

Human activities at night negatively impact Little Penguin (*Eudyptula minor*) numbers and behaviours

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The presence of humans within the natural environment is increasing worldwide. Assessing the impact of such activities on wildlife is crucial for declining populations where human disturbance adds to existing pressures. Here, we investigated how human activities at night influenced Little Penguin *Eudyptula minor* numbers and behaviours (specifically return time, number of vocalizations and time spent in vigilance) on Granite Island, a declining population in South Australia, Australia. We combined data from regular night surveys with continuous video and audio monitoring to assess the impact of human activities on the Little Penguins. The use of white light (i.e. from torches or camera flashes) by people was the most frequent activity recorded at night (recorded on 65% of the monitored nights). Fewer penguins were found on land at night when Dogs *Canis lupus familiaris* were present, but not when the number of people increased, when concerts occurred, or when white lights were used. Little Penguins were observed more often returning late from sea at night when Dogs were present and when white lights were used, but not when concerts occurred. An increase in penguin vocalizations at night correlated with the presence of Dogs and the occurrence of concerts, whereas penguins vocalized less when white lights were used. The time Little Penguins spent in vigilance did not correlate with any of the disturbances analysed. Our study also highlights the impact of coronavirus disease 2019 (COVID-19) on wildlife, as the occurrence of human activities increased significantly following the implementation of the COVID-19 health protection measures. These results add to a growing body of literature suggesting that human activities on land, and their consequent disturbance(s), may affect the numbers and behaviours of wildlife and that appropriate measures need to be developed to limit such impacts.

Keywords: anthropogenic impact, conservation, *Eudyptula minor*, management strategies, seabirds, tourism.

Human presence can disturb wildlife in many ways. Over the years, the number of locations and frequency of human visitation to natural spaces has increased significantly worldwide (Belsky *et al.* 2012, Geffroy *et al.* 2015). There are growing concerns that animals respond to this increase in human presence by increasing their time spent in avoidance or antipredator behaviour(s), thereby reducing time spent performing other behaviours that may be critical for their survival (Frid &

Dill 2002, Dyck & Baydack 2004, Ciuti *et al.* 2012, Larsen *et al.* 2014, Gaynor *et al.* 2018, Scheijen *et al.* 2021). For example, a study on the endangered Red-crowned Crane *Grus japonensis* showed that both the duration and the frequency of vigilant behaviour increased significantly in the presence of tourists (Li *et al.* 2017), which would reduce their foraging time and efficiency. The reduction in foraging time and efficiency may have a negative impact on individual fitness and eventually breeding success (Burger 1991, Verhulst *et al.* 2001, Schummer & Eddleman 2003). Evidently, further research on how human presence

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influences wildlife is required to help limit any potential negative impact that we as humans may have on nature.

Different human activities can have differing impacts on animals and create various disturbances. Some of the major concerns are mostly centred around the number of people present at a location (de la Torre *et al.* 2000, Dixon *et al.* 2021), their distance from wildlife (Holmes *et al.* 2005, Holmes 2007, Allbrook & Quinn 2020) or the noise levels produced (Buxton *et al.* 2017, Ortiz-Jiménez *et al.* 2021). Human activities around wildlife may also lead to the extensive use of artificial white lights (see Wolf & Croft 2012, Rodríguez *et al.* 2018), when searching for nocturnal animals for example, or an increase in individuals walking their Dogs *Canis lupus familiaris* around wildlife (e.g. Miller *et al.* 2001, Cortés *et al.* 2021, Beasley *et al.* 2022). Furthermore, the resulting disturbance(s) created from these human activities often do not occur independently. Noise disturbance, for example, is rarely isolated from other forms of disturbance, such as the presence of a large number of humans, their distance from wildlife, or the presence of domestic animals including Dogs (reviewed in Shannon *et al.* 2016). Combined, these human activities, and their consequent disturbance(s) on wildlife, can lead to prolonged symptoms of stress and negatively influence an individual's fitness or its reproductive success (Müllner *et al.* 2004, Ellenberg *et al.* 2006, 2007, Mortimer & Lill 2007, French *et al.* 2011, Stier *et al.* 2019), which in turn can lead to population declines (Møller 2008).

Little Penguins *Eudyptula minor* are highly susceptible to human disturbance (Klomp *et al.* 1991, Weerheim *et al.* 2003, Giling *et al.* 2008, Larcombe 2015, Carroll *et al.* 2016, Chiew *et al.* 2020; see also Seddon & Ellenberg 2008, Colombelli-Négrel & Katsis 2021), probably because they often nest close to urban development, and are regularly the target of tourism being the only penguin species that breeds on the mainland of Australia. Although globally classified as 'Least Concern' (BirdLife International 2020), Little Penguin population declines up to 80% have been recorded in South Australia over the past two decades (Wiebkin 2011, DEWNR 2016). Multiple factors are believed to be responsible for these declines, including predation on land and at sea, starvation and climate change (Wiebkin 2011, DEWNR 2016, Colombelli-Négrel & Tomo 2017,

Johnson & Colombelli-Négrel 2021, Colombelli-Négrel *et al.* 2022). Assessing human disturbance on wildlife is especially critical for declining populations that are already under threat from a variety of factors (Bell *et al.* 2020), such as in the case for Little Penguins in South Australia.

The Granite Island (South Australia, Australia) Little Penguin population declined from c. 1500 adults in 2001 to 30 adults in 2019 (Colombelli-Négrel 2020) through a combination of factors, including predation at sea by Long-nosed Fur Seals *Arctocephalus forsteri* (Bool *et al.* 2007, Reinhold 2014), predation on land by native Water-rats *Hydromys chrysogaster* and introduced Black Rats *Rattus rattus* (Bool *et al.* 2007; see also Colombelli-Négrel 2015, Colombelli-Négrel & Tomo 2017), climate change impacts on breeding success (i.e. variation in marine temperatures and wind speeds; Johnson & Colombelli-Négrel 2021) and low food availability, probably due to reduced river outflow to the ocean from the Murray Mouth (Colombelli-Négrel *et al.* 2022). Since its decline, the colony has experienced an increase in human activities at night from fewer than 2% of the monitored nights before 2016 to more than 23% of the monitored nights in 2018 (Colombelli-Négrel 2019). Human activities observed included unauthorized vehicles, Dogs (on or off leash), push bikes (Little Penguins were seen by tour guides before the study to be frightened by cyclists with lights) and people actively searching for penguins using white light (from torches and mobile phones; Colombelli-Négrel 2018, 2019, 2020). Reasons for this increase in human activities are unknown. It is suspected that it may be linked to a decrease in management measures, as well as an increase in the availability of smart phones (resulting in an increase in the use of white light) and in people wanting to experience wildlife on their own (i.e. not on a tour) or to take photographs for social media. The latter may be especially relevant during times of restriction, such as the coronavirus disease 2019 (COVID-19) health protection measures, when people were only allowed outside for exercise (Morse *et al.* 2020, Randler *et al.* 2020, Hochachka *et al.* 2021). Such human activities could potentially impact the long-term recovery of the penguins on this island.

Here, we combine data collected by tour guides with continuous video and audio recordings to investigate how different human activities influenced Little Penguin numbers and behaviours

(return time, number of vocalizations and time spent in vigilance) on Granite Island, South Australia. We first quantified which activities occurred most frequently and then assessed if these activities were linked with changes in penguin numbers and behaviours. We predicted that all human activities at night would correspond to a decrease in penguin vocalizations and fewer birds seen on land at night (see also Holmes 2007, Rodríguez *et al.* 2014, Buxton *et al.* 2017). We also predicted that these activities would lead to delays in penguin return time and increase the time that penguins spent in vigilance when returning to their nests (Sherwen *et al.* 2015, Buxton *et al.* 2017, Chiew *et al.* 2019).

METHODS

Study area

We collected data about penguin numbers and behaviours (return time, number of vocalizations and time spent in vigilance), as well as human activities, between June 2018 and June 2020 on the north shore of Granite Island, South Australia, Australia (35°37'S, 138°36'E; Fig. 1). Granite Island is a small island (c. 24 ha; approximately 500 m wide and 900 m long), 2.06 m above sea level and accessible at all times to pedestrians via a causeway. The island is uninhabited with a granite coastline and an open habitat dominated by indigenous grasses and patchy shrubs covering the lower areas. Long-term monitoring has shown that most Little Penguin nests are located on the northern shore of the island (Colombelli-Négrel 2015, 2020). During the October 2018 population census, 44 adult Little Penguins were recorded on the island (Colombelli-Négrel 2019). All other Little Penguin colonies previously located near Granite Island are now extinct (Colombelli-Négrel & Kleindorfer 2014). Granite Island is one of the top 10 most visited national parks in South Australia (DEWNR 2020), with c. 800000 people per year visiting the island. Dogs (on or off leash) are prohibited on the island.

Study species

Little Penguins are active at sea during the day and return to their colony at night, within approximately 30 min of sunset (Klomp & Wooller 1991). Little Penguins are highly susceptible to human

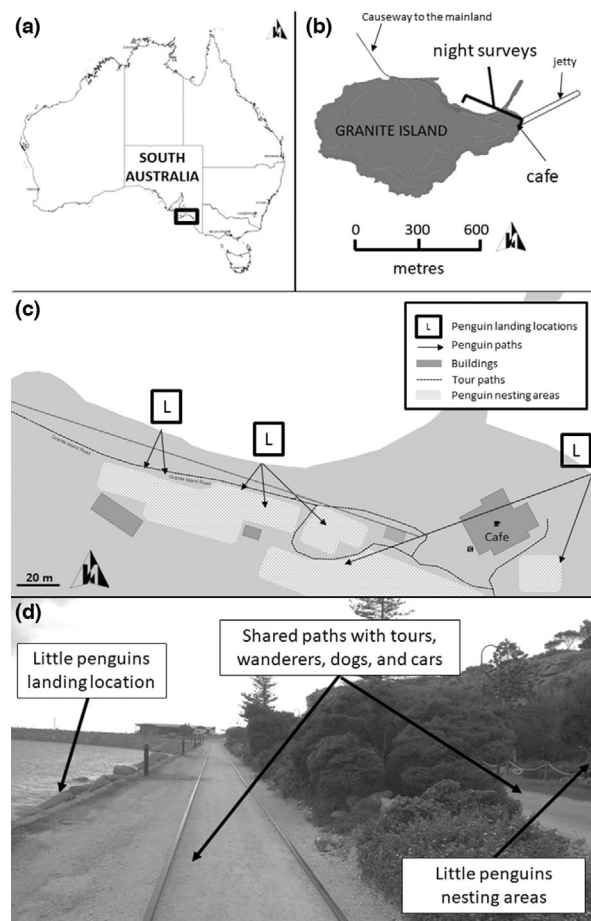


Figure 1. (a) Map of Australia with rectangle indicating the study location, Granite Island (South Australia, Australia). (b) Location of the night surveys conducted between June 2018 and June 2020 on Granite Island (South Australia, Australia). (c) Close up of the night survey location illustrating the Little Penguin landing locations, nesting areas and illuminated areas (i.e. sections of the tour path) where people interact with the penguins on the north shore of Granite Island. Night surveys occur along the tour paths, but wanderers and people walking with Dogs can be found anywhere on the penguin paths. (d) Photograph of the main night survey location illustrating one of the Little Penguin landing locations, the main nesting area, and the main illuminated paths used by people and penguins.

disturbance when they are present on land (i.e. during breeding and moulting periods; Klomp *et al.* 1991, Weerheim *et al.* 2003, Giling *et al.* 2008, Larcombe 2015, Carroll *et al.* 2016, Chiew *et al.* 2020; see also Seddon & Ellenberg 2008, Colombelli-Négrel & Katsis 2021). Little Penguins are asynchronous breeders, and on Granite Island, breeding occurs between May and February of the subsequent year (Colombelli-

Négrell 2015, 2018, Johnson & Colombelli-Négrell 2021). During incubation and the guard period (the first 2 weeks after hatching), males and females alternate between staying in the nest and foraging at sea (Chiaradia & Kerry 1999, Numata *et al.* 2000, Kemp & Dann 2001). After the guard period, both parents forage at sea until the chicks have fledged (c. 8 weeks of age; Saraux *et al.* 2011). Little Penguins are known to have a rigorous return schedule, especially during the breeding period, only to be delayed if they are unable or unwilling to return home (Chiaradia *et al.* 2007, Daniel *et al.* 2007, Rodríguez *et al.* 2016). Moulting occurs between December and April (Wiebkin 2011, Colombelli-Négrell 2018), during which adults remain within their nests for extended periods and are unable to go out to sea (Reilly & Cullen 1983). Although Little Penguins are less likely to be on land when not breeding or moulting, some still return to Granite Island outside the breeding and moulting periods to rest at night (D. Colombelli-Négrell unpubl. data).

Night surveys

We obtained nightly counts of Little Penguins as well as the occurrence and type of human activities (see methods below for the list of activities) from eight tour guides conducting regular night tours on the north shore of Granite Island. All tour guides were trained by the main senior guide (Stephen Hedges) who has 20+ years of experience observing Little Penguins on Granite Island, and the majority of the observations (94%) were completed by three of the senior guides who had 15 to 20+ years of experience working on Granite Island. These tours have been run since 2001 along a set path on the north shore, allowing visitors to observe Little Penguins returning to the island at night (Fig. 1b). Tours ran three to four nights per week all year round and lasted 1.5–2 h from sunset. All tours started with an introductory talk, away from the colony to minimize talking during the tours. Once in the colony, guides (followed by the people on the tours) slowly walked among the penguin nests to count the number of penguins and record their behaviours – there is no hiding platform on Granite Island to view the birds (see Fig. 1c and d). Penguin nests on the north shore are located within 20 m of the rocky shore where penguins arrive, and they generally arrive from

three different landing locations (whichever is closest to their nest; see Fig. 1c). Those landing locations are not ‘landing beaches’ but rocky areas where penguins have been seen to hide before crossing an illuminated and flat area that separates the landing rocks from their nests (see Fig. 1c and d). This illuminated and flat area is not protected by vegetation; penguins are therefore highly visible and exposed when crossing. This same area is used by people to wander (including those with Dogs) and by the tour guides (see Fig. 1c and d). Hence, wanderers, Dogs and people on the tours are within 20 m of the returning penguins and their nests. People on tours, however, are walking a set path and keep their distance from the birds, whereas many wanderers (including those with Dogs) are often seen closer than 1 m from the penguins. Standardized approaches to measure the Little Penguins’ ‘flee initiation distances’ (distance at which a bird flees from a perceived danger) and ‘alert distances’ (distance at which a bird becomes alert to the threat) on Granite Island showed that Little Penguins can clearly see people and alter their behaviours from 20 m away (A. Silverlake, A. Katsis & D. Colombelli-Négrell unpubl. data). When tours were not scheduled, Flinders University employed Stephen Hedges to conduct night surveys three to four nights per week (at the same frequency as the tours) to collect the same information for the same period (i.e. 1.5–2 h from sunset; Colombelli-Négrell 2020). Tours completely ceased in March 2020 as a result of the COVID-19 health protection measures but were replaced by regular Flinders University surveys to ensure continuous monitoring. Hereafter, we refer to all tours and surveys as night surveys.

During each night survey, the guide(s) or staff on duty recorded the following: (1) The total number of adult penguins seen or heard on land per night – this included those that arrived from the sea as well as those already on land (i.e. those that would have been in their nests during the day); counts were done by walking slowly and quietly back and forth along the set path of the night surveys while noting the areas where the penguins were seen on a map to avoid double counting individual birds. When several guides were on duty, they compared notes to confirm the final number of birds observed. (2) Whether the first penguin(s) seen was/were late or not (on time, late) – this was measured using the time stamp of the first bird(s) seen arriving on land from the sea; any bird

(s) first seen arriving 60 min after sunset was/were considered as late. (3) Wind speeds (obtained by the tour guides from a weather website and categorized for this study using a modified version of the Beaufort scale – calm (no wind), light (< 11 km/h), moderate (< 29 km/h), strong (< 50 km/h), gale (< 75 km/h), storm (< 102 km/h), hurricane (> 120 km/h). (4) Any human activity(ies) observed on the night – these human activities included: (i) the number of wanderers (i.e. unsupervised people) on the island, (ii) whether any Dog(s) was/were seen (yes, no) (all Dogs mentioned in this study were walked to the island by their owner(s) on or off leash and were not feral Dogs), (iii) whether people using white lights or camera flashes were seen (yes, no) – these would be people actively searching for penguins among their nests and so within less than 1 m from the penguins and included both wanderers and people on the tours as some people ignored the guidelines given by the tour guides, and (iv) the occurrence of a concert (yes, no). Concerts occurred at the café on Granite Island, which was located within the night surveys area and within 40 m from one of the main penguin landing areas (see Fig. 1c). Although these concerts often started during the late afternoon (c. 4:00 PM), they continued until late into the night, sometimes past midnight. A total of 34 concerts (4 ± 0.77 concerts per month; range 1–7) occurred during our study period between the months of November and April in both 2019 and 2020. On nights when no survey occurred but other data were collected (see below methods – infrared sensor cameras), we obtained wind speeds from the Hindmarsh Island weather station (located c. 16 km from Granite Island) via the Willy Weather website (<https://www.willyweather.co.au>) for the time the night survey would have begun if it occurred.

Automated acoustic recorders

To obtain nightly recordings of Little Penguin vocalizations, we deployed three automated acoustic recorders along the north shore between May 2019 and June 2020. The recorders were developed by the New Zealand Department of Conservation and were small (3 cm by 20 cm), light and waterproof cylinders that can record for weeks automatically with four AA batteries. We mounted the recorders to a tree trunk or pole c. 30 cm above the ground, 100 m apart. We set all

recorders to record simultaneously for 2 h every night immediately after sunset. All tracks were recorded as mono 16-bit .wav files with a sample rate of 16 kHz at 32 000 samples per second. These recorders can detect Little Penguin vocalizations within a 10-m radius (Colombelli-Négrel 2023).

We analysed all recordings with Kaleidoscope Pro v5.1.2 (Wildlife Acoustics Inc., Maynard, MA, USA). Kaleidoscope Pro uses Hidden Markov Models to detect and classify vocalizations into clusters based on their spatio-temporal similarities. Little Penguins are very territorial (Waas 1990, 1991) and vocalize mainly at night. Bray and growl calls are the most common vocalizations and are used for territory defence, mate attraction and communication between partners (Miyazaki & Waas 2003, Colombelli-Négrel & Smale 2018); hence, in this study, we focused on these calls. We constructed recognizers for Little Penguin bray and growl calls with the following parameters: (1) frequency range 50–1500 Hz, (2) minimum and maximum length of detection 0.1 and 7.5 s, respectively, and (3) maximum inter-syllable gap 0.1 s. The software accuracy was 86% on Granite Island for Little Penguin calls (Colombelli-Négrel 2023). We also manually checked a subset (10%) of recordings for accuracy using Raven Lite v2.0.1 (Cornell Lab of Ornithology, Ithaca, NY, USA) with a Hann algorithm (filter bandwidth 124 Hz, size 512 samples, time grid overlap 50, grid resolution 5.8 ms, 86.1 Hz, DTF 512 samples). These included recordings with an unusually high number of penguin calls (> 100) and recordings for which Kaleidoscope Pro found no penguin calls. We combined vocalizations from all recorders to obtain the total number of vocalizations per night.

Infrared sensor cameras

To obtain video recordings of the time Little Penguins spent in vigilance and the occurrence of human activities (i.e. the use of white lights, presence of Dogs, occurrence of concerts or numbers of wanderers) at night when the night surveys did not occur, we deployed seven infrared motion sensor cameras (Argus 2, Reolink Australia, <https://www.reolinks.com.au>) along the north shore between May 2019 and June 2020. We installed all cameras c. 30 cm above ground level. Three cameras faced landing locations and crossing zones

used by the penguins at night (determined with the help of the tour guides). The remaining four cameras were situated throughout the main area of active penguin nests at varying angles to capture the return and behaviours of the penguins as well as any potential human disturbance from human activities. We programmed all cameras to detect movements for 3 h, beginning half an hour before sunset every night. All cameras recorded audio as well as video and were set to record on the longest setting once triggered (the longest setting was 30 s; however, once triggered and if continuous movement(s) occurred, the cameras could record for up to 3 min continuously). From the recordings, we manually scored the time Little Penguins spent in vigilance (defined as the time spent stationary in an upright position, scanning the environment, or spent walking but pausing every few steps while scanning the environment) measured in seconds using the ethogram presented in Table 1. If more than one penguin was present, we averaged vigilance by the number of penguins. We then transformed the average time measured in seconds as a proportion of time (percentage of time spent in vigilance) relative to the total vigilant behaviour observed in each video recording.

Statistical analysis

We used SPSS version 22.0 for Windows (IBM, Armonk, NY, USA) for all statistical analyses. Results are presented as means \pm standard error (se). As people visiting Granite Island stopped receiving an introductory talk after March 2020, we expected a change in their behaviours while on the island. Hence, we tested for a relationship between the occurrence of human activities (yes, no) and the implementations of the COVID-19 health protection measures (from March 2020 onwards) such as people only being allowed outside for exercise (yes, no) using a χ^2 test. Wind speeds, number of people and return times were treated as categorical variables because the guides often recorded categories instead of the exact times or numbers for these variables. We combined the number of wanderers, Dog walkers and those on the tours, and categorized the total number of people as: < 5, 6–25, 26+; we included all people, not just wanderers, in our analyses because, although people on the tours were expected and asked to be quiet and not use white torches or flashes, this was often not the case. We

Table 1. Ethogram of Little Penguin behaviours identified in the video recordings obtained from seven infrared sensor cameras located on the north shore of Granite Island (South Australia, Australia) between May 2019 and June 2020.

Behaviour	Description of the behaviour	Reference(s)
Resting	Lying down, sleeping, or dozing in the absence of all other behaviours	Sherwen <i>et al.</i> (2015)
Preening	Grooming of the feathers with the bill (nibbling motion); scratching the head or the body with their feet; or shaking of the head to remove excess fluid secretions from the nasal ducts of the salt glands	Viblanc <i>et al.</i> (2011), Sherwen <i>et al.</i> (2015)
Walking	Moving at a steady pace (walking/waddling)	Sherwen <i>et al.</i> (2015)
Huddling	Stationary while near another individual	Sherwen <i>et al.</i> (2015)
Vocalizing	Emitting audible call(s) either on its own or by communicating with conspecifics	Jouventin (1982), Colombelli-Négrel & Smale (2018)
Aggressive	Aimed toward another individual, including pecking with beak or chasing the individual	Sherwen <i>et al.</i> (2015), E. Costello & D. Colombelli-Négrel pers. obs.
Vigilant	Stationary in upright position, scanning the environment or walking and pausing every few steps while scanning the environment	Sherwen <i>et al.</i> (2015), E. Costello & D. Colombelli-Négrel pers. obs.
Distressed	Either shivering continuously (wings or entire body), breathing heavily, showing pupil dilatation (when visible), and/or appearing completely frozen in an unnatural position	Holmes <i>et al.</i> (2005), Ellenberg <i>et al.</i> (2012), Schaefer & Colombelli-Négrel (2021)

included wind speeds in our analyses because it has been identified to influence the behaviours and vocalizations of seabirds, including Little Penguins (Dehnhard *et al.* 2013, Pistorius *et al.* 2015, Saraux *et al.* 2016). We used Spearman correlations, χ^2 tests and Kruskal–Wallis tests to assess

multicollinearity between our predictor variables (presence of Dog(s) (yes, no); occurrence of concert (yes, no); number of people (< 5, 6–25, 26+); use of white light (yes, no), breeding (yes, no); whether the birds were breeding or not); and wind speeds (calm, light, moderate, strong, gale, storm, hurricane)). The number of people correlated with breeding (Kruskal–Wallis $\chi^2 = 37.77$, $df = 2$, $P < 0.001$), occurrence of concert (Kruskal–Wallis $\chi^2 = 31.52$, $df = 2$, $P < 0.001$) and wind speeds ($r = -0.22$, $P < 0.0001$), whereas the use of white light correlated with breeding ($\chi^2 = 11.70$, $df = 1$, $P < 0.001$), occurrence of concert ($\chi^2 = 10.74$, $df = 1$, $P = 0.001$), presence of Dog(s) ($\chi^2 = 7.04$, $df = 1$, $P = 0.01$) and wind speeds ($r = 0.08$, $P = 0.05$). Therefore, we ran separate analyses using presence of Dog(s), occurrence of concert, breeding and wind speeds in one set of models (models (a) to (d); see Results), and the number of people and use of white light in another set of models (models (f) to (h); see Results). We square root transformed the number of vocalizations per night to conform with normality.

We used generalized linear mixed models (Zuur *et al.* 2009) to assess how our predictor variables correlated with the numbers (total number of adult penguins seen or heard on land per night, this included those arriving from the sea as well as those already on land in their nests during the day) and behaviours (return time and number of vocalizations per night) of Little Penguins. We obtained data on penguin numbers and all our fixed factors for 520 nights, data on penguin return time and all our fixed factors for 514 nights (as penguin return time was not observed on seven nights), data on penguin vocalizations and all our fixed factors for 263 nights out of the 426 nights that the recorders were deployed (due to technical failure of the recorders), and data on vigilance behaviour and all our fixed factors for 100 nights of the 426 nights that the video cameras were deployed (due to technical failure of the cameras and the fact that penguins were not present on the island or visible on the cameras every night). We analysed (1) the total number of adult penguins seen on land per night ($n = 520$ nights) with a Poisson distribution (identity link; models (a) and (e); see Results), (2) penguin return time (on time, late; $n = 514$ nights) with a binary logistic regression distribution (logit link; models (b) and (f); see Results), and (3) the number of vocalizations per night ($n = 263$ nights) with a Poisson distribution

(identity link; models (c) and (g); see Results). We included month as a random effect for all models and 'guide ID' (the name of the guide recording penguin numbers and behaviours on a given night; eight guides recorded data in this study, and when more than one guide was present, we used the name of the most senior guide) as a random effect for models (a) and (e) to account for variation in penguin counts between guides. We removed month as a random factor when analysing the time Little Penguins spent in vigilance (in seconds) to avoid overdispersion. Therefore, we used a general linear model with a Poisson distribution (identity link) to assess how our predictor variables correlated with the time Little Penguins spent in vigilance ($n = 100$ nights). We included the total number of penguins observed on land per night as a predictor when analysing penguin behaviours (return time, number of vocalizations and time spent in vigilance) to account for the influence of conspecifics on behaviours. We tested our models for overdispersion by inspecting the Pearson residuals and found no evidence for overdispersion. We used an analysis of variance to determine whether total ambient noise (dba; extracted from the automated recorders) varied with the number of people. We present the full models (including non-significant terms) for all our analyses.

RESULTS

Frequency of disturbances

We monitored a total of 520 nights across the 2-year period (June 2018 to June 2020): 462 nights before the implementation of the COVID-19 health protection measures (June 2018 to March 2020) and 58 nights after the implementation of these measures (March 2020 to June 2020). Before the implementation of the COVID-19 health protection measures (June 2018 to March 2020), the tour guides recorded 12 155+ people at night, with on average 25 ± 0.85 se people per night (range 0–142 people per night; these included people booked on the tours as well as wanderers). After the implementation of the COVID-19 health protection measures (March 2020 to June 2020), the tour guides recorded 1217+ people at night, with on average 11 ± 1.60 se people per night (range 0–101 people per night). Across the 2 years of the study (June 2018 to June 2020), human activities (number of

people, presence of Dog(s), occurrence of concert, use of white light) recorded by the guides occurred on 20% of the monitored nights before the COVID-19 health protection measures and on 64% of the nights after the measures were implemented (overall on 25% of the monitored nights; 129/520 nights; Fig. 2a). The most common activity during the 129 nights was the use of white light (occurring on average on 65% of the nights with recorded human activities: 51% of the nights before the COVID-19 health protection measures and 100% of the nights after the measures; Fig. 2b, see also Supporting Information Fig. S1A, B). It was not uncommon to observe multiple human activities on a single night, and other common activities included: (1) concert (occurring on 16% of the monitored nights, all before the COVID-19 health protection measures) and (2) the presence of Dog(s) (occurring on average on 5% of the monitored nights: 4% of the nights before the COVID-19 health protection measures and 5% of the nights after the COVID-19 health protection measures; Fig. 2b). Other human activities that occurred less frequently (<1% of the monitored nights) included unauthorized cars, fishermen walking with trolleys, and push bikes. The occurrence of human activities was significantly higher after the implementation of the COVID-19 health protection measures ($\chi^2 = 8.08$, $P = 0.004$; see also Fig. 2). We also recorded the presence of two Red Foxes *Vulpes vulpes* on 24 June 2020 (Supporting Information Fig. S1C,D), which killed two-thirds of the penguin population (assessed via direct observations by Stephen Hedges and evidence from necropsy analyses on the carcasses).

Little Penguin behaviours

We found that fewer penguins on land were observed on the north shore when Dogs were present at night in the same area (Fig. 3a; Table 2). There was no difference in penguin numbers between nights with and nights without a concert (Table 2) and between nights with and nights without the use of white lights (Fig. 3b; Table 3). We found no correlation between penguin numbers and the number of people (Fig. 4c; Table 3), whether the birds were breeding or not (Table 2), wind speeds (Table 2), or the identity of the guide on duty (Model (a): Wald $Z = 0.12$, $P = 0.90$;

Model (e): Wald $Z = 0.53$, $P = 0.60$). Penguin numbers, however, differed between months, with fewer penguins seen in February and March (Model (a): Wald $Z = 2.15$, $P = 0.03$; Model (e): Wald $Z = 2.25$, $P = 0.02$; Fig. 4a).

Penguins were more often observed late when Dog(s) were present compared with when Dogs were absent (Fig. 3d; Table 2) and when white lights were used (Fig. 3f; Table 3). We also found evidence of a strong suppression effect between number of people and penguin return time, with a negative correlation in Table 3 when the number of people increased above 26, despite the positive relationship observed in Fig. (3e). Penguins' return time did not correlate with the occurrence of concerts (Table 2), breeding season (Table 2), the number of penguins present on land at night (Table 2), wind speeds (Table 2) or months (Model (b): Wald $Z = 0.64$; $P = 0.52$; Model (f): Wald $Z = 0.92$; $P = 0.35$).

Penguins vocalized more when Dogs were present on the island (Fig. 3g; Table 2), at lower wind speeds (Fig. 4b; Table 2) and at nights with concerts (Table 2), accounting for the number of penguins present on land that night (Table 2). Similar to our results for penguin return time, we found evidence of a strong suppression effect between number of people and penguin vocalizations at night, with a negative relationship observed in Table 3 despite the positive relationship observed in Fig. (3h). Penguins vocalized less at night during the non-breeding season (Fig. 4c; Table 2) or when white lights were used (Fig. 3i; Table 3). Penguin vocalizations correlated significantly with month, with more vocalizations per night recorded between October and January (Fig. 4a; Model (c): Wald $Z = 1.89$, $P = 0.05$; Model (g): Wald $Z = 2.14$, $P = 0.03$). Total ambient noise (dbA) increased as the number of people increased (analysis of variance: $F_{3,426} = 2.92$; $P = 0.03$).

We obtained 1413 videos with footage of Little Penguins and randomly selected 293 videos (21%) for analysis. Penguins were more vigilant during the non-breeding season than during the breeding season (Fig. 4d; Table 2). The proportion of time Little Penguins spent in vigilance at night did not correlate with the presence of Dogs (Table 2), the occurrence of concerts (Table 2), wind speeds (Table 2), the number of penguins present (Table 2), the number of people (Table 3) or the use of white light (Table 3).

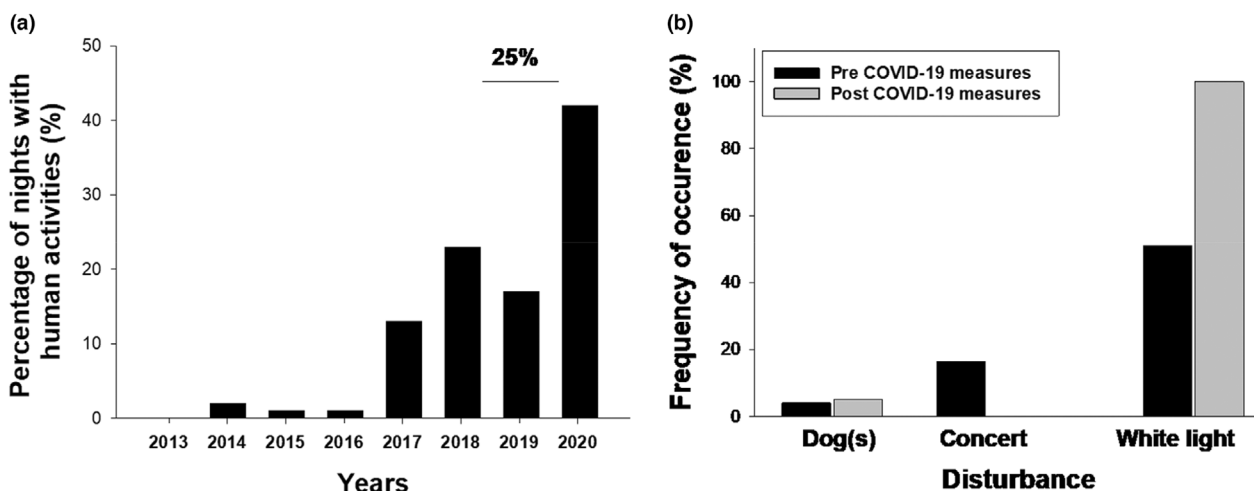


Figure 2. (a) Percentage of surveyed nights with human activities between January 2013 and June 2020. The activities were recorded on Granite Island (South Australia, Australia) to assess how different human activities influenced Little Penguin numbers and behaviours (vocalizations, return time and vigilance). The percentage presented above 2018–2020 (25%) indicates the percentage of nights with human activities during our study period (June 2018 to June 2020; 2 years). Data for 2013–2017 were collected as described and extracted from Colombelli-Négrel (2018, 2019, 2020). (b) Frequency of occurrence (%) of the three most common human activities (presence of Dog(s), occurrence of concerts and the use of white lights) observed on Granite Island (South Australia, Australia) between June 2018 and June 2020.

DISCUSSION

Penguins are one of the most threatened groups of seabirds (Croxall *et al.* 2012), and a popular attraction for tourism leading to increased interactions with humans and their associated disturbances (Boersma *et al.* 2020). Although some individuals or species can habituate to visitors (Walker *et al.* 2006, Ellenberg *et al.* 2009, 2012, Villanueva *et al.* 2012, Pichegru *et al.* 2016), disturbance at poorly managed colonies may result in adverse effects on individuals (McClung *et al.* 2004, Ellenberg *et al.* 2007, Bell *et al.* 2020; see also Schaefer & Colombelli-Négrel 2021). In this study, we investigated the occurrence of human activities at night on Granite Island (South Australia, Australia) and whether the disturbance arising from these activities was associated with the changes in numbers and behaviours of the Little Penguin population. We identified that fewer penguins were found on land at night when Dogs were present and that penguins were observed more often returning late from sea at nights when Dogs were present and when white lights were used. Our findings suggest that appropriate measures need to be developed to limit the impacts that human activities can have on wildlife, especially as peoples' attitudes and

behaviours toward nature-based activities are changing because of the COVID-19 pandemic (Morse *et al.* 2020, Randler *et al.* 2020, Hochachka *et al.* 2021).

We identified that the presence of Dogs was associated with fewer penguins on land at night. Penguins were also observed more often returning late from sea at night when Dogs were present and when white lights were used. Dogs can have detrimental effects on seabirds (Banks & Bryant 2007, Lenth *et al.* 2008), including Little Penguins (Dann & Norman 2006, Priddel *et al.* 2008, Braidwood *et al.* 2011, Van Dooren 2011). Although no Dog predation has been reported recently on Granite Island and, while we acknowledge that this was not an experimental study, these results suggest that Little Penguins could be avoiding the area when Dogs were on the island, especially considering that, on Granite Island, people walk their Dogs within the colony where they are visible and close to the penguins, even from the sea (see Fig. 1d). The fact that Dog owners continue to walk their Dogs on the island despite the Dog restrictions (Colombelli-Négrel 2018, 2019, this study) raises concerns regarding Dog owners' awareness that their Dogs can be a threat to seabirds (Bridson 2000, see also Williams *et al.* 2009).

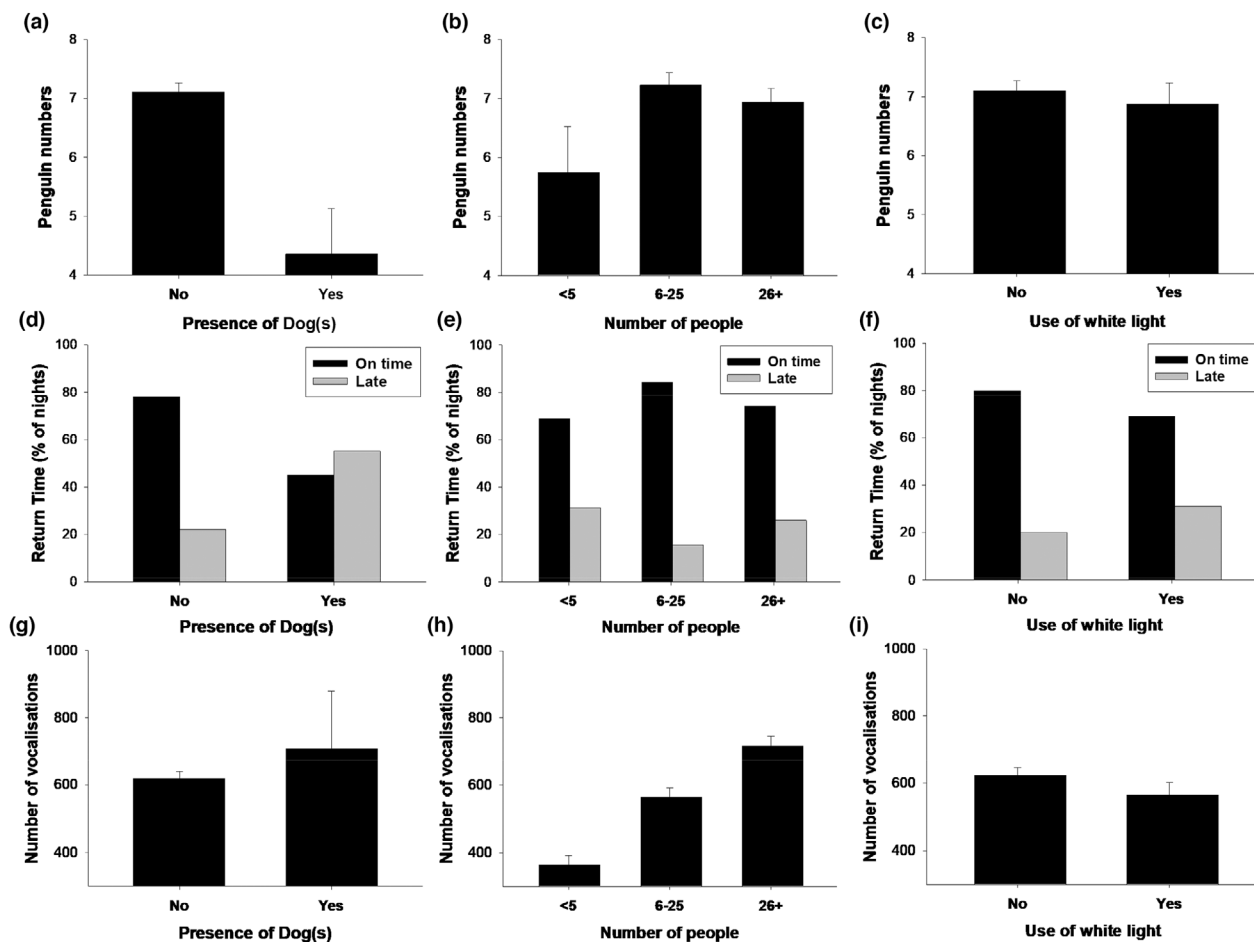


Figure 3. Human activities and Little Penguin numbers and behaviours (mean \pm standard error (se)) on Granite Island (South Australia, Australia) between June 2018 and June 2020. The figure presents: the number of penguins seen or heard per night on land in relation to: (a) the presence of Dog(s) (yes, no), (b) the number of people (< 5, 6–25, 26+) and (c) the use of white light (yes, no); Little Penguin return time (on time, late) in relation to (d) the presence of Dog(s), (e) the number of people and (f) the use of white light; and the number of vocalisations per night in relation to (g) the presence of Dog(s), (h) the number of people and (i) the use of white light.

Similarly, the increase in the use of white light observed in this study causes concerns regarding the attitudes held by both tourists and locals. Previous studies showed that artificial lights can disorientate seabirds, thereby increasing their risk of physical trauma and mortality (Le Corre *et al.* 2002, Rodríguez *et al.* 2014). Although white light directed straight into their eyes may be detrimental to Little Penguins, ambient and indirect lights may offer increased visibility to avoid obstacles and facilitate their movement on land (Rodríguez *et al.* 2018). This has been demonstrated on Phillip Island (Victoria, Australia), where penguins preferred lit paths over dark paths

to reach their nests (Rodríguez *et al.* 2018). Yet this study showed that penguins were more often observed late at night when white lights were used, which aligns with an experimental study on Lipson Island (South Australia, Australia) showing that fewer Little Penguins returned to the island when the light was turned on (L. Iasiello & D. Colombelli-Négrell unpubl. data). Further experimental research investigating the impacts that different types of artificial light, including duration and direction of light source, have on penguins is required (see also Rodríguez *et al.* 2016).

Anthropogenic noise (including human voices) can disrupt and mask vocal communication in

Table 2. Results of the generalized linear mixed models (models (a), (b) and (c)) and general linear model (model (d)) used to assess how Dog presence (yes, no), the occurrence of concert (yes, no), breeding (yes, no) and wind speeds (calm, light, moderate, strong, gale, storm, hurricane) correlated with (a) the total number of adult penguins seen on land per night ($n = 520$ nights), (b) their return time (on time, late; $n = 514$ nights), (c) the number of penguin vocalizations per night ($n = 263$ nights) and (d) the proportion of time Little Penguins spent in vigilance ($n = 100$ nights) on Granite Island, South Australia (Australia), between June 2018 and June 2020.

Model	Estimate	se	t value	P value
(a) Number of adult penguins per night ($n = 520$)				
<i>Intercept</i>	5.70	± 1.88	3.03	0.003
Presence of dog	-1.73	± 0.61	-2.85	0.005
Occurrence of concert	0.45	± 0.47	0.94	0.35
Breeding	0.04	± 0.64	0.06	0.95
Wind speeds calm – light	1.16	± 1.81	0.64	0.52
Wind speeds light – moderate	1.36	± 1.80	0.75	0.45
Wind speeds moderate – strong	1.65	± 1.80	0.92	0.36
Wind speeds strong – gale	0.58	± 1.82	0.32	0.75
Wind speeds gale – storm	1.58	± 1.85	0.85	0.39
Wind speeds storm – hurricane	5.13	± 3.04	1.69	0.09
(b) Return time ($n = 514$)				
<i>Intercept</i>	-11.81	± 228.47	-0.05	0.96
Presence of dog	1.54	± 0.64	2.41	0.02
Occurrence of concert	-0.53	± 0.53	-1.00	0.32
Breeding	-0.32	± 0.30	-1.08	0.28
Wind speeds calm – light	10.23	± 228.47	0.45	0.96
Wind speeds light – moderate	10.72	± 228.47	0.47	0.96
Wind speeds moderate – strong	10.24	± 228.47	0.45	0.96
Wind speeds strong – gale	10.37	± 228.47	0.45	0.96
Wind speeds gale – storm	10.51	± 228.47	0.46	0.96
Wind speeds storm – hurricane	11.65	± 228.47	0.51	0.96
Number of penguins per night	0.02	± 0.03	0.69	0.49
(c) Number of vocalizations per night ($n = 263$)				
<i>Intercept</i>	335.35	± 61.01	5.50	< 0.0001
Presence of dog	289.47	± 12.62	22.93	< 0.0001
Occurrence of concert	120.86	± 9.41	12.84	< 0.0001
Breeding	-231.63	± 105.08	-2.20	0.03
Wind speeds calm – light	273.41	± 6.96	39.27	< 0.0001
Wind speeds light – moderate	244.58	± 5.93	41.24	< 0.0001
Wind speeds moderate – strong	259.66	± 6.20	41.87	< 0.0001
Wind speeds strong – gale	118.60	± 7.03	16.87	< 0.0001
Number of penguins per night	14.79	± 0.60	24.87	< 0.0001
(d) Time spent in vigilance ($n = 100$)				
<i>Intercept</i>	8.32	± 6.25	1.33	0.19
Presence of dog	-2.36	± 4.73	-0.50	0.62
Occurrence of concert	0.27	± 2.65	0.10	0.92
Breeding	4.35	± 2.05	2.12	0.04
Wind speeds calm – light	-6.21	± 6.11	-1.02	0.31
Wind speeds light – moderate	-1.30	± 6.16	-0.21	0.83
Wind speeds moderate – strong	-4.03	± 6.22	-0.65	0.52
Wind speeds strong – gale	-4.88	± 6.40	-0.76	0.45
Number of penguins per night	-0.04	± 0.21	-0.19	0.85

We analysed the data for (a), (c) and (d) with Poisson distributions (identity link), and for (b) with a binary logistic regression distribution (logit link). Month and guide ID were used as random factors for model (a) and month was used as a random factor for models (b) and (c). We included the total number of penguins observed on land per night as a predictor when analysing penguin behaviours (return time, vocalizations, vigilance) to account for the influence of conspecifics on behaviours. Significant results are presented in bold. Abbreviation: se, standard error.

birds (Kleist *et al.* 2016, Buxton *et al.* 2017), especially for species that communicate at low frequencies, such as Little Penguins (Warren

et al. 2006, Francis *et al.* 2011, Dowling *et al.* 2012). More people on land is likely to be linked to additional loud noises, as suggested by

Table 3. Results of the generalized linear mixed models (models (e), (f) and (g)) and general linear model (model (h)) used to assess how the number of people (< 5, 6–25, 26+) and the use of white light (yes, no) correlated with (e) the total number of adult penguins seen on land per night ($n = 520$ nights), (f) their return time (on time, late; $n = 514$ nights), (g) the number of penguin vocalizations per night ($n = 263$ nights) and (h) the proportion of time Little Penguins spent in vigilance ($n = 100$ nights) on Granite Island, South Australia (Australia), between June 2018 and June 2020.

Model	Estimate	se	<i>t</i> value	<i>P</i> value
(e) Number of adult penguins per night ($n = 520$)				
Intercept	6.90	± 0.60	11.49	< 0.0001
Number of people (< 5) – (6–25)	–0.23	± 0.53	–0.43	0.67
Number of people (6–25) – (26+)	0.20	± 0.25	0.81	0.42
Use of white light	0.32	± 0.28	1.15	0.25
(f) Return time ($n = 514$)				
Intercept	–0.93	± 0.20	–4.68	< 0.0001
Number of people (< 5) – (6–25)	0.17	± 0.50	0.34	0.73
Number of people (6–25) – (26+)	–0.87	± 0.23	–3.77	< 0.0001
Use of white light	0.48	± 0.25	1.94	0.05
(g) Number of vocalizations per night ($n = 263$)				
Intercept	642.06	± 52.56	12.22	< 0.0001
Number of people (< 5) – (6–25)	–206.48	± 5.04	–40.98	< 0.0001
Number of people (6–25) – (26+)	–53.62	± 3.54	–15.16	< 0.0001
Use of white light	27.63	± 3.38	8.18	< 0.0001
(h) Time spent in vigilance ($n = 100$)				
Intercept	4.01	± 1.42	2.80	< 0.001
Number of people (< 5) – (6–25)	2.72	± 281	0.97	0.34
Number of people (6–25) – (26+)	1.84	± 1.59	1.16	0.25
Use of white light	1.77	± 1.63	1.08	0.28

We analysed the data for (e), (g) and (h) with a Poisson distribution (identity link), and for (f) with a binary logistic regression distribution (logit link). Month and guide ID were used as random factors for model (e), and month was used as a random factor for models (f) and (g). Significant results are presented in bold. Abbreviation: se, standard error.

the fact that the total ambient noise increased as more people were present at night. Here, we found that Little Penguins called more on nights when Dogs were present but found a negative correlation between the number of people and penguin vocalizations. Yet this was under a strong suppression effect, suggesting an interactive effect with other human activities. Therefore, it is still possible that Little Penguins produced more calls at night when Dogs were present (as Dogs would always be accompanied by their owners and thus people) to compete with a noisy environment (Little Penguins do not have alarm calls, and we recorded brays and growls, which are used for communication between partners; Miyazaki & Waas 2003, Colombelli-Négrel & Smale 2018). This idea is further supported by the fact that Little Penguins also vocalized more when concerts occurred or when wind speeds increased, both of which would increase background noise. Further studies investigating the impacts of anthropogenic noise and the number of people present on penguin communication are needed to fully answer this question.

An increase in vigilance due to human presence and anthropogenic noise has been observed in several species of seabirds including penguins (Holmes *et al.* 2005, 2006, Sherwen *et al.* 2015, Buxton *et al.* 2017, French *et al.* 2019, Chiew *et al.* 2020). From an evolutionary point of view, seabirds should perceive humans as potential predators and respond accordingly (the ‘risk–disturbance’ hypothesis; Frid & Dill 2002, Beale & Monaghan 2004). Yet, in this study, we did not find any correlation between human activities and the proportion of time Little Penguins spent in vigilance. This may be because the recorded activities did not occur at the exact time the penguins returned to their nests or because most of the vigilant behaviours were scored from a single camera, located under the boardwalk. The boardwalk could have provided a protected path for the penguins as habitat can influence how animals respond to the presence of people (Li *et al.* 2017). Future studies should also account for the sex, age, experience and even personalities of the penguins, as these factors are known to influence individuals’ responses to human disturbance

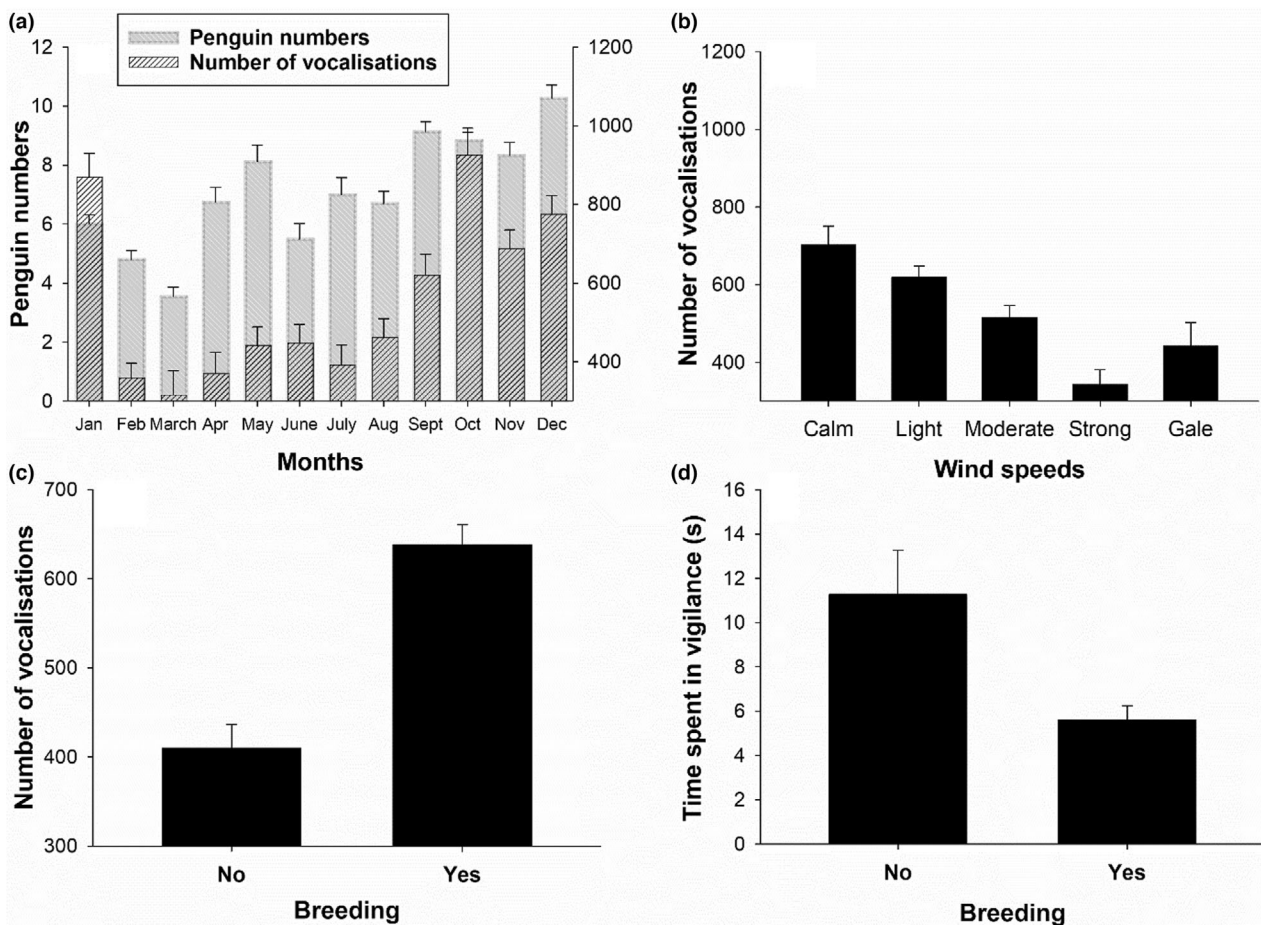


Figure 4. Variation in Little Penguin numbers and behaviours (mean \pm standard error (se)) in relation to wind speeds, breeding and months on Granite Island (South Australia, Australia) between June 2018 and June 2020. The figure presents: (a) the number of penguins seen or heard per night on land (grey) and the number of vocalizations per night (hashed grey) in relation to the months of the year; (b) the number of vocalizations per night in relation to wind speeds (calm, light, moderate, strong, gale); (c) the number of vocalizations per night in relation to the breeding period (whether the birds were breeding or not); and (d) the proportion of time Little Penguins spent in vigilance in relation to the breeding period (whether the birds were breeding or not).

(Ellenberg *et al.* 2009, 2012, Pichegru *et al.* 2016, Colombelli-Négrel & Katsis 2021).

When facing potential threats or disturbances, wild and captive penguins have been shown to display avoidance behaviours, alter their travel path or delay their return to their nest (Wilson *et al.* 1991, Culik & Wilson 1995, Wright 1998, Chiew *et al.* 2020; see also Ellenberg 2017). Here, we found that Little Penguins returned later to their nests when Dogs were present on the island or when white lights were used. As mentioned before, human activities and disturbances often do not occur independently (reviewed in Shannon *et al.* 2016) and quantifying the effects of a single activity on wildlife is challenging. It is therefore

possible that the observed delays were not simply the result of the presence of Dogs or white lights but to the combination of all human activities. This is because the presence of Dogs co-occurred with the use of white lights and tended to correlate with the number of people recorded at night (see Statistical analysis section). In support of this idea, we found several suppression effects, suggesting that the different human activities interact with each other. Hence, the delays in return to the colony and changes in behaviours observed in our study could be the result of Little Penguins avoiding people, Dogs, white lights or all of them combined, and remains to be experimentally tested.

Human presence can be positive in some seabird colonies (Hentati-Sundberg *et al.* 2021) and human disturbance may not have any immediate severe consequences for penguin survival – compared with the Red Fox predation recorded in this study for example – from a conservation point of view, but we need to consider that even subtle and low levels of human disturbance could have cumulative and negative consequences for individual breeding success and survival, which may ultimately affect the long-term persistence of the colony (Seddon & Ellenberg 2008, Ellenberg & Seddon 2009; see also Ellenberg 2017, Schaefer & Colombelli-Négrel 2021). A delay in a penguin's return time, for example, especially during breeding when they need to feed their chicks, could decrease their time spent providing parental care or resting, which in turn would influence not only their individual fitness but also their breeding success (see also Ellenberg 2017). In addition, when animals are continuously exposed to stressful factors, they can enter a chronic state of stress (Cyr & Romero 2007), which can lead to stress-related diseases (Mortimer & Lill 2007), alter or disrupt their behaviours (Burger & Gochfeld 1993, Angelier *et al.* 2008), or impact their fitness (McClung *et al.* 2004, Lupien *et al.* 2009). Combined with other pressures from their environment, regular human disturbances could therefore have serious consequences for the long-term survival of a population, especially for those that already experience a high number of other threats (Boal *et al.* 2007, Colombelli-Négrel 2015, Colombelli-Négrel & Tomo 2017, Johnson & Colombelli-Négrel 2021, Colombelli-Négrel *et al.* 2022), such as the Granite Island population.

Management implications

The findings from this study further our understanding of how human activity may influence penguins (Ellenberg *et al.* 2007, Cannell *et al.* 2016, Chiew *et al.* 2019). This is particularly important as, during 2020 when the COVID-19 health protection measures were put in place, we noted an increase in human activities on Granite Island. This is probably due to people only being allowed outside for exercise, as many locals living in Victor Harbour, South Australia (Australia), use Granite Island for

exercise. Recent studies showed that people interested in nature-based activities, such as bird-watching, became more localized in their activities during the pandemic (Randler *et al.* 2020, Hochachka *et al.* 2021) and had more time for such leisure activities than before the pandemic (Randler *et al.* 2020). Our study specifically highlights that appropriate measures need to be developed to limit the impacts that human activities can have on wildlife. First, it is important to educate the local community about Little Penguin (and seabird) conservation and to generate awareness about the impacts of our actions on seabirds (Gill 2007). Conducting workshops and training days, for example, could engage and increase awareness within the community. Another important aspect to consider is the implementation of clear signage demonstrating which human activities can negatively influence wildlife, as this was successful in reducing unwanted human behaviours in other studies (Kratovichil & Schwammer 1997, Sherwen *et al.* 2014, Marschall *et al.* 2017). The reinforcement of the no-dog rule and educating Dog owners could help with preventing Dogs on the island, while complete restriction of people at night would help minimize human disturbances, particularly at times of increased vulnerability (i.e. Little Penguin breeding and moulting periods). Physical barriers to reduce visual and acoustic interactions between people and penguins may also be considered as they are commonly used as a mitigation tool to reduce noise levels (Slabbekoorn & Ripmeester 2008). Additionally, this study highlights the importance of ongoing monitoring for declining populations as the night surveys and constant video monitoring ensured that the Red Fox attacks could be detected and dealt with promptly. Although fox predation has only been recorded three times on Granite Island since the 1900s, the drastic impact that these events had on the population has warranted the installation of a fox-proof gate in 2022 to fully prevent the access of introduced predators to the island. Future studies should investigate how each specific human activity influences individuals, their long-term fitness and how other factors (such as age or experience with humans) may influence an individual's response to such disturbances (and hence their ability to persist).

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AUTHOR CONTRIBUTIONS

Emily Costello: Data curation; formal analysis; validation; visualization; writing – original draft; writing – review and editing. **Diane Colombelli-Négrel:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing.

ETHICAL NOTE

The project was approved by Flinders University Animal Welfare Ethics Committee (No. E449) and supported by a scientific permit (Y26040) to conduct the research.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

Data Availability Statement

Data are available on the Flinders University data repository at DOI: [10.25451/flinders.22344688](https://doi.org/10.25451/flinders.22344688)

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Photographs captured by the infrared sensor cameras showing people using white light at night via (A) a phone and (B) a torch and camera flash; and two Red Foxes under the boardwalk (C) and checking a Little Penguin nest (D) on Granite Island, South Australia (Australia), between May 2019 and June 2020.