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RESEARCH ARTICLE

Little penguins select more isolated nest boxes for breeding, but lay date influences breeding success

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Abstract

Little penguins (*Eudyptula minor*; known as kororā in te reo Māori, the Indigenous language of Aotearoa New Zealand) depend on terrestrial environments for nesting, breeding, and molting, spending approximately 20% of their lives on land. Therefore, little penguins may select breeding habitats that could improve breeding success or survival. However, selection and its consequences differ across colonies because of varying threats and habitat contexts, requiring examination at the colony scale. We investigated the habitat and nest box characteristics influencing little penguin breeding ecology during the 2022 and 2023 breeding seasons at the Pōhatu/Flea Bay colony on Banks Peninsula, New Zealand. Using weekly monitoring data from 194 nest boxes, we applied generalized linear models and occupancy models to assess how these characteristics influenced breeding nest box selection, hatching success, and fledging success. Additionally, we explored the influence of breeding timing and hard tick (*Ixodes eudyptidis*) abundance in the hatching and fledging success models. Little penguins selected more isolated nest boxes for breeding, with >75% breeding probability at nest boxes >2 m from a neighbor. Older nest boxes were selected slightly preferentially for breeding,

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potentially increasing little penguins' exposure to ticks as these boxes had higher tick presence. Breeding success was primarily influenced by the timing of egg laying, where hatching success declined with later lay dates in the 2022 and 2023 breeding seasons. Fledging success decreased by approximately 50% across the lay period in 2022 but remained high (>75%) across similar lay dates in 2023. Our results suggest that nest box characteristics may be related to little penguin breeding nest box selection, whereas hatching and fledging success may be more influenced by timing of breeding and factors not included in our models. We recommend that nest boxes be placed at least 2 m from neighboring boxes within the breeding colony and that older boxes should be preserved where possible. Integrating continued monitoring with wider ongoing conservation efforts in an adaptive management framework is crucial to refining nest box placement and enhancing breeding success.

KEYWORDS

conservation, *Eudyptula minor*, fledging success, hatching success, *Ixodes eudyptidis*, little penguins, nest box selection, New Zealand, ticks

Breeding habitat selection is a key ecological process for many species and can have direct implications for the survival and fitness of individuals (e.g., European polecat [*Mustela putorius*; Lodé 2011], greater sage-grouse [*Centrocercus urophasianus*; Gibson et al. 2016], least tern [*Sternula antillarum*; Catlin et al. 2019], piping plover [*Charadrius melodus*; Catlin et al. 2019], and moose [*Alces alces*; Blouin et al. 2021]). Seabirds rely heavily on terrestrial environments for the nesting and breeding phases of life, and therefore often select breeding habitats that optimize reproduction, increase offspring survival, and minimize energy expenditure (Buckley and Buckley 1980, Colombelli-Négrel 2019). Such selection helps to improve evolutionary fitness (Furness and Monoghan 1987). Studies of various seabird species have demonstrated selection for specific breeding habitat features, such as vegetation cover, substrate type, and isolation from disturbances and intra-specific competition (Seddon and Davis 1989, Ratz 2019, Pagenaud et al. 2022, Colombelli-Négrel and Iasiello 2023, Momberg et al. 2023), some of which have also been linked to improved reproductive outcomes (Stokes and Boersma 1998, Colombelli-Négrel and Iasiello 2023). For instance, Magellanic penguins (*Spheniscus magellanicus*) in Argentina had greater breeding success when nests had more vegetation cover (Stokes and Boersma 1998), with experimental results suggesting that an increase in cover reduced the likelihood of egg detection by predators and created more shade, protecting chicks from high temperatures. Vegetation cover has similarly been found to be important for yellow-eyed penguins (*Megadyptes antipodes*), where penguins selected nests that had dense vegetation cover to protect adults and chicks (Seddon and Davis 1989). In addition to habitat features influencing nest site selection and success in seabirds, intra-specific competition for nesting sites and territoriality can also inform decisions on site selection, with individuals often engaging in aggressive interactions with conspecifics over nest sites or mates (Penney 1968, Stokes and Boersma 2000, Dann and Norman 2006). Such nest-site-level competition can reflect the competition experienced by seabirds at broader ecological scales; for example, there is a growing body of literature providing evidence that there is a zone of food depletion around seabird colonies, as suggested by Ashmole's halo hypothesis (Ashmole 1963, Dann and Norman 2006, Gaston et al. 2007, Weber et al. 2021, Lazarus et al. 2024), which can increase intra-specific competition for food resources and influence individuals' breeding success.

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Breeding success in seabirds can also be influenced by environmental variability preceding and during the breeding season (Weimerskirch et al. 2001, Nevoux et al. 2008, Cannell et al. 2012, Agnew et al. 2015), prey availability (Becker et al. 2007, Sherley et al. 2013), and extreme weather events (Newell et al. 2015, Marcelino et al. 2020, Piatt et al. 2020, Cannell et al. 2024). For example, extreme temperatures during marine heatwave events can influence reproductive outcomes by altering prey distributions, often leading to more chick mortality due to starvation, where such extremes can impact breeding success independently of local habitat quality (Cannell et al. 2012, Carroll et al. 2015, Glencross et al. 2021). In addition to environmental stressors, the role of ecto-parasites, such as hard ticks (Acari: Ixodidae), on breeding success is important to consider. During the prolonged periods that seabirds spend at nesting sites throughout breeding and molting, their exposure to ticks can increase (Mangin et al. 2003). Through blood feeding, ticks can transmit pathogens and drain nutrients from adults or chicks, potentially reducing breeding success (Major et al. 2009, Sanz-Aguilar et al. 2020). The influence of ticks on breeding success has been explored in several seabird species such as black-browed albatross (*Thalassarche melanophris*; Bergström et al. 1999, Militão et al. 2024), Cassin's auklets (*Ptychoramphus aleuticus*; Morbey 1996), Guanay cormorants (*Phalacrocorax bougainvilliorum*; Duffy 1983), Peruvian booby (*Sula variegata*; Duffy 1983), Peruvian brown pelican (*Pelecunus occidentalis thagus*; Duffy 1983), and storm petrels (*Hydrobates pelagicus*; Sanz-Aguilar et al. 2020), where breeding success was negatively affected by hard ticks in most cases. However, there remain few studies on penguin species and the influence of ticks, with several of these studies focusing on king penguins (*Aptenodytes patagonicus*; Gauthier-Clerc et al. 1998, 2003; Mangin et al. 2003). King penguins observed with ticks at Possession Island, part of the Crozet Archipelago, showed reduced breeding success compared to individuals without ticks (Mangin et al. 2003). Years with greater infestation levels led to poor condition in several dozen individuals, with some cases leading to death (Gauthier-Clerc et al. 1998, Mangin et al. 2003). Little penguins (*Eudyptula minor*; known as kororā in te reo Māori, the Indigenous language of Aotearoa New Zealand) in Australia and New Zealand have been documented carrying tick loads (Jansen van Rensburg 2010, Moon et al. 2019, Wells et al. 2025), with a negative association found between little penguin body condition and ectoparasite load across 15 local populations in Tasmania, Australia (Wells et al. 2025). However, few studies have investigated the effect of tick load on little penguins' reproductive success because of difficulties in gaining accurate estimates of tick prevalence and their ecological influence or because tick abundances are too low (ranging from 0-5 individuals per nest) to examine any effects (Jansen van Rensburg 2010).

Little penguins are an example of a species influenced by breeding habitat selection (Clitheroe 2021), environmental variability (Mattern and Wilson 2018), and exposure to ticks (Jansen van Rensburg 2010, Wells et al. 2025). These burrow-nesting seabirds are distributed around the coastal regions of Aotearoa New Zealand, southern mainland Australia, and their offshore islands (Mattern and Wilson 2018). Little penguins, like all seabirds, are an important biological indicator for their environment (Furness 1997, Geurts 2006) and are currently listed as at risk-declining in New Zealand on the New Zealand Threat Classification System (Robertson et al. 2017). Although little penguins are still listed as least concern by the International Union for Conservation of Nature Red List (BirdLife International 2020), several local populations have declined within their broader distribution (Challies and Burleigh 2004, Mattern and Wilson 2018, Clitheroe 2021, Nikitine et al. 2022, Cannell et al. 2024). Such declines have been attributed to a range of anthropogenic threats (Priddel et al. 2008, Cannell et al. 2016, Mattern and Wilson 2018), spanning the terrestrial and marine environments, including predation, habitat degradation, over-fishing, and climate change (Perriman and Steen 2000, Perriman et al. 2000, Mattern and Wilson 2018, Cannell et al. 2024). In response to habitat degradation, and as a terrestrial conservation tool, landowners, researchers, and colony managers have installed artificial nest boxes in many colonies to provide secure nesting sites for little penguins (Klomp et al. 1991, Lalas et al. 1999, Perriman and Steen 2000, Sutherland and Dann 2014, Clitheroe 2021). The nest boxes have the added benefit of allowing for greater accessibility during monitoring, research, and conservation activities. To support conservation programs of little penguins, it is important to broaden understanding of their ecology at the colony scale (here defined as the patterns and processes observed within a single colony), considering varying threats and habitat contexts that might affect colonies differently. While some

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research has investigated aspects of their terrestrial environment, such as breeding habitat selection (Clitheroe 2021, Colombelli-Négrel and Iasiello 2023), much of this work has focused on Australian colonies, including Phillip Island, Penguin Island, and several other locations across Western Australia, South Australia, New South Wales, and Tasmania (Weerheim et al. 2003, Schumann et al. 2013, Colombelli-Négrel 2019, Clitheroe 2021, Colombelli-Négrel and Iasiello 2023). Comparatively limited research exists for New Zealand colonies (Allen et al. 2011, Braidwood et al. 2011, Ratz 2019). New Zealand little penguin colonies differ from those in Australia, with unique threats and habitat dynamics, taxonomic and morphological differences, and no large colonies as are found in some parts of Australia, such as Phillip Island (Braidwood et al. 2011, Grosser et al. 2015, Mattern and Wilson 2018).

We investigated the role of terrestrial habitat and nest box characteristics on the breeding ecology of little penguins at Pōhatu/Flea Bay, New Zealand, over 2 breeding seasons (2022 and 2023). Our objectives were to 1) investigate the factors influencing tick presence at nest boxes, 2) determine the habitat and nest box characteristics that may influence little penguin nest box selection for breeding, and 3) explore whether hatching and fledging success is affected more by nest box characteristics and tick presence or by the timing of egg laying. We predicted that older nest boxes in close neighboring areas would have more ticks (Jansen van Rensburg 2010, Blunsden and Goodenough 2023), with cracks, crevices, and old nest material providing ideal habitat for ticks (Niebuhr et al. 2013). We also predicted that little penguins would select nest boxes with medium-height vegetation (such as shrub coverage) and those located farther from neighboring boxes to minimize intraspecific competition, such as territoriality or competition for mates or nests (Stokes and Boersma 2000, Dann and Norman 2006, Mattern and Wilson 2018, Colombelli-Négrel and Iasiello 2023). Finally, we predicted that lower fledging success would be associated with greater tick presence because of their role in disease transmission and influences on body condition, and predicted lower hatching and fledging success with later laying weeks because of the possible shift in resource availability and environmental conditions later in the breeding season (Jansen van Rensburg 2010, Carroll et al. 2015).

STUDY AREA

Pōhatu/Flea Bay (43° 52' S, 173° 0'E) is located on the southeastern side of Banks Peninsula, South Island, New Zealand (Figure 1), approximately 90 km southeast of Christchurch. Most of the area surrounding the bay is a working sheep and cattle farm, first established in 1843. The bay is surrounded on either side by steep hills over 200 m above sea level, with a more gradual slope at the head of the bay. Geological features include volcanic rock formations characteristic of Banks Peninsula's volcanic origins (Hampton and Cole 2009), and rocky intertidal zones that support marine biodiversity. Pōhatu has a temperate, maritime climate, with an average annual rainfall of 1,000 mm from 2009 to 2024, based on data from the nearest weather station at Akaroa (~12 km; National Institute of Water and Atmospheric Research [NIWA] 2024*a*). Mean monthly temperature ranged from 9°C in July to 18°C in February (NIWA 2024*a*). The terrestrial landscape consisted of grasslands, patchy shrubland, dense shrubland with a mix of remnant and re-established native vegetation such as kānuka (*Kunzea robusta*), pine (*Pinus* spp.) tree shelterbelts, rocky shore platforms, and some man-made structures. Each land cover type provided varying degrees of cover and shade for nesting little penguins, with the rocky beaches and intertidal zones playing an important role in providing access to the sea for foraging.

Pōhatu supports one of the largest little penguin colonies on mainland New Zealand, with an estimated minimum count of 928 breeding pairs as of a nest survey conducted in 2020 (Nikitine et al. 2022, Hickcox et al. 2026). Natural burrows are distributed mostly around the head of the bay and the eastern side (Helps Pōhatu Conservation Trust, personal communication). Possibly as a consequence of anthropogenic threats, such as fisheries interactions and invasive mammalian predators, the little penguin population in Pōhatu appears to have been declining for the last decade (Nikitine et al. 2022, Hickcox et al. 2026), reflecting trends seen in many other little penguin colonies (Stevenson and Woehler 2007, Colombelli-Négrel 2015, Mattern and Wilson 2018, Clitheroe 2021, Nikitine et al. 2022, Hickcox et al. 2026). Over 200 artificial nest boxes have been installed within the colony across habitat characteristics, including variations in slope, vegetation type and height, aspect, and

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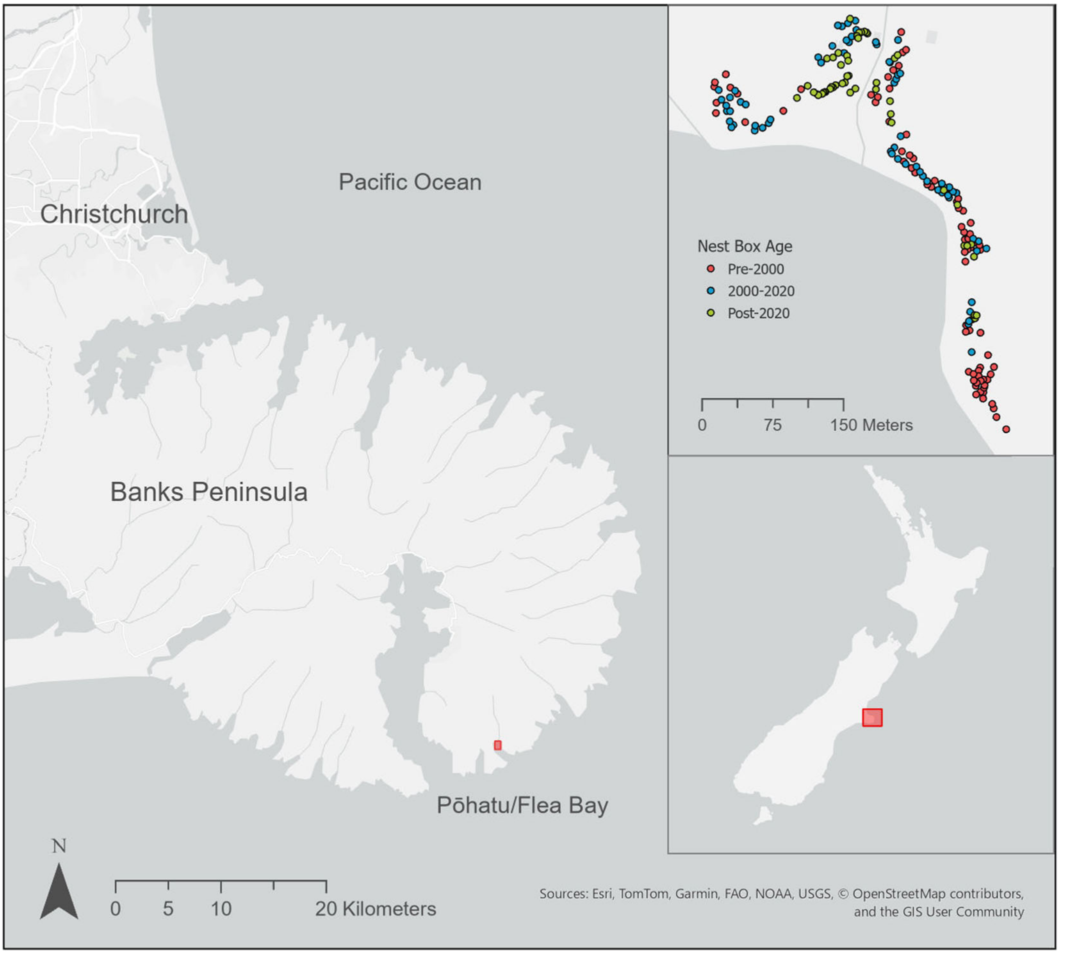

FIGURE 1 Pōhatu/Flea Bay, located on the southeastern side of Banks Peninsula, South Island, New Zealand, where the little penguin colony in this study is located. A zoomed-in extent of the bay is shown in the top right, with the locations of the 194 nest boxes colored by nest box age class (red = pre-2000, blue = 2000–2020, and green = post-2020).

proximity to neighboring nests. In 2022, the Helps Pōhatu Conservation Trust initiated a long-term penguin monitoring program at Pōhatu that works alongside other management efforts, including invasive predator control of stoats (*Mustela erminea*) and other introduced species, and habitat restoration to safeguard this little penguin colony. Complementing these terrestrial efforts, the Pōhatu Marine Reserve became the first marine reserve to be established on the east coast of the South Island in 1999 (Barr 1999). Covering 215 ha, the reserve helps to improve the protection of the marine ecosystems that support little penguins and other species at sea.

METHODS

Study design

We collected data in collaboration with the Helps Pōhatu Conservation Trust through their monitoring and research program. The program involves weekly monitoring of artificial nest boxes in one section of the colony (the area

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where nest boxes have been installed, which does not include the wider area of surrounding natural burrows) during the breeding season (August–February at the Pōhatu colony), and monitoring every 2 weeks during the non-breeding season. During monitoring, each nest box is checked for the presence of adults, eggs, and chicks, and behavioral status is noted (breeding, molting, or loafing [when a penguin is resting and not displaying behaviors connected to breeding, molting, or feeding]). Biological information is recorded in custom libraries on the open-source Memento Database app (NZ Penguin Initiative 2020). We categorized nest box status as used for breeding or unused for breeding, where the latter includes nest boxes that remained empty during the breeding season and those that had loafing penguins present but no observations of eggs or chicks. In addition to the observational monitoring, marking of little penguins has been carried out since October 2022 using an 8-mm Trovan Radio Frequency Identification (RFID) transponder inserted with a needle into the back of the neck. Each individual observed during monitoring is scanned using an electronic identification reader (Gallagher Animal Management, Hamilton, New Zealand), and the unique transponder ID is recorded for that individual. All microchipping is performed by permitted individuals certified by the NZ National Bird Banding Scheme. In this study, we used data from the 2022-2023 and 2023-2024 breeding seasons (referred to throughout as the 2022 and 2023 seasons, respectively) from 194 nest boxes, which excludes 29 nest boxes that were installed after the 2022 season and 7 nest boxes that were either replaced between the 2022 and 2023 breeding seasons or removed for maintenance or replacement at the time of recording nest box variables. We considered the breeding season to coincide with the first observation of eggs and the last observation of chicks at the nest boxes (22 August 2022–23 February 2023 and 23 August 2023–26 February 2024, for the 2022 and 2023 seasons, respectively).

Tick occupancy

During weekly monitoring in the 2023 breeding season, we visually scored tick (*Ixodes eudyptidis*) presence at each nest box (excluding ticks directly on penguins) on a scale from 0 to 2, where 0 indicated no visible ticks, 1 represented a few ticks (<~10 ticks), and 2 represented many visible ticks (>~10 ticks). We separately scored presence or absence of ticks directly on penguins. Nest boxes were generally monitored in a similar order each week, such that tick scores for individual boxes were recorded at approximately the same time of day across sampling weeks. Scoring was conducted by multiple observers from the monitoring team, all of whom had comparable experience with identifying ticks, ensuring they could reliably distinguish between categories 1 and 2. We presumed that 0 scores (absences of ticks) would largely be due to imperfect detection (MacKenzie et al. 2004). To test our confidence in the 0 scores, we conducted additional intensive tick surveys during the breeding season at a subset of 47 nest boxes that were scored a tick presence score of 0 (i.e., ticks were absent) during weekly monitoring for at least 2 consecutive weeks, and we prioritized boxes where either penguins were present or signs of recent penguin activity were visible during that period. We used these tick surveys solely as a validation step and did not include the data in subsequent modeling. We used a range of search techniques during the surveys, such as sifting nest material and surrounding dirt using a sieve and white tray, investigating cracks and crevices in the box using an LED electric torch, and visually checking around the nest box sides and lid. The techniques used at each nest box varied depending on the type of nest material and presence of penguins. Empty nest boxes were surveyed for 10 minutes, prioritizing nest boxes that had signs of recent penguin activity (e.g., fresh feces). At occupied boxes where an individual penguin was being removed for weighing or microchipping, we limited the survey to the time the bird was out of the box to avoid causing additional stress. We also conducted some intensive tick surveys at occupied nest boxes where the individual was not removed from the box. In these cases, material was only sifted from outside the nest box and was not taken from the nest itself, and visual checks inside the nest box were brief to minimize disturbance. These 2 types of searches were timed and then standardized based on search length. We selected this overall method for thoroughness and to minimize the disturbance to individuals at the nest. Between May and June 2024, 14 of those 47 nest boxes were revisited for a follow-up intensive tick survey to investigate

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tick detectability outside the summer breeding season, prioritizing those with signs of recent penguin activity and following the same method as the original surveys.

Models of tick occupancy

We used a single-species (ticks) single-season occupancy model (MacKenzie et al. 2002) to explore tick presence at 194 little penguin nest boxes during the 2023 breeding season. We selected this approach because tick presence is difficult to ascertain, and it is reasonable to expect that any observer could miss detections because the ticks are small (1–6 mm) and easily confused with mud, dirt, rocks, and other insects. Single-season occupancy models have 2 components, occupancy probability (ψ) and detection probability (*p*), and account for imperfect detection (MacKenzie et al. 2002, Bailey et al. 2014).

From the occupancy models, we extracted predicted probabilities for tick occupancy across the nest boxes and used this as a predictor variable in the fledging success models (Table S1). As tick data were only available for 2023, we assumed consistency in tick prevalence between breeding seasons and included the 2023 tick data for each season in our analysis (Gómez-Díaz et al. 2008). We used weekly tick score data collected during the monitoring period from 24 October 2023 to 26 February 2024. This timeframe began 2 weeks after tick scoring commenced (to ensure consistent scoring was occurring) and extended until the last recorded chick fledged (marking the end of the breeding season). We converted nest box tick scores (0–2) to presence (1) or absence (0) for the occupancy model, with tick scores of 1 and 2 representing presence and 0 remaining as presumed absence. For any cases where ticks were observed on the penguin but not the nest box, we included the observation as a tick presence (1) for the occupancy model. We pooled data into weekly surveys (19 total weeks) to address inconsistencies caused by occasional multiple monitoring of some nest boxes within the same week, and stored data as encounter histories.

We investigated the influence of several variables on the probability of detection and the probability of occupancy of ticks at nest boxes. We included mean daily temperature (°C) from the previous week, time of day, and daily penguin presence as detection covariates, all of which change between survey periods. We sourced mean daily temperature data from the Akaroa weather station (NIWA 2024*b*) and averaged mean daily temperature across the week before each survey date. This variable provided an overall representation of thermal conditions during the week preceding each survey, which are known to influence tick activity and development (Ogden et al. 2021). Although specific thermal requirements for development are not known for *I. eudyptidis*, another nest-dwelling Ixodid tick in New Zealand (*I. anatis*) has an optimal developmental temperature between 10°C and 15°C (Bansal et al. 2021). We obtained time of day for each tick record from the weekly monitoring data, where we expected the temperature and humidity fluctuations associated with time of day to influence tick detectability (Vail and Smith 2002). Daily penguin presence was a binary variable using weekly monitoring data, where presence of an adult or chick at the time of the tick survey was equal to 1, and the absence of penguins was equal to 0. We expected ticks to be out and visible at nest boxes to feed when penguins were present, rather than be dormant and buried in nest material as typically occurs when penguins are absent (Ramos et al. 2001, Jansen van Rensburg 2010).

We included vegetation height, nest box age, mean penguin presence, and distance to the nearest nest box as tick occupancy covariates in the models. We categorized vegetation into 3 levels (low, medium, and high) based on the height of vegetation either directly above or within a 1-m radius of the nest box. Low describes nest boxes only surrounded by grasses or low-lying weeds, medium describes those with shrubbery surroundings, and high describes those with tall tree cover. We categorized 3 nest boxes located under carports or sheds as having high vegetation because the environment most resembled the dense cover provided by tall pines or other trees, even though they are not naturally occurring. We categorized nest box age based on approximate installation decade (pre-2000, 2000–2020, and post-2020; Helps Pōhatu Conservation Trust, personal communication). Older nest boxes typically had more cracks and crevices because of the type of wood used and their longer exposure to the

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elements, whereas newer nest boxes were generally made with smoother plywood (Figure S1). We calculated mean penguin presence for each nest box across the 2022 and 2023 breeding seasons by averaging the penguin presence values (where 0 = penguins absent, and 1 = adults or chicks present) recorded for each nest box across those time periods. We calculated the shortest linear distance to the nearest neighboring nest box in meters using global positioning system (GPS) waypoints, which we collected for each nest box using a Garmin Etrex 10 GPS device (Garmin, Auckland, New Zealand) in ArcGIS Pro (version 2.9.2; Esri, Redlands, CA, USA).

We fitted 37 candidate models with different combinations of occupancy and detection covariates using the RPresence 1.15.13 package (MacKenzie and Hines 2018; Table S2), representing all *a priori* candidate sets based on our variable hypotheses. We used Akaike's Information Criterion (AIC) and associated weights to determine the most parsimonious model (Anderson 2008). However, if multiple models were within 2 ΔAIC of the best-supported model, we selected the more parsimonious model for generating predictions, unless additional predictors had a significant influence on the response or there was strong biological justification based on previous literature. We ran a Mackenzie and Bailey goodness-of-fit test (MacKenzie and Bailey 2004) in RPresence using the occMod function.

Little penguin breeding models

We calculated the following variables for each monitored nest box for the 2022 and 2023 breeding seasons: 1) nest box selection for breeding, a binary variable that describes whether we observed eggs or chicks at a nest box at least once from August through February (the time of year of egg-laying and chick-rearing), 2) hatching success, the number of chicks that hatched over the total number of eggs laid in a clutch (either 0 [0/1 or 0/2], 0.5 [1/2], or 1 [1/1 or 2/2]), and 3) fledging success, the number of chicks that survived and left the nest successfully over the total number of chicks hatched in a clutch, again either 0, 0.5, or 1 (Table S1). To assess fledging success, we restricted our analysis to nests with naturally fledging chicks (i.e., nests that did not receive any interventions such as supplementary feeding or rehabilitation).

Covariates

In 2022, we collected data for 3 nest box variables, 6 habitat variables, and one additional breeding variable to investigate how these were related to nest box selection for breeding, hatching success, and fledging success (Table S1). Each variable was shown to be a relevant predictor for nest box selection and breeding success in previous studies on little penguins and other penguin species (Braidwood et al. 2011, Ratz 2019, Clitheroe 2021, Colombelli-Négrel and Iasiello 2023). The 3 nest box variables included 1) approximate nest box age, as used for the tick occupancy models, 2) nest box volume, where length × width × height measurements were recorded for each nest box (measurements were taken from the outside of the nest box to minimize additional disturbance to birds inside the boxes), and 3) nest box entrance type, which was categorized as either a tunnel or no tunnel design (Figure S1).

We recorded 6 habitat variables for each nest box. We categorized vegetation height as in the tick occupancy models and compared photographs of a random subset of nest boxes between the 2022 and 2023 seasons to confirm that vegetation height did not change substantially between the years of study. We measured the aspect of the nest box entrance using the Compass application on an Apple smartphone (Apple, Cupertino, CA, USA), with the device placed on top of the nest box to take the measurement. We categorized nest boxes as either north or south facing (north = 271–90 degrees; south = 91–270 degrees) to test whether exposure to different wind conditions (colder, southerly winds or warmer, prevailing northwesterly winds) may influence box selection and breeding success. We recorded slope of the terrain, measured in degrees, using an Abney level directly adjacent to the nest

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box and collected GPS waypoints for each nest box. We calculated the shortest linear distance to the nearest neighboring nest box and the shortest linear distance from the shoreline to each nest box in ArcGIS Pro (Esri) using Google satellite imagery (Google, Mountain View, CA, USA) to delineate the shoreline.

We also included week of egg laying in models examining hatching and fledging success to explore the potential influence of unexplained variation in success, beyond what nest box and habitat characteristics could explain (Table S1). We assumed the week of egg laying was the week before the first observation of eggs during weekly monitoring, which occurred on a Monday or Tuesday. We also included the probability of tick occupancy as a predictor for fledging success.

Nest box selection, hatching success, and fledging success

We used generalized linear mixed-effects models (GLMM) to investigate how nest box selection for breeding, hatching success, and fledging success response variables were related to terrestrial habitat and nest box characteristics, tick presence, and week of egg laying. We constructed models using the lme4 1.1.35.4 (Bates et al. 2015) and glmmTMB 1.1.9 packages (Brooks et al. 2017) in RStudio (R x64 version 4.3.3; R Core Team 2023). Our use of GLMMs enabled us to include nest box as a random effect and to model non-normal response types, such as little penguin breeding parameters that were binary or represented proportions; we used binomial distributions for the nest box selection for breeding models and specified a logit link function. Hatching success and fledging success models were initially overdispersed, so we used a beta-binomial distribution instead (Harrison 2015). In all models, we included season (year) as a fixed effect and nest box ID as a random effect to account for repeated sampling. Season, nest box age, nest box entrance type, vegetation height, and aspect were factors with multiple levels. We log-transformed distance to shore and distance to nearest nest box to normalize the relationship between distance and the response variables. To fix model convergence warnings, as these variables were on largely different scales, we centered and scaled slope, distance to shore, distance to nearest nest box, nest box volume, tick occupancy, and week of egg laying, transforming the data to have a mean of 0 and standard deviation of 1. We examined all variables for multicollinearity using variance inflation factor (VIF) analyses with the function vif from the car 3.1.2 package (Fox and Weisberg 2019). Additionally, we used generalized variance inflation factor (GVIF) analyses for assessing collinearity of categorical variables and a threshold of VIF or GVIF > 5 to indicate concerning multicollinearity (Fox and Monette 1992, Kim 2019). Following VIF analyses, we included only variables that were orthogonal (Table S1) in models together.

We formulated sets of *a priori* candidate models for each breeding response variable, with 29 models for nest box selection for breeding (Table S3), 28 for hatching success (Table S4), and 35 for fledging success (Table S5). We developed the sets of candidate models with an exploratory approach, based on what we considered to be plausible, biologically relevant representations of how the system operates. Our approach allowed us to focus on combinations of predictors that were likely to be meaningful, while avoiding overly complex or redundant models. The candidate models tested combinations of main effects and interactions between some of these effects. We evaluated the interaction between aspect and nest box entrance type in our nest box selection and hatching and fledging success models to explore whether the effect of entrance type (tunnel vs. no tunnel) varied depending on the direction the nest box faced, as both factors could influence microclimate and exposure. We also evaluated the interaction between week of egg laying and season in our hatching and fledging success models to determine whether the influence of timing on breeding outcomes varied by year, potentially reflecting interannual differences in environmental conditions. Lastly, we evaluated interactions between tick occupancy and slope, and tick occupancy and vegetation height in our fledging success models to explore whether the effect of tick occupancy varied with factors that may influence drainage, shading, and microclimate of nest boxes. We used AIC and associated weights to determine the most parsimonious model and deemed models with a ΔAIC < 2 as competitive with similar explanatory power (Anderson 2008). We evaluated the fit of the most parsimonious candidate models for each

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response variable using the DHARMa 0.4.6 package (Hartig 2018), simulated and plotted model residuals from each model (Figures S2–S4), and tested for dispersion, uniformity, and zero inflation.

RESULTS

Tick occupancy

The most frequent tick score recorded during weekly surveys was 0, followed by 1 and then 2 (Figure S5). The greatest average tick score for a nest box across the 19 survey weeks was 0.83, and the least was 0. The greatest average tick score across all nest boxes in a week was 0.37 in week 1, while the least was 0.02 in week 19, reflecting the general trend observed with presence of ticks in these weekly scores decreasing over the breeding season (Figure S6). The selected single-season occupancy model indicated that tick occupancy at little penguin nest boxes was influenced by nest box age (Figure 2A) and mean penguin presence (Figure 2B), while tick detection was influenced by daily penguin presence and previous weekly mean temperature (Figure 2C; Table S6). The next best model had a ΔAIC of 3.58 (Table S6) and a goodness-of-fit test indicated the top model fit the data ($\hat{c}$ = 0.99, $P = 0.15$).

Nest boxes installed from 2020 onwards showed the least tick occupancy (Figure 2A), and confidence intervals on the post-2020 coefficient did not overlap zero ($\beta = -1.75$ [95% CI = −2.71, −0.80]; Table S7), indicating strong evidence for a reduction in tick presence in newer boxes. The probability of tick occupancy for nest boxes installed between 2000–2020 did not differ from the reference (pre-2000), with confidence intervals on the 2000–2020 coefficient overlapping zero ($\beta = -0.43$ [95% CI = −1.39, 0.52]; Table S7). Probability of tick occupancy was greater in nest boxes with a higher mean penguin presence ($\beta = 3.28$ [95% CI = 1.13, 5.44]; Table S7; Figure 2B). Tick detection probability decreased with increasing mean temperatures in the week before each survey date ($\beta = -0.10$ [95% CI = −0.14, −0.07]), and was greater for nest boxes with penguins (adults or chicks) present ($\beta = 1.77$ [95% CI = 1.47, 2.08]) compared to empty boxes ($\beta = -0.87$ [95% CI = −1.62, −1.12]; Figure 2C; Table S7). Our intensive

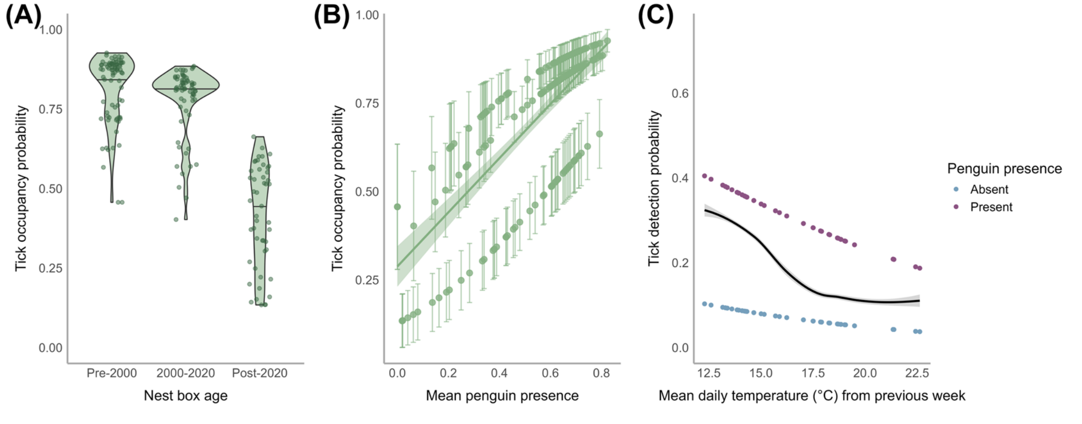

FIGURE 2 Tick occupancy probability across 194 little penguin nest boxes during the 2023 breeding season (23 August 2023–26 February 2024) at Pōhatu on South Island, New Zealand, in relation to nest box age (A), mean penguin presence across the 2022 and 2023 breeding seasons (B), and tick detection probability in relation to mean daily temperature (°C) from the previous week (C). Three levels of nest box age are shown: pre-2000 ($n = 79$), 2000–2020 ($n = 66$), and post-2020 ($n = 49$), and the colored shading in A indicates the density of data points across tick occupancy probability values. The error bars in B indicate the standard error of the tick occupancy estimates based on the best-supported occupancy model, and the shading in B and C indicates the associated 95% confidence intervals.

tick surveys supported our model findings, showing more ticks detected in occupied boxes compared to empty ones (Table S8). Our intensive surveys also highlighted the low likelihood that the 0 scores during weekly monitoring were true 0 s; when we increased search effort, we found ticks in 57.4% of the surveyed boxes previously recorded as having 0 ticks (Table S8).

Nest box selection for breeding

Across 194 nest boxes, there were 164 boxes used for breeding and 30 boxes unused for breeding in the 2022 season (Figure S7), and 149 boxes used for breeding and 45 boxes unused for breeding in the 2023 season (Figure S8). Our best supported model for little penguin nest box selection for breeding included distance to nearest nest box (in meters, log scale), nest box age, nest box volume, season, and the random effect of nest box ID (Table 1). The variance of the random intercept for nest box ID was estimated at 1.579 (SD = 1.256).

Log distance to nearest nest box had a positive influence on likelihood of nest box selection for breeding, with little penguins more likely to breed in more isolated boxes (>90% probability of breeding in nest boxes that were 10 m from a neighbor in both seasons; Table 2; Figure 3A). Regarding nest box age, observations from 2022 and

TABLE 1 Model selection of the top 3 candidate models describing little penguin nest box selection for breeding during the 2022 and 2023 breeding seasons (22 August 2022–23 February 2023 and 23 August 2023–26 February 2024, respectively) at Pōhatu on South Island, New Zealand. The null model is also shown for comparison. All models include nest box ID as a random effect. We show the difference in Akaike Information Criterion values between each model and the best-supported model (ΔAIC), the number of parameters in the model (*K*), and the proportion of variance explained by the model (R^2).

Model		ΔAIC	Weight	*K*	R^2
1	Nest box age + log (distance to nearest nest box) + nest box volume + season	0.00[a]	0.77	6	0.42
2	Nest box age + nest box volume + season	4.59	0.08	5	0.32
3	Nest box age + nest box volume + nest box entrance type + aspect + season	5.44	0.05	7	0.32
28	1 (null model)	27.46	<0.01	1	0.25

[a]Lowest AIC score = 354.48.

TABLE 2 Model coefficients, confidence intervals (CI), standard error (SE), and *P* values within the best-supported model to describe little penguin nest box selection for breeding during the 2022 and 2023 breeding seasons (22 August 2022–23 February 2023 and 23 August 2023–26 February 2024, respectively) at Pōhatu on South Island, New Zealand.

Variable	Estimate (lower 95% CI, upper 95% CI)	SE	*P*
Intercept: Nest box age (pre-2000), season (2022)	2.33 (1.45, 3.21)	0.45	<0.01
Nest box age (2000–2020)	0.75 (−0.16, 1.67)	0.47	0.11
Nest box age (post-2020)	−0.92 (−1.86, 0.01)	0.48	0.05
Log distance to nearest nest box	0.47 (0.10, 0.82)	0.19	0.01
Nest box volume	0.36 (−0.10, 0.82)	0.23	0.12
Season (2023)	−0.59 (−1.20, 0.02)	0.31	0.06

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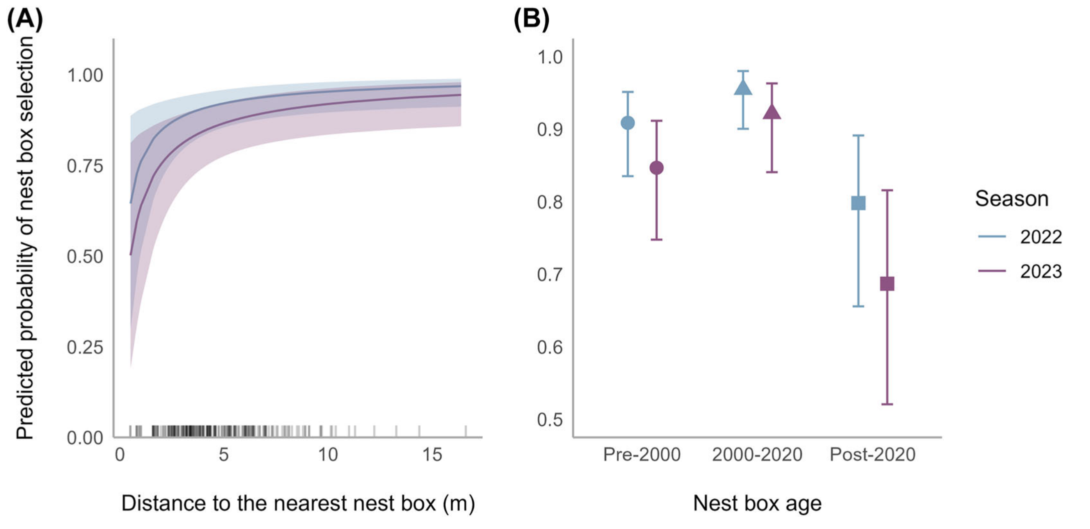

FIGURE 3 Little penguin predicted probability of nest box selection for breeding at 194 nest boxes at Pōhatu on South Island, New Zealand, in relation to distance to nearest nest box (A) and nest box age (B) during the 2022 and 2023 breeding seasons (22 August 2022–23 February 2023 and 23 August 2023–26 February 2024, respectively). Error bars and colored shading indicate the associated 95% confidence intervals. The bars at the bottom of A indicate observed distance values. Three levels of nest box age are shown: pre-2000 ($n = 79$), 2000–2020 ($n = 66$), and post-2020 ($n = 49$). Predicted probabilities are based on the best supported model, which included nest box age, nest box volume, distance to nearest nest box, and season as predictor variables.

2023 indicated that nest boxes installed between 2000–2020 were more frequently selected for breeding (88.8%), followed by pre-2000 (82.8%), and then post-2020 (69.5%). Our best-supported model suggested that selection was lowest for nest boxes installed after 2020, but confidence intervals around the coefficient were wide and overlapped 0 (Table 2; Figure 3B). The variable for season also had confidence intervals overlapping zero in the selected model ($\beta = -0.59$ [95% CI = −1.20, 0.02]; Table 2). Despite the nest box volume variable additionally having confidence intervals overlapping zero ($\beta = 0.36$ [95% CI = −0.10, 0.82]; Table 2), with uncertainty about the direction or magnitude of its effect, its inclusion in all top candidate models based on AIC and model weights indicates that it contributes to explaining variation in little penguin nest box selection for breeding relative to other models.

Hatching success

From 170 clutches in the 2022 breeding season across 194 nest boxes, 26 were unsuccessful in hatching, 30 were partially successful with 1 out of 2 eggs hatching, and 114 were fully successful (Figure S9). From 154 clutches in the 2023 breeding season, 16 were unsuccessful, 23 were partially successful, and 115 were fully successful (Figure S10). There were 3 closely competing models for understanding little penguin hatching success (Table S9), all of which included season, nest box volume, and week of egg laying. Despite nest box volume having confidence intervals overlapping zero in all 3 models (e.g., model 1: $\beta = 0.02$ [95% CI = −0.32, 0.29]; Table S10), its inclusion in all top candidate models based on AIC indicates that it contributes to explaining variation in little penguin hatching success relative to other models. Season was included in all candidate models to account for the inclusion of 2 seasons of data, but there was no evidence that it influenced hatching success, with confidence intervals overlapping zero (model 1: $\beta = 0.27$ [95% CI = −0.22, 0.77]; Table S10). Week of egg laying had a negative influence

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on hatching success, with earlier lay weeks associated with greater hatching success (model 1: $\beta = -0.11$ [95% CI = −0.19, −0.02]; Table S10).

Despite the top 3 models competing closely (Table S9), we selected the most parsimonious model (model 2) because the entrance type did not influence hatching success when included in model 1 ($\beta = 0.43$ [95% CI = −0.16, 1.02]), and there was a lack of support for an interaction between week of egg laying and season as included in model 3 ($\beta = -0.05$ [95% CI = −0.22, 0.11]; Table S10). Using predictions generated from model 2, hatching success was greatest for those nests where eggs were laid at the end of August, declining from approximately 0.90 to below 0.75 for those nests where eggs were laid in December, a trend observed in 2022 and 2023 (Figure 4). The random intercept for nest box ID had a variance of 0.799 (SD = 0.894).

Fledging success

Across the 194 nest boxes, there were 145 clutches with chicks in 2022, and 138 in 2023 (Figures S11–S12). The exclusion of clutches that received interventions resulted in data from 95 clutches in 2022 and 129 clutches in 2023. Of the remaining dataset, there were 24 unsuccessful clutches in 2022 compared to 9 in 2023, 11 clutches where 1 out of 2 chicks fledged successfully in 2022 compared to 15 in 2023, and 59 completely successful clutches in 2022 compared to 104 in 2023.

There were 2 closely competing models for understanding little penguin fledging success (Table 3), both of which included season, nest box volume, and week of egg laying. We chose model 2 for generating predictions based on parsimony and the lack of strong evidence for an effect of entrance type when included in models. The random intercept for nest box ID had a variance of <0.001 (SD ≤ 0.001). The influence of week of egg laying on fledging success varied by season, with fledging success greater in 2023 compared to 2022 (Figure 5). In 2022, fledging success decreased rapidly with later lay weeks, whereas fledging success was fairly constant and high in 2023 (Figure 5). Nest box volume had confidence intervals overlapping zero in both models (e.g., model 1: $\beta = 0.13$ [95% CI = −0.21, 0.46]; Table 4); however, its inclusion in the top four candidate models based on AIC indicates that it likely contributes to explaining variation in little penguin fledging success.

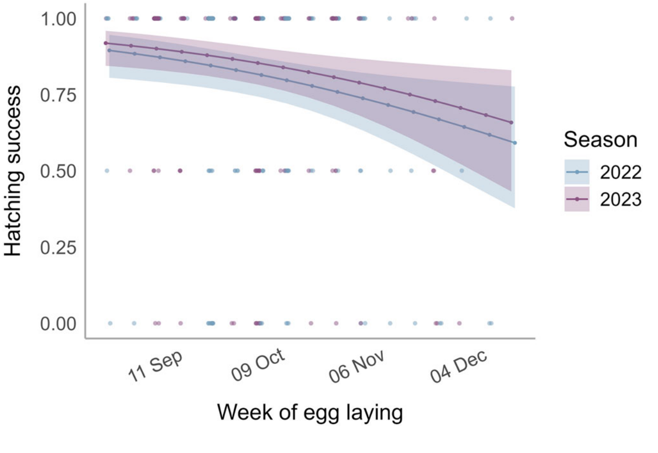

FIGURE 4 Relationship between predicted little penguin hatching success and week of egg laying, for the 2022 season (blue; 22 August 2022–23 February 2023) and 2023 season (purple; 23 August 2023–26 February 2024) at Pōhatu on South Island, New Zealand. The plotted line shows the predicted probability of hatching success based on the best supported model, with the shaded area indicating the 95% confidence intervals. Also plotted are the raw data points.

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TABLE 3 Model selection of the top 5 candidate models for describing fledging success of little penguins at Pōhatu on South Island, New Zealand, for the 2022 and 2023 breeding seasons (22 August 2022–23 February 2023 and 23 August 2023–26 February 2024, respectively). The null model is also included for comparison. All models include nest box ID as a random effect. We show the difference in Akaike Information Criterion values between each model and the best-supported model (ΔAIC), the number of parameters in the model (K), and the proportion of variance explained by the model (R^2).

Model		ΔAIC	Weight	K	R^2
1	Nest box volume + nest box entrance type + week of egg laying × season	0.00[a]	0.33	6	0.81
2	Nest box volume + week of egg laying × season	0.68	0.23	5	0.79
3	Nest box volume + nest box entrance type + week of egg laying + season	2.26	0.11	5	0.78
4	Nest box volume + nest box entrance type + season	3.24	0.07	4	0.75
5	Nest box volume + week of egg laying + season	3.74	0.05	4	0.73
34	1 (null model)	31.90	<0.01	1	0.32

[a]Lowest AIC score = 319.51.

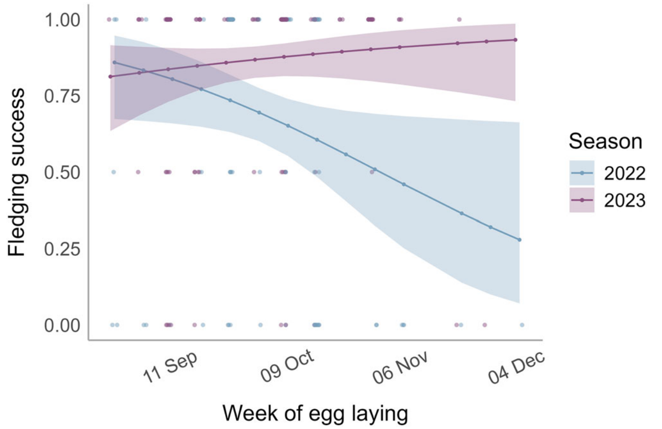

FIGURE 5 Relationship between predicted little penguin fledging success and week of egg laying for the 2022 season (blue; 22 August 2022–23 February 2023) and 2023 season (purple; 23 August 2023–26 February 2024) at Pōhatu on South Island, New Zealand. The plotted lines and dots show the predicted probability of fledging success based on the selected model, with the shaded area and bars indicating the 95% confidence intervals. Also plotted are the raw data points.

DISCUSSION

Our study provides insights into how nest box placement and possibly nest box age influence little penguin nest box selection for breeding at Pōhatu/Flea Bay, and whether these and other nest box characteristics, along with breeding timing and tick abundance, affect hatching and fledging success. Penguins were more likely to select more isolated nest boxes for breeding, with a >75% breeding probability at nest boxes >2 m from a neighbor, and may be less likely to breed in newer nest boxes. Hatching and fledging success were primarily influenced by week of egg laying. Results support our prediction that success would decline with week of egg laying, though this trend was only observed for fledging success in one breeding season. Additionally, we found that tick presence was lower in newer nest boxes and in those with penguins absent, but contrary to our hypothesis and previous work

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TABLE 4 Model coefficients, confidence intervals (CI), standard error (SE), and *P* values for the top 3 candidate models for fledging success of little penguins at Pōhatu on South Island, New Zealand, across the 2022 and 2023 breeding seasons (22 August 2022–23 February 2023 and 23 August 2023–26 February 2024, respectively).

Model	Variable	Estimate (Lower 95% CI, Upper 95% CI)	SE	*P*
1	Intercept: Nest box entrance type (no tunnel), season (2022)	0.42 (−0.07, 0.92)	0.25	0.09
	Nest box entrance type (tunnel)	0.51 (−0.11, 1.13)	0.31	0.10
	Nest box volume	0.13 (−0.21, 0.46)	0.17	0.46
	Week of egg laying	−0.58 (−1.16, 0.01)	0.30	0.05
	Season (2023)	1.33 (0.69, 1.97)	0.33	<0.01
	Week of egg laying × season (2023)	0.82 (0.03, 1.62)	0.41	0.04
2	Intercept: Season (2022)	0.65 (0.24, 1.07)	0.21	<0.01
	Nest box volume	0.18 (−0.16, 0.51)	0.17	0.31
	Week of egg laying	−0.62 (−1.20, −0.04)	0.30	0.04
	Season (2023)	1.33 (0.69, 1.96)	0.32	<0.01
	Week of egg laying × season (2023)	0.88 (0.10, 1.67)	0.40	0.03
3	Intercept: Nest box entrance type (no tunnel), season (2022)	0.48 (0.06, 1.06)	0.25	0.05
	Week of egg laying	−0.14 (−0.48, 0.30)	0.19	0.46
	Nest box entrance type (tunnel)	0.57 (−0.05, 1.19)	0.31	0.06
	Season (2023)	1.13 (0.48, 1.68)	0.30	<0.01
	Nest box volume	0.13 (−0.17, 0.51)	0.17	0.43

(Sanz-Aguilar et al. 2020), observed tick presence was not related to fledging success. Together, these findings provide valuable colony-scale insights into little penguin breeding ecology, offering immediate recommendations for conservation at Pōhatu whilst also contributing to the broader body of research on little penguins (Johannesen et al. 2002, Jansen van Rensburg 2010, Allen et al. 2011, Clitheroe 2021).

The selection of nest boxes farther from neighbors potentially reflects an avoidance of intraspecific competition, social interactions, or cuckoldry from non-partners during breeding (Chiaradia 1999). Though little penguins in a previous study at Penguin Island were found to have a greater proportion of breeding nests within 5 m of neighboring nests (Clitheroe 2021), little penguins nesting in rock-based burrows across colonies in South Australia were found to have the highest success when they had fewer neighbors, suggesting a potential benefit to selecting nest sites with fewer conspecifics close by (Colombelli-Négrel 2019). Such selection for nesting sites with reduced intra-specific competition is often important for non-burrowing penguin species, such as the Magellanic penguin (*Spheniscus magellanicus*; Stokes and Boersma 2000), possibly because of the greater prevalence of fights, non-breeding prospectors, and nest predation in high-density areas (Stokes and Boersma 2000, Sherley et al. 2014). While proximity to neighboring boxes was the most evident factor influencing little penguin nest box selection for breeding in the present study, our observations across 2022 and 2023 suggest newer nest boxes had a lower occurrence of breeding events, despite this trend not being conclusive in our models. New nest boxes often take time to be used, as penguins typically show high fidelity to previous nest sites rather than seeking new ones, particularly if their previous breeding was successful (Reilly and Cullen 1981, Rogers and Knight 2006, Mariné and Bernard 2020). For instance, at Otago Peninsula, New Zealand, 72% of birds returned to their previous breeding nest, and nest fidelity increased with individual breeding success in the previous year (Johannesen et al. 2002). The lower use of newer nest boxes has been further observed in research conducted at Pilots Beach, New Zealand (Ratz 2019) and Phillip Island, Australia (Sutherland and Dann 2014), where older nest boxes (deployed for >7 years) were preferentially used for breeding. However, to draw more definitive conclusions on such patterns of newer versus older nest box use for breeding at Pōhatu, and to better understand the influence of other characteristics investigated in our models but not found to have large effects, a longer period of data collection will be required. With only 2 breeding seasons of data in the present study, we may not have captured the full extent of factors influencing selection. Additionally, incorporating spatial components to understand patterns of nest site selection across the colony will be important for providing further insights into how little penguins use their terrestrial environment, but this was beyond the scope of the present study.

Our study differs from previous work by also examining the effect of tick presence on fledging success. The use of occupancy modeling allowed us to account for imperfect detection of ticks, addressing a key limitation in traditional species monitoring approaches (MacKenzie et al. 2002). From the occupancy models, we found ticks had lower occupancy in newer nest boxes, potentially because they had fewer cracks and crevices, which can provide ideal habitat for the ticks (Niebuhr et al. 2013). Additionally, as observed in previous research and suggested in our study, penguins have a high likelihood of breeding in older nest boxes (Sutherland and Dann 2014, Ratz 2019), which may result in more tick presence at these older boxes, as these ectoparasites rely on feeding on blood from the penguins (Jansen van Rensburg 2010). When penguins are absent from nest boxes for prolonged periods, however, ticks can remain dormant in the soil, where nest boxes with older nest material may be more established for them to live in (Espinaze Pardo 2019). The absence of an observed relationship between tick presence and fledging success in this study may be a result of several factors. For example, the intensity of tick infestations may not have reached a threshold necessary to influence breeding success during the study period (Jansen van Rensburg 2010). Additionally, the nature of our occupancy model, with nest box age being a categorical predictor, meant that occupancy estimates for nest boxes were partially grouped into 3 levels, which may have influenced the relationships that could be observed. With the post-2020 nest box age class being the only one in which we could be confident in the estimated patterns of tick occupancy, we acknowledge that uncertainty in tick occupancy estimates for the older nest boxes may influence our interpretation of the relationship between tick occupancy and fledging success. It is also likely that the effects of ticks may manifest in more subtle ways, through sub-lethal impacts such as reduced chick growth rates or compromised immune function (Ramos et al. 2001, Jansen van Rensburg 2010), which were not assessed in this study. Furthermore, the intensive surveys we conducted revealed that ticks were often present even in cases where they were undetected during weekly checks. As a result, the cases where nest boxes were scored as 0 are likely to represent false negatives, meaning model outputs should be interpreted cautiously and can be considered conservative estimates of tick presence, highlighting the need for improved methods for detecting and estimating tick load.

While little penguin nest box selection for breeding may be influenced by specific nest box characteristics, hatching and fledging success appeared to be more strongly influenced by week of egg laying. The observed decline in hatching success with week of egg laying across breeding seasons is consistent with the idea that early breeders benefit from better conditions earlier in the season, such as more abundant food resources or more favorable weather (Buckley and Buckley 1980). For many seabirds, this is a prevailing trend, where earlier lay date is associated with increased breeding success (Pezzo et al. 2001, Paredes et al. 2002, Cannell et al. 2012). Fledging success was also influenced by week of egg laying in our study, but there was a clear difference between seasons. The strong decline in fledging success with later lay week during the 2022 season is likely attributed again to external environmental factors, notably the marine heatwave event that occurred across New Zealand over the 2022 breeding season (NIWA 2022). It is well understood that prolonged periods of elevated sea surface temperatures can disrupt marine ecosystems, leading to reduced prey availability (Chiaradia and Kerry 1999;

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Cannell et al. 2012, 2024; Carroll et al. 2015). The 2022 event indeed coincided with a period of increased chick starvation and mortality at Pōhatu, where those hatched later likely overlapped with times of decreased prey availability due to the warmer water temperatures, leading to nest abandonment (Helps Pōhatu Conservation Trust, personal communication). In contrast, fledging success during 2023 saw a slight increase with later week of egg laying. Some previous studies have observed similar scenarios, with breeding success improving with later relative week of egg laying at Pōhatu (Allen et al. 2011). An explanation for the lack of a decrease in fledging success with later week of egg laying could be that adults breeding later may have better body condition, having spent longer feeding prior to laying eggs and thus may be less energetically stressed (Allen et al. 2011). Additionally, fledging success is likely influenced by other factors not assessed by our models, such as the length of the guard stage, which plays a crucial role in chick survival (Chiaradia and Kerry 1999, Allen et al. 2011), the number of short and long foraging trips throughout the chick rearing period (Saraux et al. 2011), and the quality of parental care (Chiaradia and Kerry 1999, Saraux et al. 2011, Riechert and Becker 2017), which could also affect hatching success. Conversely, even though intervention during the 2023 season was minimal in comparison to 2022, this may have masked a potential decrease in fledging success if the natural outcome of those chicks were to dictate the relationship observed. The clear difference in fledging success patterns between the 2 seasons highlights the critical influence of broader environmental conditions on breeding outcomes and success, beyond the scope of habitat or nest box characteristics (Carroll et al. 2015). This influence is particularly apparent in years of extreme environmental conditions, and these are likely to only increase in frequency in the coming years (Chiaradia and Kerry 1999, Robinson et al. 2005, Ummenhofer and Meehl 2017, Cannell et al. 2024).

Our work provides an important step towards understanding little penguin breeding ecology, particularly the relationships between nest box selection, environmental variability, and ectoparasites. While the 2022 and 2023 breeding seasons provided valuable environmental comparisons, longer-term data would enhance our understanding of interannual variability and its effects on reproductive success (Inchausti et al. 2003, Carroll et al. 2015, Cannell et al. 2024), and any effects of parasite load. As more years of data become available, further research at the colony scale, inclusive of natural burrows, is recommended to better capture long-term patterns and trends at the interplay among these factors. Incorporating measures of the broader environmental conditions into models would help clarify their influence on breeding success and overall fitness (Carroll et al. 2015, Cannell et al. 2024). While not the primary focus of our study, the inclusion of week of egg laying highlights the importance of exploring these factors further. Our study also establishes a baseline understanding of tick presence at nest boxes at Pōhatu, providing a foundation for refining methodologies to define thresholds of tick occupancy and guide management strategies. Future research should explore the effects of tick presence through manipulative experiments and continued long-term monitoring to determine their potential impacts on little penguin survival and breeding success. Such studies will be crucial for assessing the broader ecological role of ectoparasites in this system (Jansen van Rensburg 2010).

MANAGEMENT IMPLICATIONS

Our results provide information for colony managers to refine nest box placement and offer insights into the mechanisms influencing breeding success at this little penguin colony. We suggest that when new nest boxes are installed, these should be placed at least 2 m apart from neighboring boxes to increase their likelihood of being selected for breeding; however, newly installed nest boxes may take longer to become occupied for breeding, regardless of their placement or design. Therefore, where possible, preserving older nest boxes could be beneficial, as observations suggest these may be used more frequently for breeding, likely owing to breeding nest fidelity. Although ticks were also more commonly found in these older boxes, further research is required to fully understand the relationship between ticks and breeding success or chick survival before direct management recommendations can be made. Developing standardized survey methods and continuing to incorporate tick monitoring into ongoing management efforts is an important first step.

The strong influence of lay timing on hatching and fledging success, and the clear difference in fledging success patterns between the 2 breeding seasons, highlight the important role of external environmental conditions on breeding success. Ongoing monitoring will be critical to better understand these patterns, with long-term data necessary to enhance our understanding of interannual variability in breeding outcomes for little penguins. It will be important to integrate continued monitoring with wider ongoing conservation efforts to refine nest box placement and enhance breeding success.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Monitoring and research at the Pōhatu colony is permitted under a Department of Conservation New Zealand Wildlife Act Authority granted to the Helps Pōhatu Conservation Trust (94750-FAU) and the University of Canterbury (103681-FAU). All handling of animals was approved by the University of Canterbury's Animal Ethics Committee (protocol AEC2023-02R).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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