealand veterinary journal, 65(6): 332-337.

Stahel, C. and Gales, R. (1987). Little penguin: fairy penguins in Australia. New South Wales University Press, Australia.

Stephens, P. A., Houston, A. I., Harding, K. C., Boyd, I. L. and McNamara, J. M. (2014). Capital and income breeding: the role of food supply. Ecology, 95(4): 882-896.

Sutherland, D. R. and Dann, P. (2014). Population trends in a substantial colony of Little Penguins: three independent measures over three decades. Biodiversity and Conservation, 23(1): 241-250.

Sutherland, D. R., Dann, P. and Jessop, R. E. (2014). Evaluation of artificial nest sites for long-term conservation of a burrow-nesting seabird. The Journal of Wildlife Management, 78(8): 1415-1424.

Sutton, G. J., Hoskins, A. J., Berlincourt, M. and Arnould, J. P. Y. (2017). Departure time influences foraging associations in little penguins. PLoS One 12(8): e0182734.

Waas, J. R. (1990). An analysis of communication during the aggressive interactions of little blue penguins (*Eudyptula minor*). In Penguin biology (pp. 354-376). Academic Press.

Weimerskirch, H. (1998). How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. Journal of Animal Ecology, 67(1): 99-109.

Wells, M. R., Philips, A., Lea, M. A. and Carver, S. (2025). Spatial Variation in Body Condition of a Coastal Sentinel, the Little Penguin, Reflects Marine and Terrestrial Factors. Ecology and Evolution, 15(5), e71361.

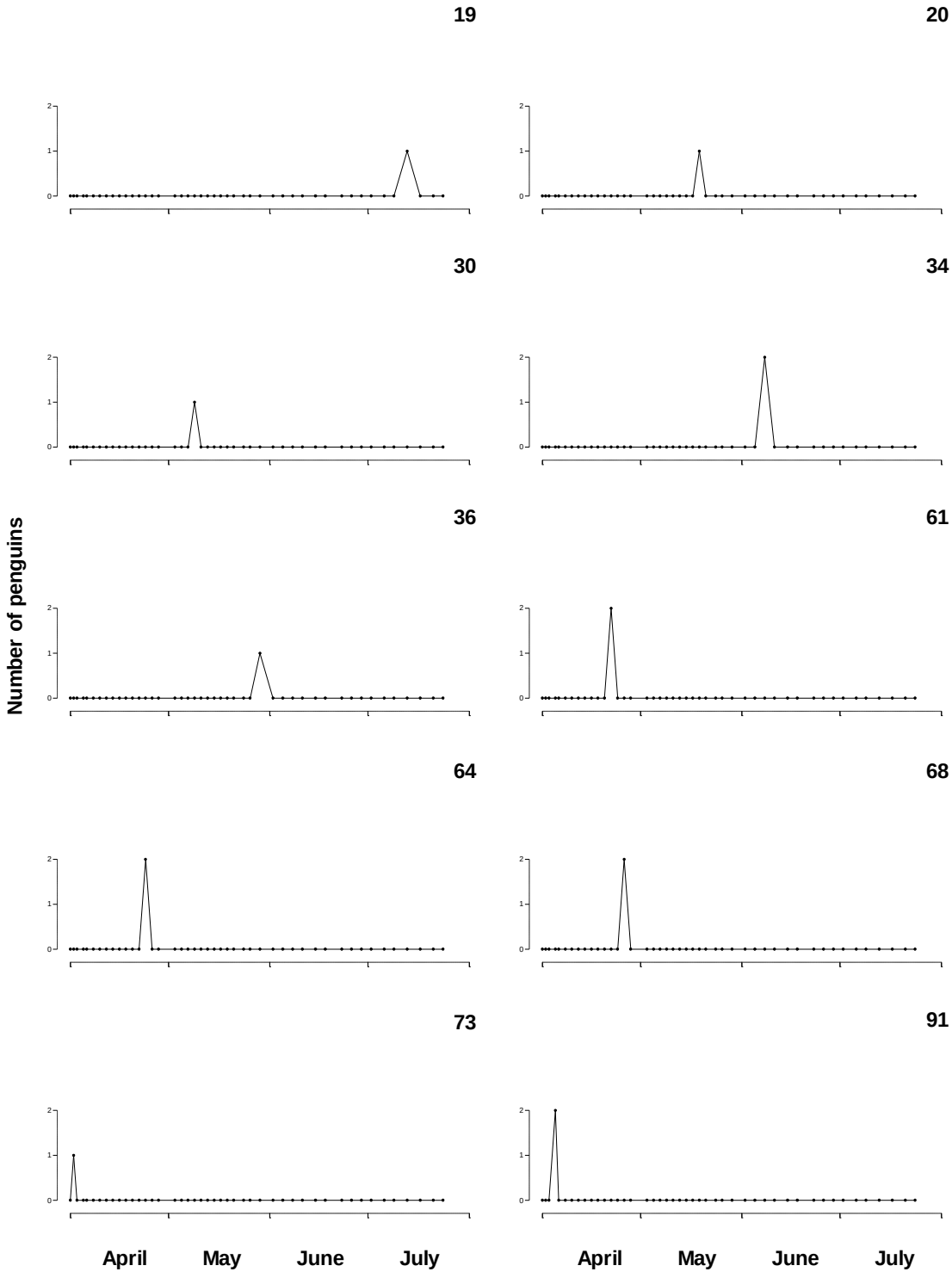
Whiteman, J. P., Newsome, S. D., Bustamante, P., Cherel, Y. and Hobson, K. A. (2021). Quantifying capital versus income breeding: New promise with stable isotope measurements of individual amino acids. Journal of Animal Ecology, 90(6): 1408-1418.

Wilhelm, S. I. and Storey, A. E. (2002). Influence of cyclic pre-lay attendance on synchronous breeding in common murres. Waterbirds 25(2): 156-163.

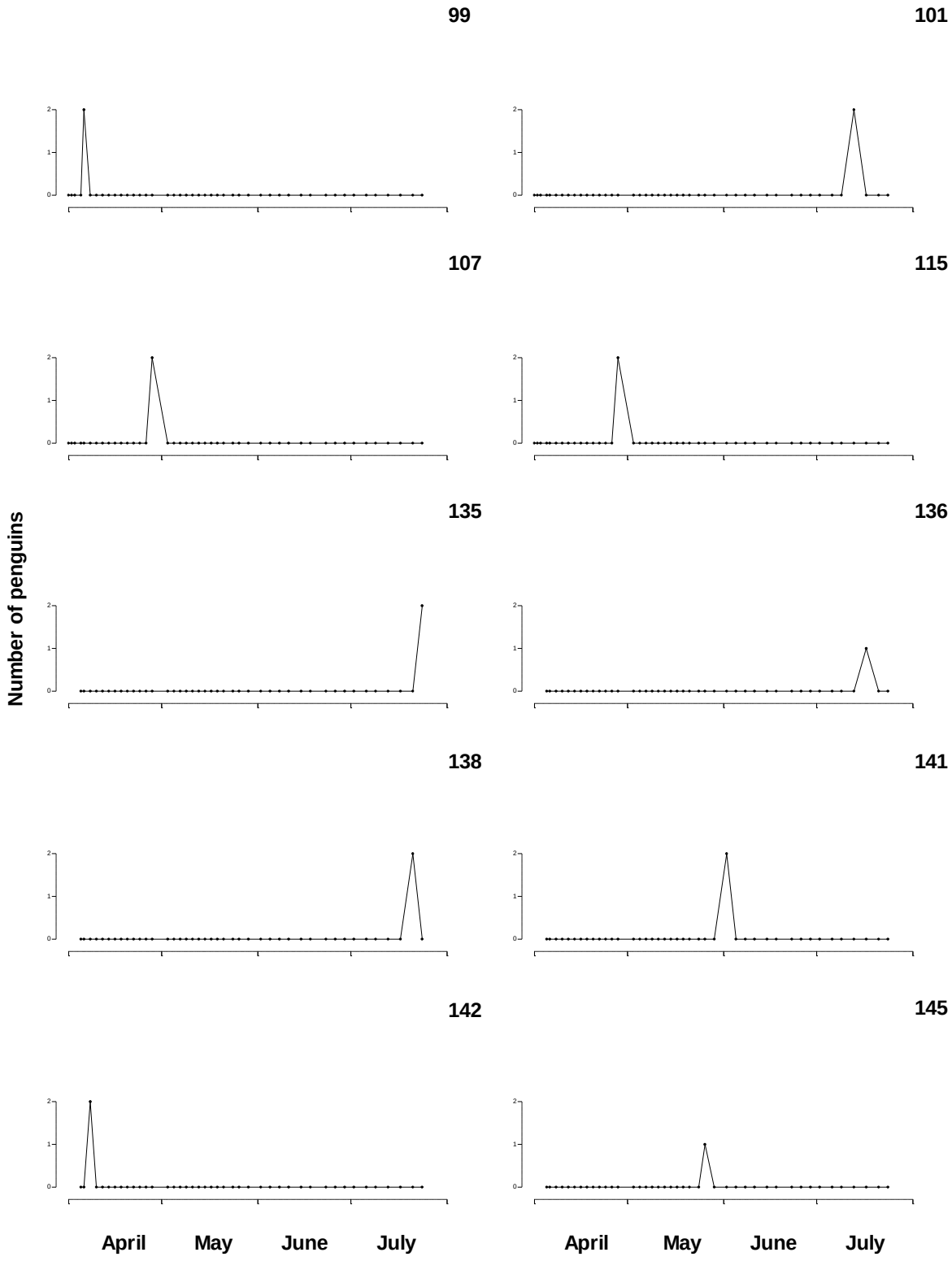
Yamamoto, T., Takahashi, A., Yoda, K., Katsumata, N., Watanabe, S., Sato, K. and Trathan, P. N. (2008). The lunar cycle affects at-sea behaviour in a pelagic seabird, the streaked shearwater, Calonectris leucomelas. Animal Behaviour, 76(5): 1647-1652.

6. Appendix

6.1 Appendix 1. Graphs showing numbers of penguins present in nestboxes that had penguins present on one day of nestbox checks (21 nestboxes).

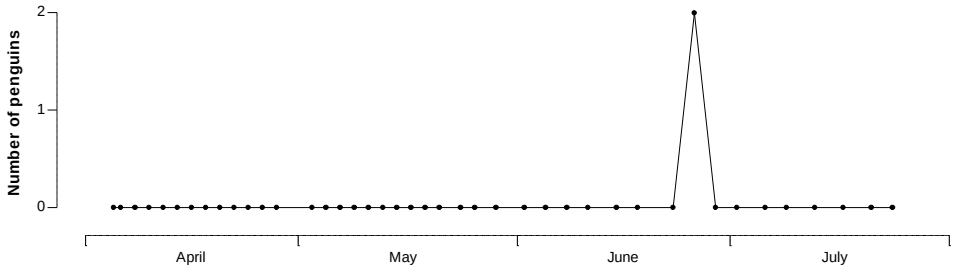


Appendix Fig. 6.1. Numbers of penguins present in nestboxes.



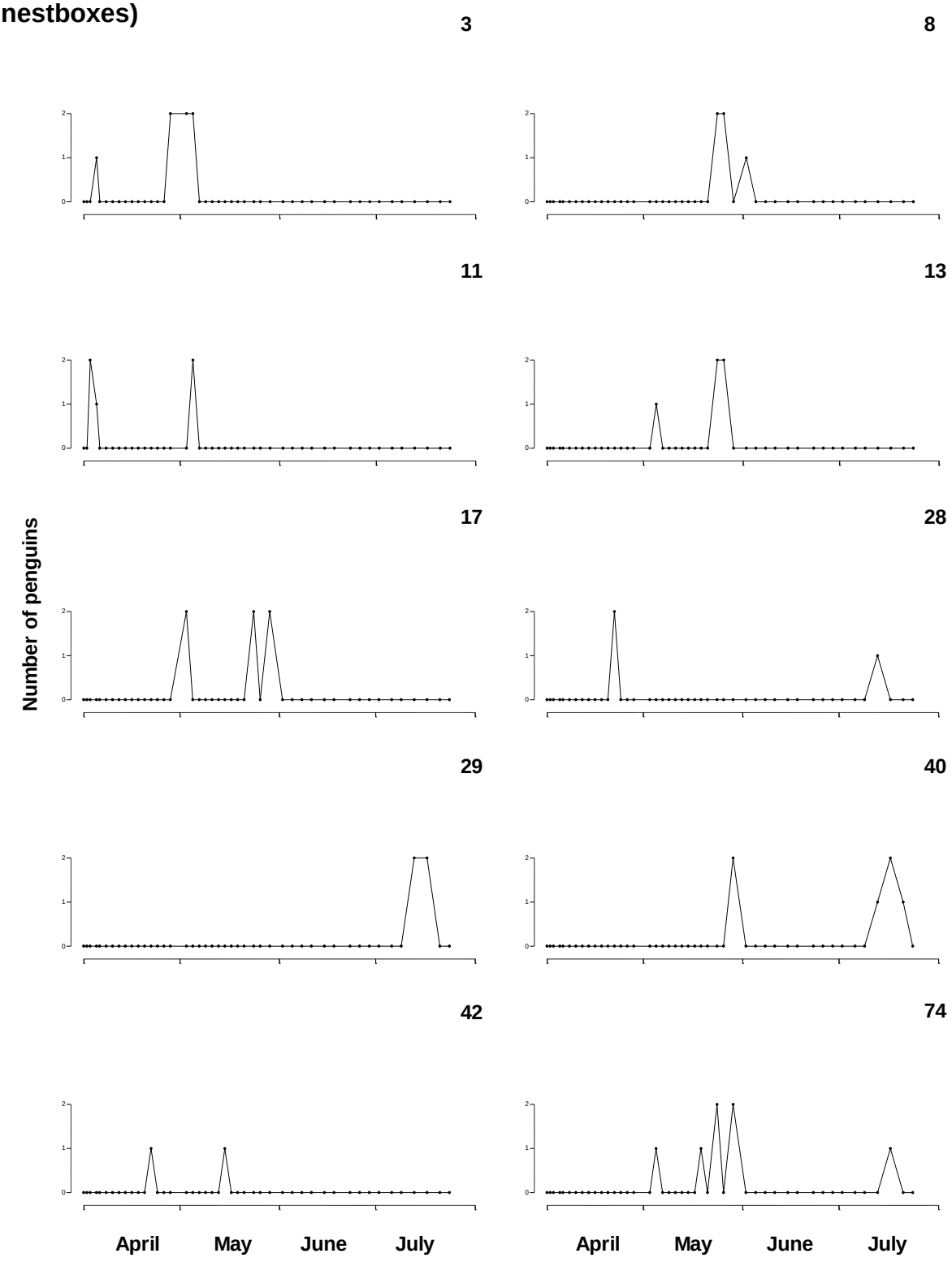
Appendix Fig. 6.2. Number of penguins present in nestboxes.

150

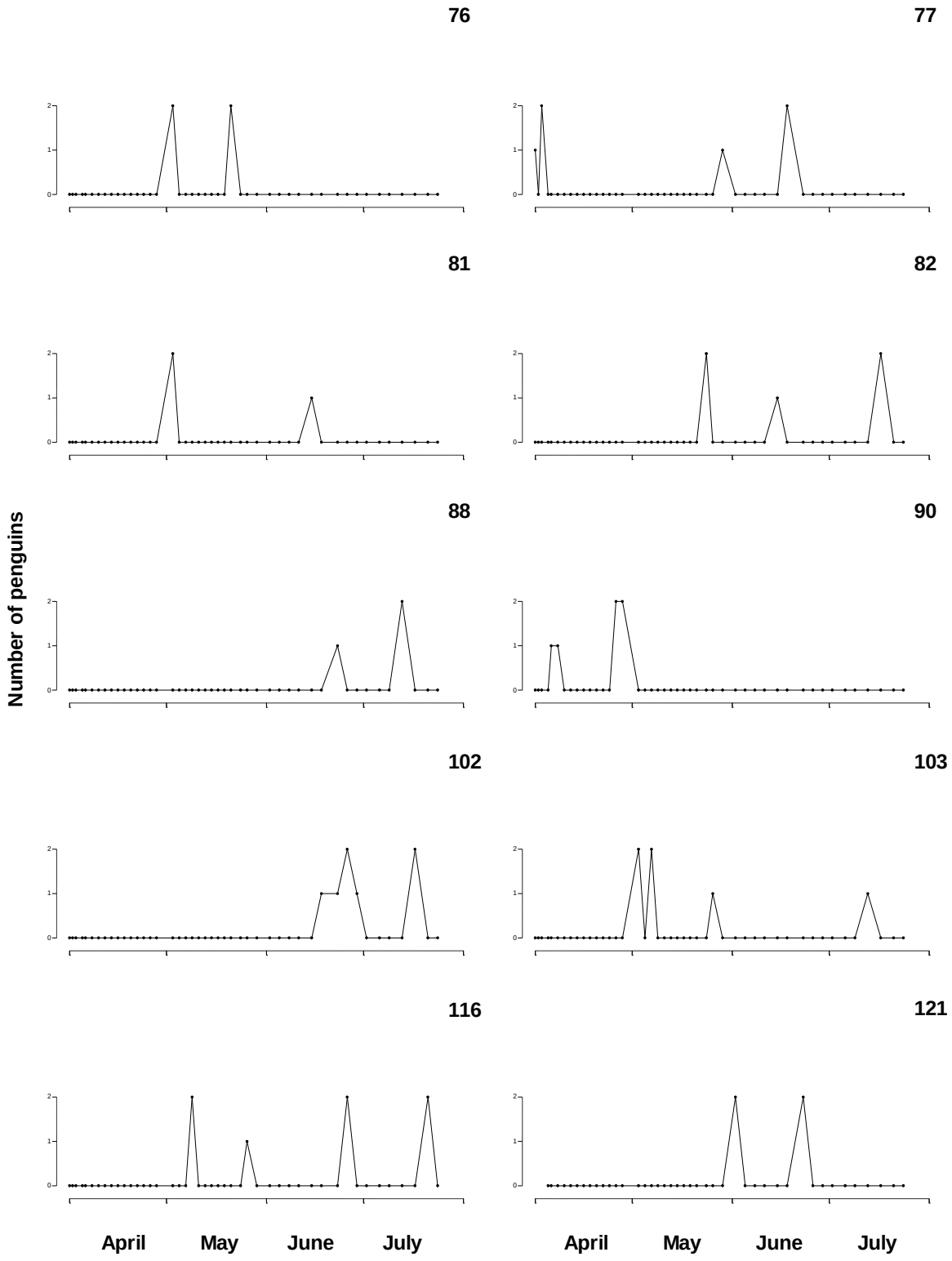


Appendix Fig. 6.3. Number of penguins present in nestboxes.

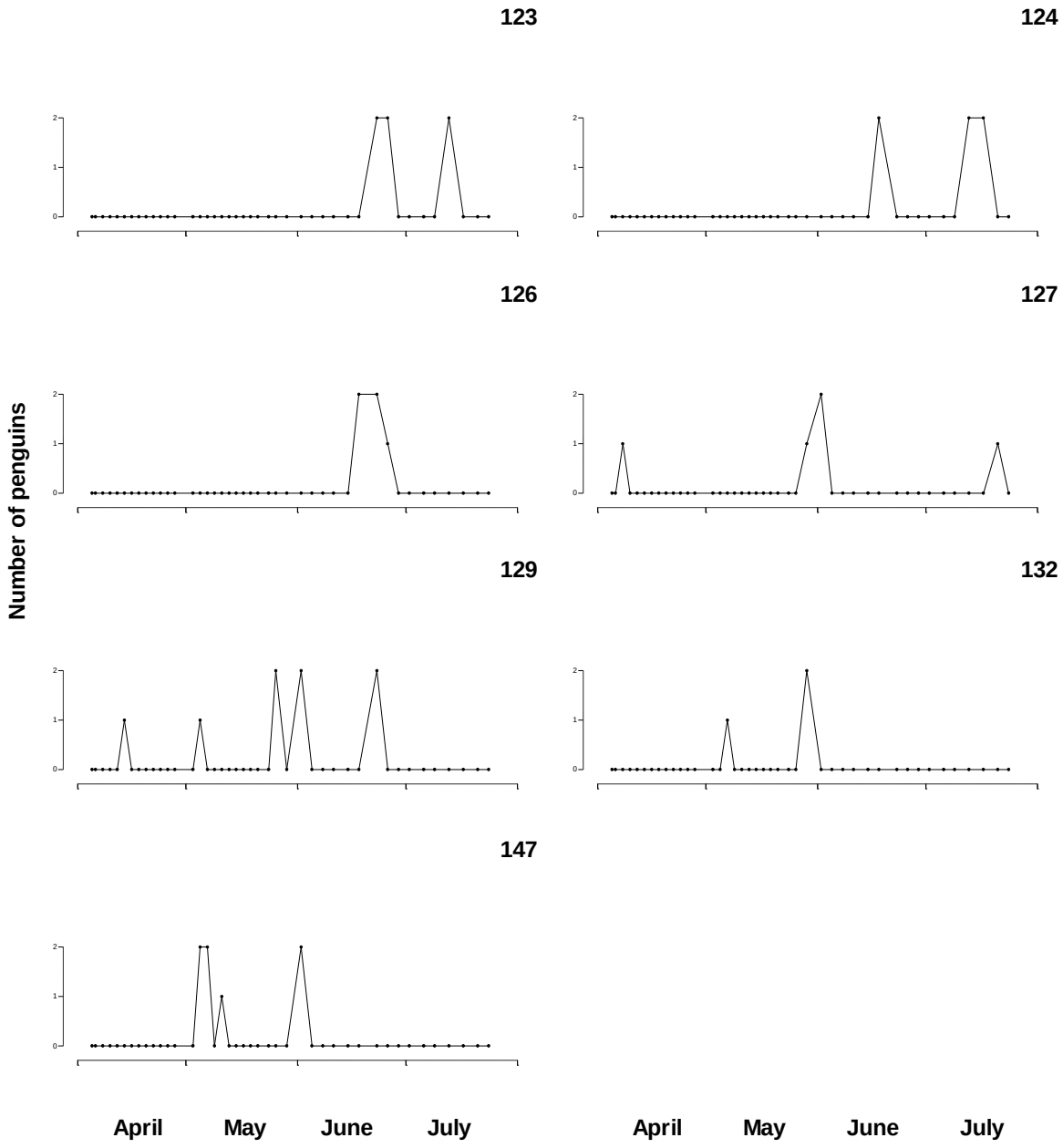
6.2 Appendix 2. Graphs showing numbers of penguins present in nestboxes that had penguins present on two to five days of nestbox checks (27 nestboxes)



Appendix Fig. 6.4. Number of penguins present in nestboxes.

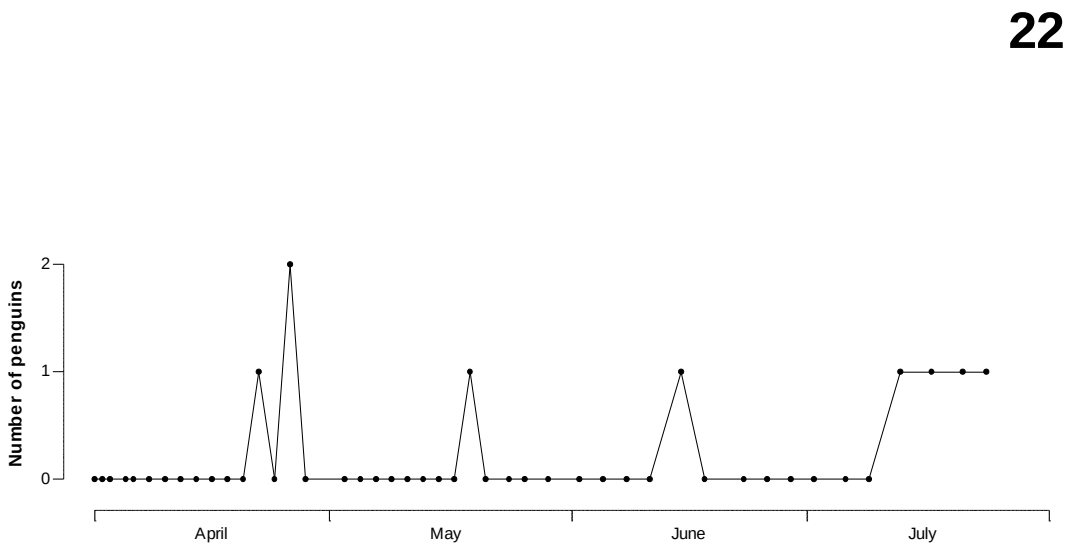


Appendix Fig. 6.5. Number of penguins present in nestboxes.



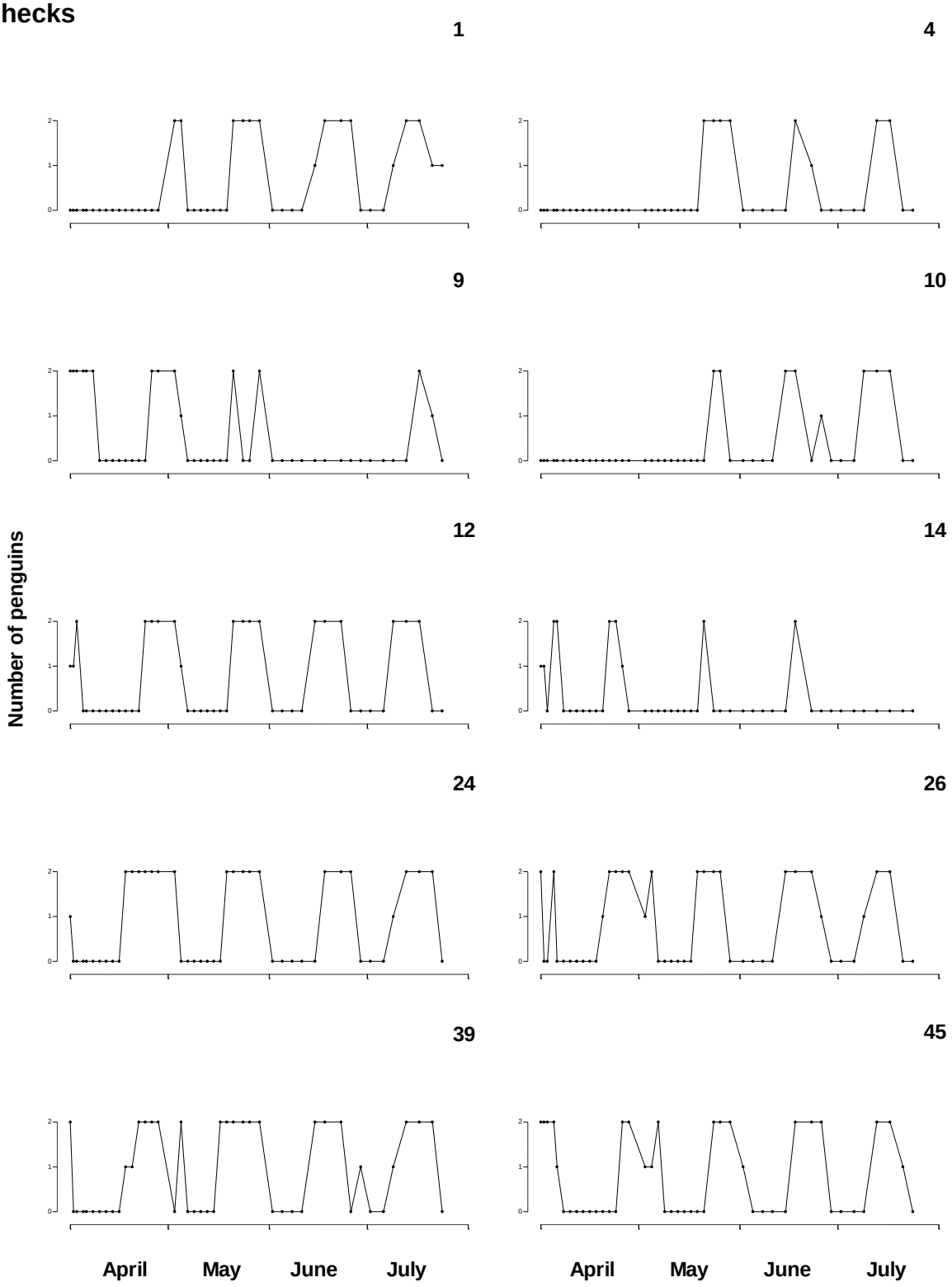
Appendix Fig. 6.6. Number of penguins present in nestboxes.

6.3 Appendix 3. Graph showing numbers of penguins present in a nestbox that regularly had one penguin present on days of nestbox checks

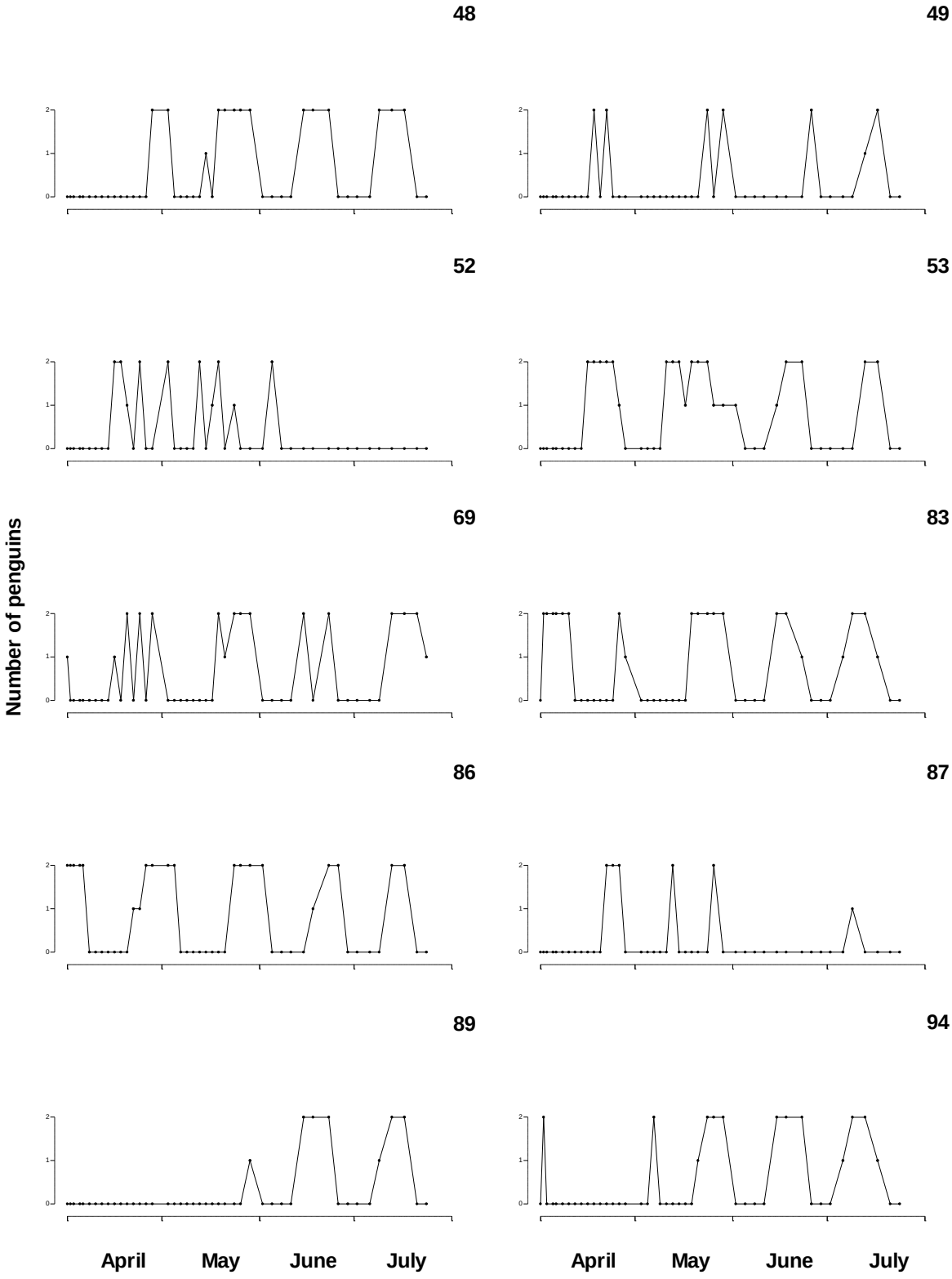


Appendix Fig. 6.7. Number of penguins present in nestboxes.

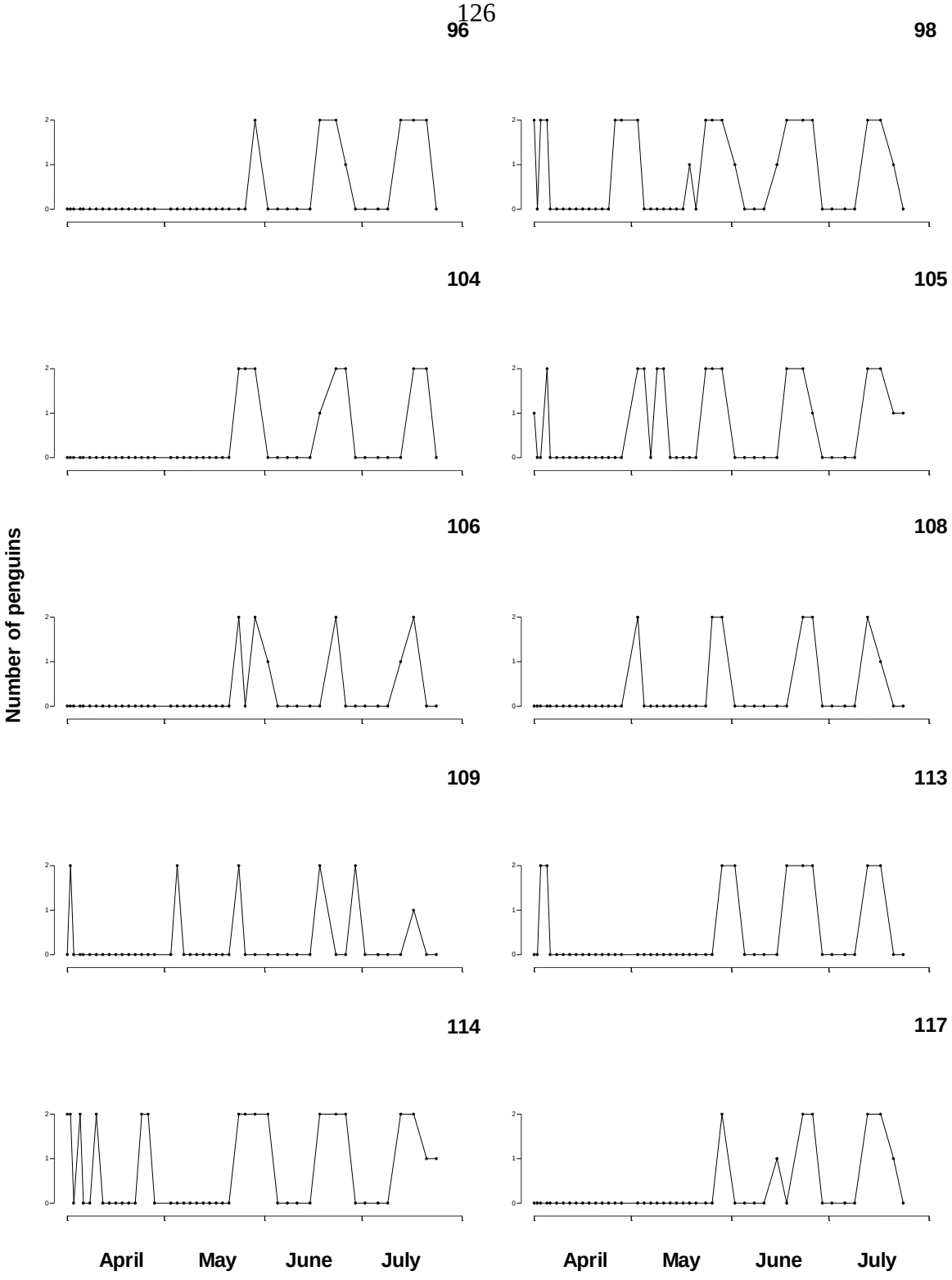
6.4 Appendix 4. Graphs showing numbers of penguins present in nestboxes that regularly had two penguins present (32 nestboxes) on days of nestbox checks



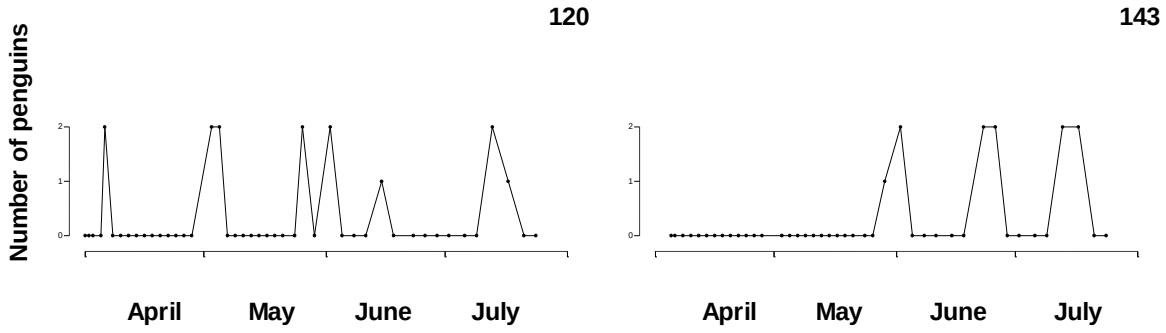
Appendix Fig. 6.8. Number of penguins present in nestboxes.



Appendix Fig. 6.9. Number of penguins present in nestboxes.

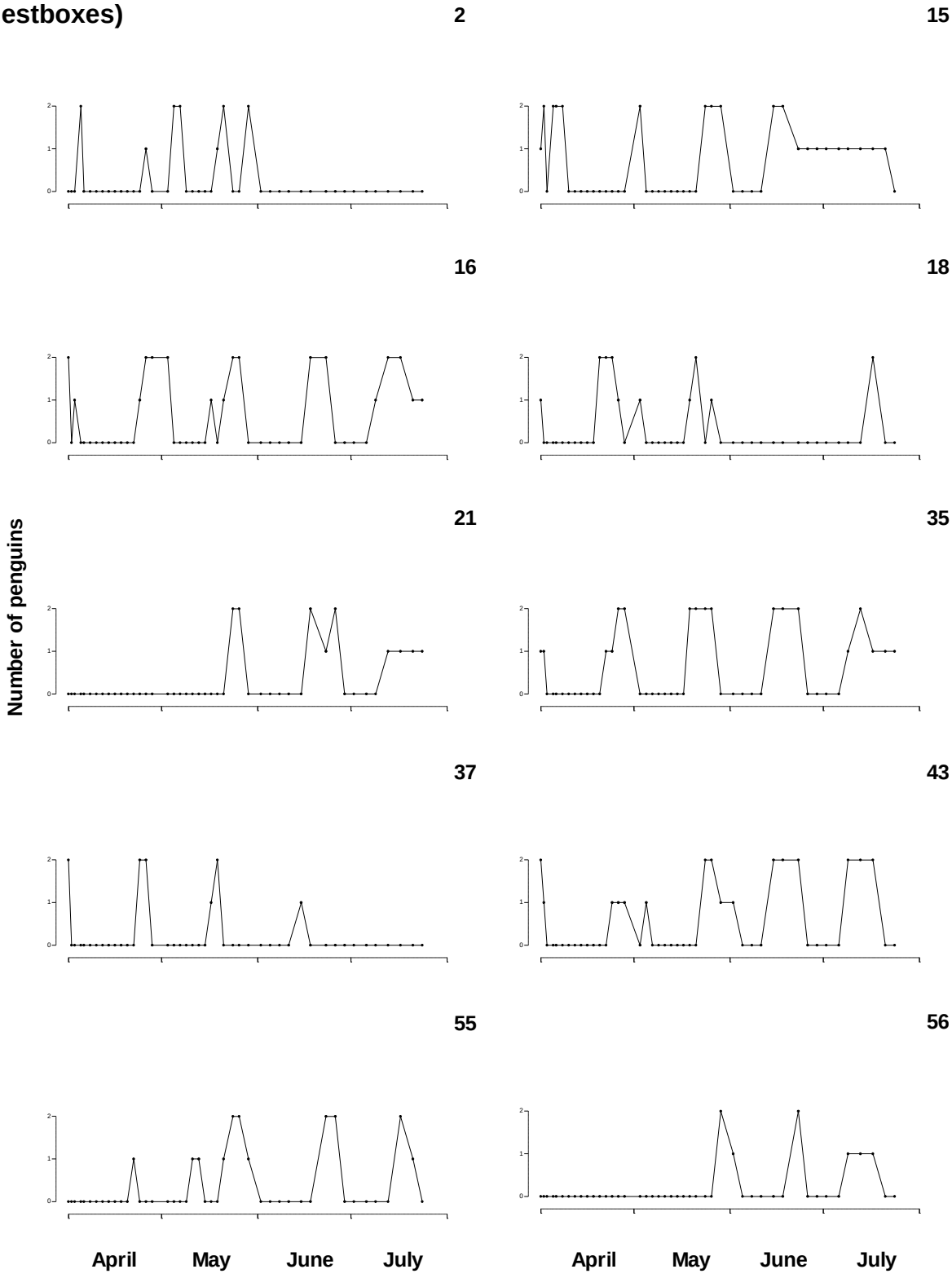


Appendix Fig. 6.10. Number of penguins present in nestboxes.

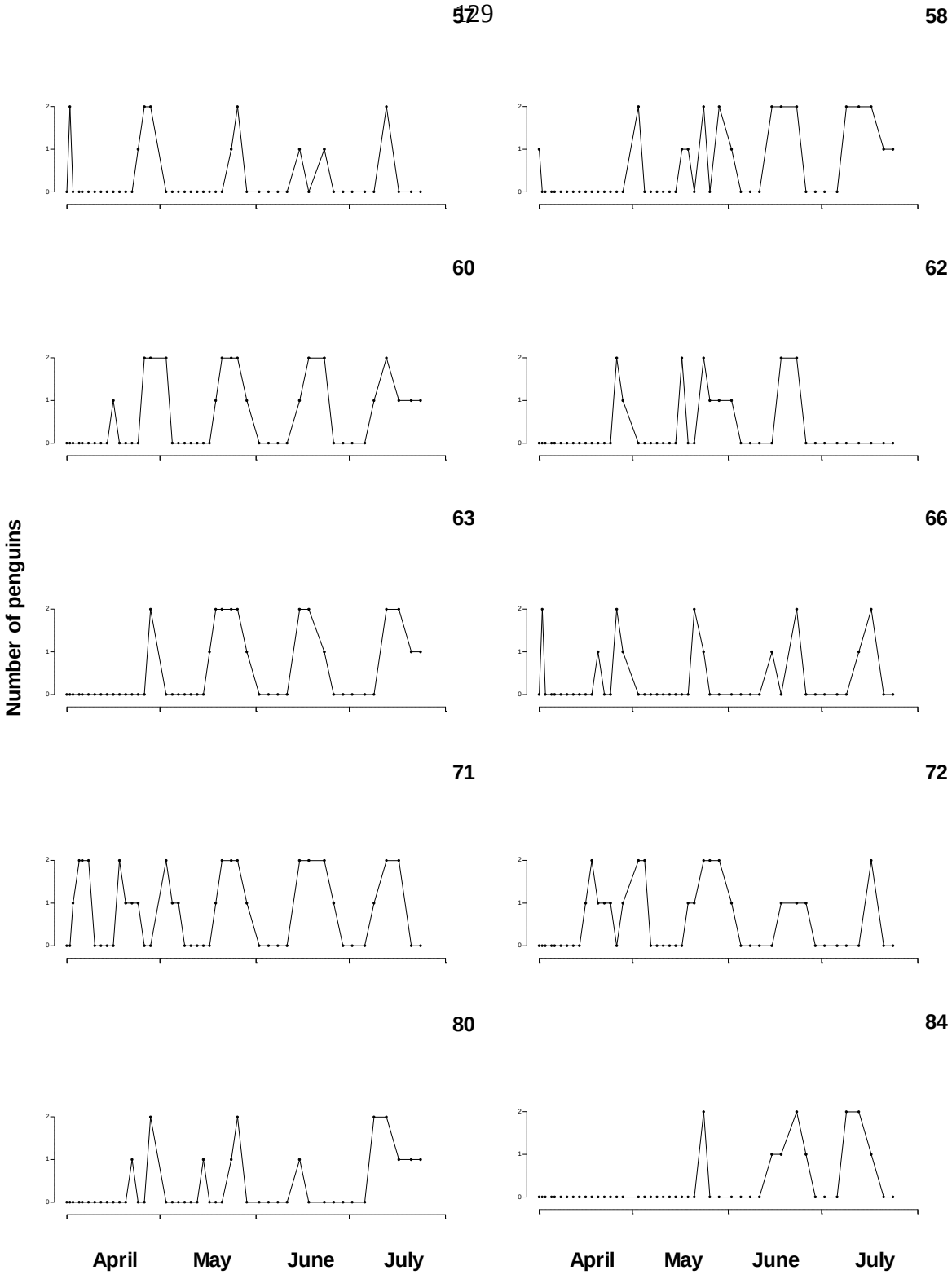


Appendix Fig. 6.11. Number of penguins present in nestboxes.

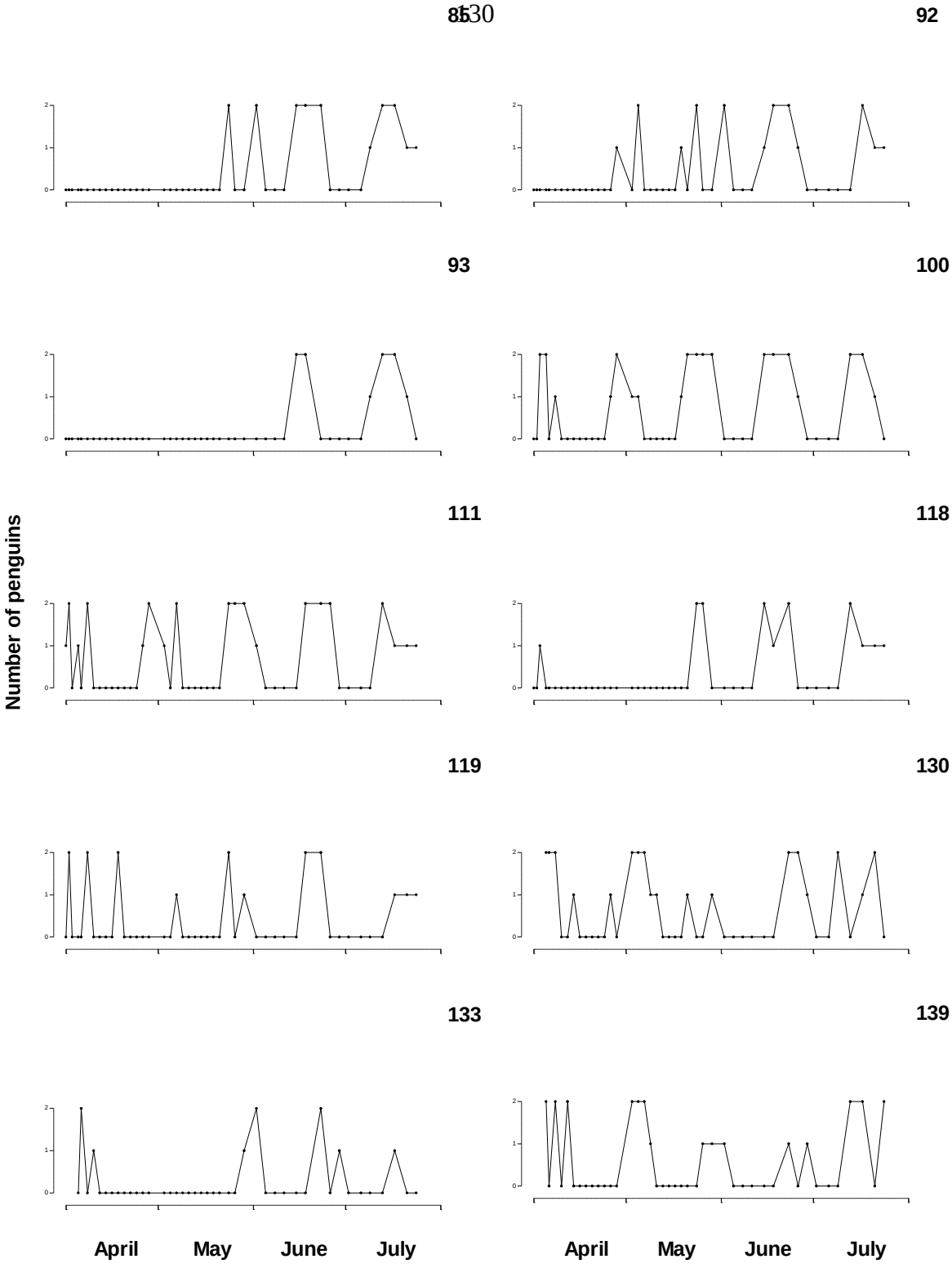
6.5 Appendix 5. Graphs showing numbers of penguins present in nestboxes that regularly had one or two penguins present on days of nestbox checks (30 nestboxes)



Appendix Fig. 6.12. Number of penguins present in nestboxes.



Appendix Fig. 6.13. Number of penguins present in nestboxes.



Appendix Fig. 6.14. Number of penguins present in nestboxes.