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The diving behaviour of little penguins in Western Australia predisposes them to risk of injury by watercraft

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Abstract

1. The most western little penguin colony globally, and the most northern in Western Australia (WA) is found on Penguin Island, WA. The penguins use coastal bays that are also used extensively by recreational watercraft. These penguins have been found to either dive predominantly to shallow depths of 1–5 m or to depths >8 m. It is thus hypothesized that (a) both the shallow and deeper diving penguins can potentially be disturbed or injured by these watercraft but that the risk will differ between the two diving strategies, and (b) that risk of injury for both is greater during the summer and autumn, when people are more likely to use watercraft.
2. This was tested by attaching data loggers to little penguins during chick rearing and by investigating necropsy records. Diving activity was studied for the very shallow and relatively deeper diving penguins separately, and we considered the penguins were vulnerable to interactions with watercraft when they were within the top 2 m of the water column or at the surface.
3. Shallow-diving penguins executed >1,200 dives per day, 64% of dives occurred within the top 2 m, and they were vulnerable for approximately two-thirds of their time at sea. The deeper diving penguins executed fewer dives. Almost half of dives were to ≥10 m, yet they were vulnerable for almost one-third of their time at sea. Their post-dive recovery was also longer. Thus, the risk of interaction from watercraft differs depending on the diving behaviour.
4. This study highlights the potential impact to little penguins throughout Australia and New Zealand.

KEYWORDS
behaviour, birds, coastal, marine park, recreation, shipping

1 | INTRODUCTION

The little penguin (*Eudyptula minor*) colony on Penguin Island, Western Australia (WA), is the largest in the state, with approximately 1,500–2,400 adults (Cannell et al., 2011). It is also the most western little penguin colony globally, and the most northern in WA. It has been recognized as having the highest conservation status of all marine fauna groups locally (Department of Conservation and Land Management, 2003), and of all major penguin colonies Australia-wide (Dann, Cullen, & Weir, 1996). This relatively small and edge-of-range colony is also genetically distinct from other colonies in WA (J. Sinclair, B. L. Cannell, W. B. Sherwin, S. J. Bradley, and R. D. Wooller unpublished data), and these traits may negatively influence this colony's long-term viability.

Little penguins from this colony travel and feed in bays within 30 km from the island during chick rearing (Bradley, Cannell, &

Wooller, 1997; B. L. Cannell, unpublished data) and much further away during incubation, up to 200 km (B. L. Cannell, unpublished data). However regardless of distance from the colony, the penguins generally remain within approximately 10 km of the coast during both the incubation and guard phase foraging trips (B. L. Cannell, unpublished data). These bays and coastal areas are also used extensively for recreational water-based activities, including fishing, boating, wind surfing, kite surfing, and water skiing. An estimated 11,000 recreational fishing boats alone were surveyed to use these bays in 1996–1997 (Sumner & Williamson, 1999). However, since the survey in 1996, the population in the Rockingham area, adjacent to Penguin Island, has almost doubled to nearly 110,000 people. The number of fisher hours has increased by 15% in just under a decade since the survey, and the areas used by recreational fishers have also increased (Sumner, Williamson, Blight, & Gaughan, 2008). Boat ownership in this area is the second highest of all 30 local government areas that comprise the Perth metropolitan region (Department of Planning and Infrastructure, 2009). Moreover, the rate of boat ownership is increasing in all government areas (Department of Planning and Infrastructure, 2007, 2009), and the population in Rockingham is expected to increase by a further 50% by 2023 (http://forecast.id.com.au/rockingham). It is therefore reasonable to assume that human usage of the local coastal waters will also increase.

The issue is what effect the increasing human population, and hence number of craft, may have on the penguins. It is possible that the penguins may avoid the watercraft, either by diving out of their range or by utilizing different areas, as found in other marine fauna (e.g. Allen & Read, 2000; Bellefleur, Lee, & Ronconi, 2009; Lusseau, 2003; Mikola, Miettinen, Lehikoinen, & Lehtilä, 1994; Tyne, Johnston, Rankin, Loneragan, & Bejder, 2015). However, the type of avoidance response and the efficacy of these strategies is influenced by vessel speed (Hazel, Lawler, Marsh, & Robson, 2007; Miksis-Olds, Donaghay, Miller, Tyack, & Reynolds, 2007), the dive depth of the animal, and the local bathymetry (Edwards et al., 2016). For example, shallow water makes the location of a sound source more difficult and can potentially result in inappropriate avoidance behaviour (Miksis-Olds et al., 2007). This is particularly relevant for little penguins, because as well as diving to depths of 10 m or more when foraging (e.g. Bethge, Nicol, Culik, & Wilson, 1997; Chiaradia, Ropert-Coudert, Kato, Mattern, & Yorke, 2007; Gales, Williams, & Ritz, 1990; Kato, Ropert-Coudert, Gremillet, & Cannell, 2006; Ropert-Coudert, Chiaradia, & Kato, 2006; Ropert-Coudert, Kato, Naito, & Cannell, 2003), they also forage within shallow depths. In fact, some penguins from Penguin Island preferentially foraged within the top 1–5 m, and on multiple days (Ropert-Coudert et al., 2003). In addition, little penguins dive only to shallow depths when travelling, with little surface time and sustain this pattern for several hours (Bethge et al., 1997; Gales et al., 1990). This means that for much of their time at sea they may not be diving deeper than the typical draft of the recreational watercraft. Also, as air-breathing divers, penguins come to the surface to breathe and rest; this time on the surface increases with the duration of the previous dive (Chappell, Shoemaker, Janes, Bucher, & Maloney, 1993; Kooyman, 1989), but it is also conditioned by the expected duration of the subsequent dives (Wilson, 2003). Therefore, penguins are potentially at risk of being hit by watercraft, whether they are utilizing shallow depths in the water column or spending longer on the surface after deeper dives. Indeed, physical trauma was found to be the most prevalent cause of mortality in a recent study of little penguins from this region (Cannell et al., 2016).

We suggest that the little penguins' foraging and travelling behaviour puts them into conflict with the human use of the area and that their diving strategy may influence the likelihood of interactions. As recreational boating is most popular in the austral summer and autumn (Ryan et al., 2015; Sumner & Williamson, 1999), it is hypothesized that the risk of injury may also vary according to the season. This reasoning/hypothesis was tested in two ways. First, both the diving behaviour of shallow and deeper-diving penguins when travelling and foraging and their behaviour at the surface was described. The seasonality of the incidence of traumatic injury was then investigated and related to the level of boating activity. Although there are many studies on the interactions of marine mammals and turtles with watercraft (e.g. Allen & Read, 2000; Laist, Knowlton, Mead, Collet, & Podesta, 2001; Nowacek, Wells, & Solow, 2001; Parks, Warren, Stamieszkin, Mayo, & Wiley, 2011; Wells & Scott, 1997), this paper is novel in detailing the implications of avian diving strategy on the risk of interactions with vessels.

2 | MATERIALS AND METHODS

Data loggers (49 mm × 15 mm, 14 g in the air, including batteries; Little Leonardo, Tokyo, Japan) were attached to three female and three male little penguins from Penguin Island, WA (32.31°S, 115.69°E; Figure 1), during their breeding season in 2001 (as described by Ropert-Coudert et al., 2003). The 12-bit-resolution data loggers recorded dive depth every second with a 0.1 m accuracy. All the penguins were rearing chicks between 2 and 6 weeks old, and fieldwork followed ethical guidelines approved by Murdoch University Animal Ethics Committee under permit 880R/01. Diving data were collected from three birds for 1 day, one bird for 2 days, and two birds for 3 days. Once the birds were recaptured, the loggers were removed and the data were downloaded. Data were analysed using a customized macro in Igor Pro software (WaveMetrics 5.0, Lake Oswego, OR, USA,). Based on the resolution of the devices, the dive threshold was set at 0.5 m.

Data from these penguins showed the existence of two different diving strategies: a shallow diving strategy to depths <5 m and a deeper diving strategy to >8 m (Ropert-Coudert et al., 2003). Consequently, the dive patterns and activity were analysed separately for the shallow and deeper divers. To determine usage of the water column throughout the day, each dive was placed in one of four depth categories (based on local bathymetry: 0.5–2 m, 2–4 m, 4–10 m, and ≥10 m), according to the maximum depth of each dive. As little penguins are visual predators (Cannell & Cullen, 1998) and the depth of dives could be related to the amount of light penetrating the water column, the average proportion of dives in each depth category was

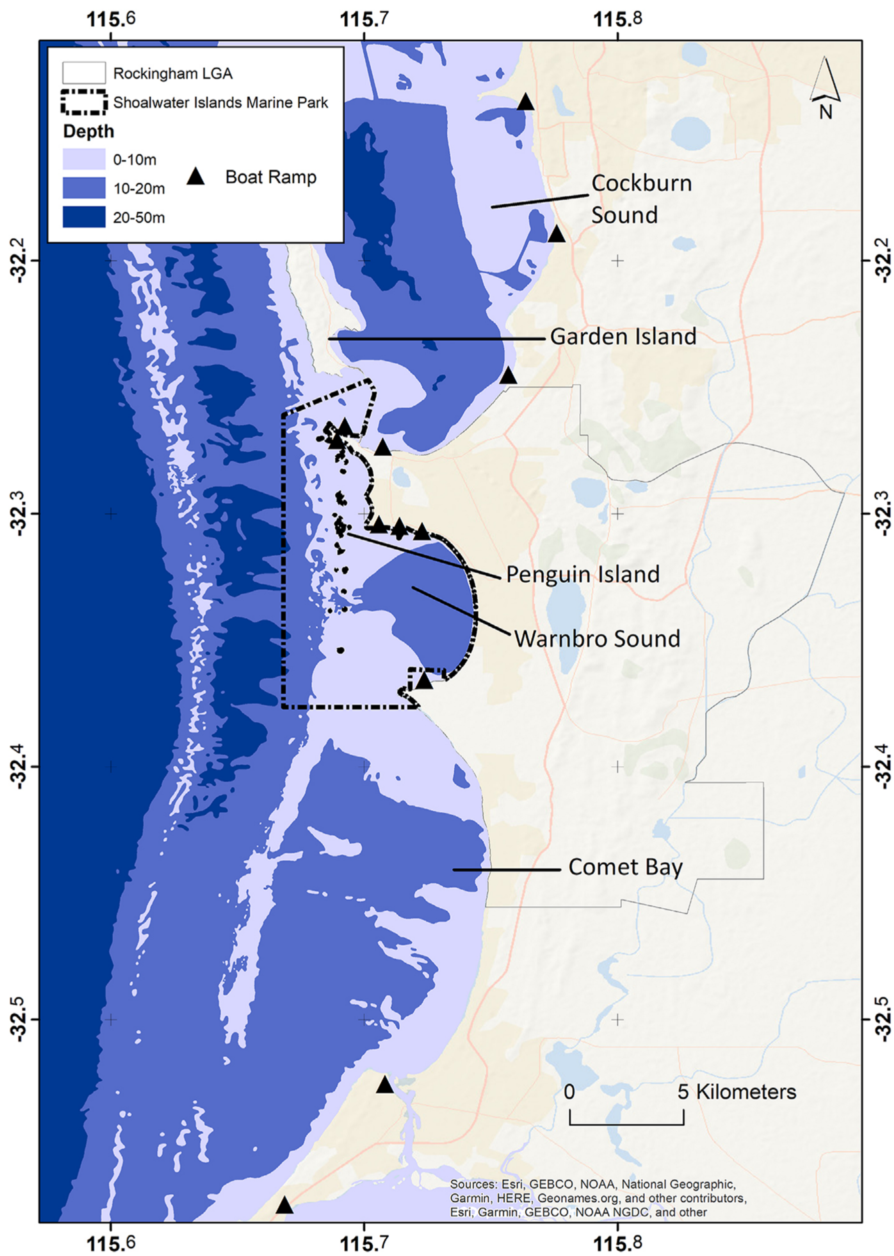

FIGURE 1 Location of Penguin and Garden islands, Western Australia, and the bathymetry within Cockburn Sound, Warnbro Sound, and Comet Bay. The Shoalwater Islands Marine Park is indicated by the hatched line, and the 12 boat ramps or boat launching areas in close proximity to Penguin Island are shown

determined for each hour for the shallow and deep-diving birds. Dives within the top 2 m with no abrupt variations in descent or ascent rate (>0.25 m s^{-1}) or dives with no undulations in depth at the bottom phase were classified as travelling dives (Kato et al., 2006). All other dives were classified as foraging (including search) dives. The average proportion and duration of travelling dives were calculated using data from all trips for each of the penguins. The time each penguin spent at the surface between dives (i.e. the recovery and anticipation time) was also determined for individual dives as well as after a bout of dives, with the bout identified using a log-survivorship curve (Gentry & Kooyman, 1986).

All statistical analyses were performed using R 3.1.2 (R Core Team, 2014). Summary statistics were performed in R package plyr (Wickham, 2011) and are reported as mean ± 1 SD (unless otherwise stated). Variation in the time spent underwater each hour was initially investigated using generalized additive mixed models, using the R package mgcv (Wood, 2004). The time each penguin spent underwater every hour can be highly variable due to factors not easily measured, and each dive does not necessarily represent a physiological or behavioural limit. For instance, the time underwater can be affected by factors such as the light penetration, the age of the bird (middle-aged little penguins had shorter dives than younger and older birds—Zimmer, Ropert-Coudert, Kato, Ancel, and Chiaradia (2011)—but it was not possible to age the birds in the study), prey distribution, and the aerobic dive limit of each bird, which itself is dependent on several factors (Wilson, Shepard, Laich, Frere, & Quintana, 2010). Thus, when comparing the proportion of each hour spent underwater within diving strategy type, such potential unmeasured sources of variation were accounted for and any physiological or behavioural limit to diving was estimated using quantile regression (Cade & Noon, 2003). A non-linear form of neural-network-based quantile regression was used to appropriately model the non-linear relationship in the data. It was applied using the package qrnn (Cannon, 2011), and estimates were based around the 50% quantile. Linear mixed models (LMMs) and generalized linear mixed models (GLMMs) were used to determine differences in dive variables between the two diving strategies, accounting for the influence that the individual bird may have on the data. The models were applied using the functions lmer and glmer, respectively using the package lme4 (Bates, Maechler, Bolker, & Walker, 2015). Least-squares means of fixed effects, which are adjusted for means of other factors in the model, were computed using the package lsmeans (Lenth, 2015). To test for differences in both the duration and proportion of travelling dives throughout the day and between diving strategies, the data were pooled into blocks of time based on three criteria: the proportion of each hour spent underwater; general ambient light levels; and the dominant behaviour for the period, identified as either travel or foraging. This resulted in four time categories: (1) departure from the colony (5:00–9:00 a.m.), (2) morning (9:00 a.m.–noon), (3) afternoon (noon–4:00 p.m.), and (4) return to the colony (4:00–6:00 p.m.). Differences in the duration of travelling dives were tested using a GLMM with a Poisson distribution and a log link function, with bird identification (ID) and day (i.e. 1, 2, or 3) as random effects. Time category and diving strategy were included as fixed effects. Differences in the proportion of travelling dives throughout the day were tested using an LMM after checking for overdispersion in the residuals. Each bird was given a unique ID. Bird ID and a dummy code to differentiate single or repeat trips were included as random effects. We included time category and diving strategy, with an interaction, as the fixed effects. The least-squares means were then obtained to (a) determine if the shallow or deeper divers performed significantly more travelling dives in different time categories, and (b) compute pairwise comparisons of the proportion of each time category spent travelling within diving strategy, with *P* values adjusted using the Tukey honest significant difference method. To test for differences in the recovery surface intervals following a bout of dives throughout the day, the data from only the first day of diving were pooled into the same four blocks of time categories, natural log transformed due to non-normal distributions, and analysed using an LMM. Bird ID was included as a random effect, whereas block of time and diver strategy, with an interaction, were included as the fixed effects. The least-squares means were then obtained to determine if the shallow or deeper divers spent significantly more time at the surface in different blocks of time.

Nautical sunrise and sunset data were obtained from Geoscience Australia (http://www.ga.gov.au/geodesy/astro/sunrise.jsp).

2.1 | Periods of increased vulnerability to interactions with watercraft

Penguins are most vulnerable to interactions with watercraft when they are either on the surface or within the top 2 m of the water column. The consecutive number of seconds that a penguin was found within the top 2 m was obtained for travelling dives, other dives with a maximum depth within 2 m but not classified as travelling dives, and the ascent and descent phases of deeper dives. The total time per hour of increased vulnerability for each diving strategy was then determined by first summing the length of time each penguin was either on the surface or in the top 2 m and then averaging this across both diving strategies. As the time–depth data recorders did not record surface activity before the first dive or after the last dive, only data from 6:00 a.m–6:00 p.m. were included. Differences in the amount of time the shallow and deep diving penguins were vulnerable each hour were tested using an LMM, with bird ID and day number as random effects and diving strategy and hour of day as fixed effects.

2.2 | Seasonality of traumatic injury

A total of 168 little penguins were collected from 2004 to 2012. They were recovered from the colonies on Penguin Island and neighbouring Garden Island (32.23°S, 115.69°E; Figure 1), as well as from the foreshores of south-west WA. These penguins were either injured and subsequently died or were recovered as carcasses. Potential seasonal effects on collection of dead or injured penguins were reduced as the islands have daily ranger presence throughout the year, and, in 2006–2009, additional weekly checks throughout the year were undertaken at the mainland beaches from 32.16°S, 115.77°E to 32.51°S, 115.74°E. The carcasses showing little decomposition were taken to the veterinary department of Murdoch University and necropsied if cause of death was not obvious (see Cannell et al., 2016). The date of recovery for those birds that were both in a reasonable condition and identified to have a traumatic injury was used to identify the season of occurrence (summer: December–February; autumn: March–May; winter: June–August; spring: September–November).

The proportion of deaths attributed to trauma was determined for each season, and differences between all seasons were tested using a chi-squared test. A Marascuilo procedure was then performed to determine which seasons had significantly different proportions of trauma deaths.

3 | RESULTS

3.1 | Time of dives, dive rate, and time spent underwater

All the penguins exhibited diurnal diving behaviour, with first dives recorded between 5:30 and 6:00 a.m. (nautical sunrise 5:19–5:22 a.m. from 16 to 18 September 2001) and the last dives between 6:00 and 8:00 p.m. (nautical sunset 7:02–7:04 p.m. from 16 to 18 September 2001).

The shallow-diving birds (n = 4) performed an average of 1430 ± 144 dives during their day at sea and spent 30 ± 5% of their total time at sea underwater. They performed most of their dives

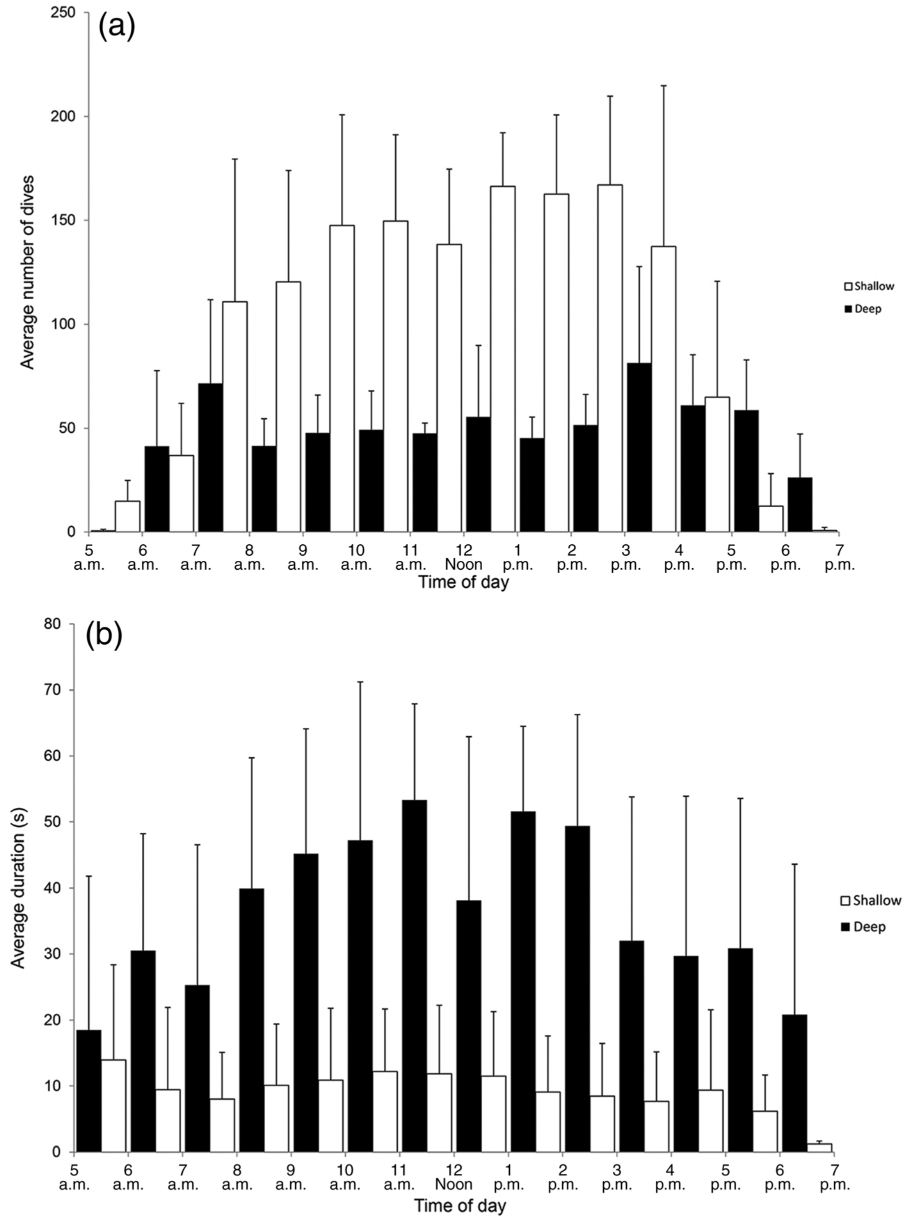

FIGURE 2 The average hourly diving parameters (±*SD*) of shallow and deep-diving little penguins from Penguin Island: (a) number of dives per hour; (b) duration of dives in seconds

between 8:00 a.m. and 5:00 p.m. (Figure 2a) and dived an average of 144 ± 51 times an hour during this period. The average duration of dives each hour did not vary greatly between 6:00 a.m. and 7:00 p.m., lasting for 10 ± 1 s (Figure 2b). However, the proportion of each hour that birds spent underwater was not evenly distributed across the whole day. From 9:00 a.m. to 4:00 p.m. the penguins spent approximately half of each hour underwater. Before 9:00 a.m. and after 4:00 p.m. the amount of time they spent underwater decreased to less than a third of each hour (Figure 3a).

The deeper-diving penguins (n = 2) performed fewer dives than the shallow-diving penguins (mean dives per day: 679 ± 213) but almost doubled their time underwater while at sea (mean proportion of day underwater: 57 ± 9%). The number of dives performed per hour by the deeper-diving penguins remained relatively constant from 6:00 a.m. to 6:00 p.m. (Figure 2a), with the penguins diving an average of 52 ± 27 times per hour in this period. The average duration of the dives changed across the day (Figure 2b), and the penguins executed longer dives, averaging 46 ± 3 s between 8:00 a.m. and 3:00 p.m. Like the shallow-diving penguins, time of day affected the time spent underwater, and the deep-diving penguins spent more time on the surface before 9:00 a.m. and after 5:00 p.m. compared with the rest of the day (Figure 3b). Between 9:00 a.m. and 5:00 p.m. they spent, on average, two-thirds of each hour underwater (Figure 3b).

3.2 | Travelling dives

Almost two-thirds of all the dives by the shallow-diving penguins were to depths within the top 2 m (Figure 4a), and 68% of these were travelling dives. In contrast, only a quarter of all the dives by the deep-diving penguins were to this depth range (Figure 4b), but 90% of these were travelling dives. All penguins travelled throughout the day

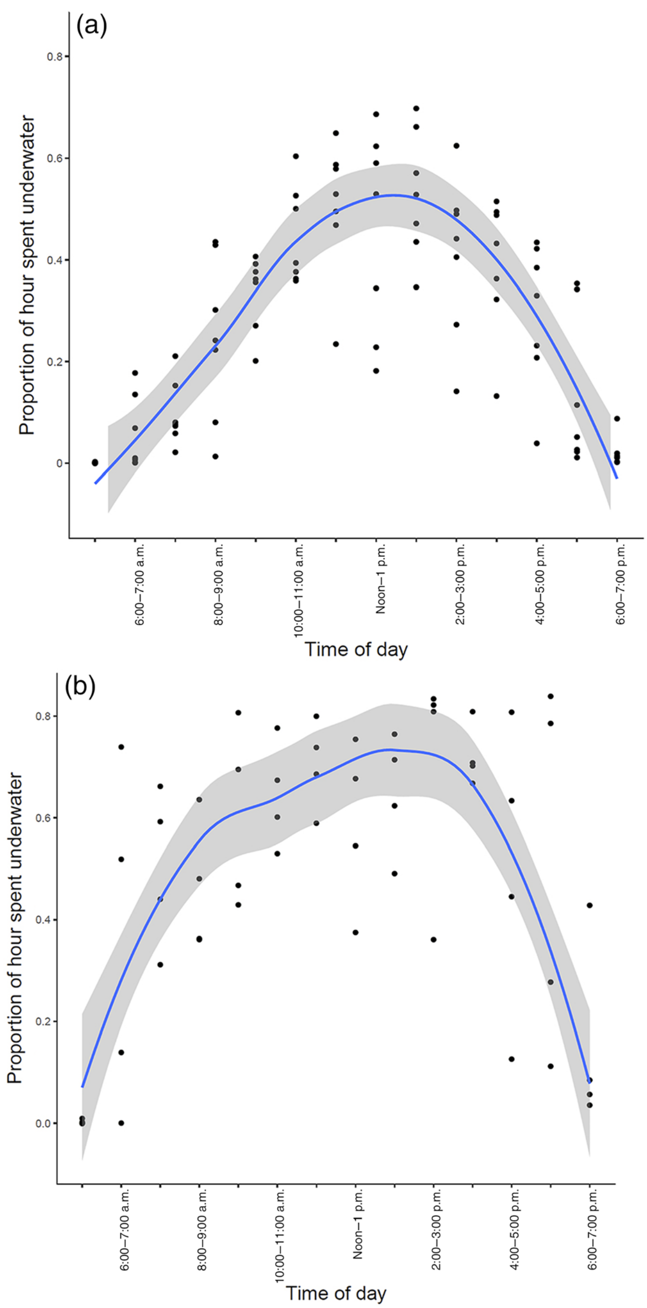

FIGURE 3 The proportion of each hour spent under water by (a) shallow-diving little penguins and (b) deep-diving little penguins. The solid line in each graph shows the 50% quantile regression

and, not surprisingly, all travelled more when departing from and returning to the colony (Figure 5, Table 1). However, the shallow-diving birds not only travelled more throughout the day than the deep-diving birds did(Figure 5) but also executed a similar proportion of travelling dives in both the afternoon and return journey to the colony (Table 1). There was no difference in the average duration of the travelling dives of the two groups: 2.7 ± 1.7 s for shallow-diving penguins (range 1–18 s) and 2.3 ± 2.2 s for the deep-diving penguins (range 1–17 s) (GLMM, z = 0.059, P = 0.953). However, the duration of travelling dives differed throughout the day, with the penguins executing shorter travelling dives in the afternoon (GLMM, z = −4.415, P < 0.001) and return to the colony (GLMM, z = −2.357, P = 0.0184).

3.3 | Depth of dives and effect of time of day

The proportion of dives by the shallow diving penguins in the top two metres gradually decreased each hour to just under half of all dives between 11:00 a.m. and noon, and thereafter increased (Figure 4a). Time of day also affected the proportion of dives executed by the deep-diving penguins to depths ≥10 m, with the proportion increasing until 2:00 p.m. and thereafter decreasing (Figure 4b). Even though the shallow-diving birds mainly dived within the top 4 m, all the penguins dived to depths greater than 4 m, and did so at least once per hour between 07:00 a.m. and 6:00 p.m. (Figure 4a).

3.4 | Post-dive and post-bout surface intervals

The time the birds spent on the surface after a dive ranged from 1 to 3,813 s. The frequency of occurrence of surface time intervals was unimodal for shallow-diving penguins at 1–5 s (Figure 6a) and for deeper-diving penguins at 11–15 s (Figure 6b). All penguins spent periods of 3 min or more at the surface, and though these occurred throughout the day, the highest frequency occurred before 9:00 a.m. and then after 4:00 p.m. Of all the surface intervals ≥3 min, the majority lasted between 3 and 10 min, but 17% ranged between 10 and 20 min, 4% were between 20 and 30 min, and 3% were greater than 30 min.

Bouts of dives occurred throughout the day, and the post-bout surface intervals generally ranged from 73 to 154 s (Table 2). However, there was a significant difference in the post-bout surface intervals between the blocks of time (χ^2 = 14.44, df = 3, P < 0.01), and there was also a significant interaction between diving strategy and block of time (χ^2 = 19.148, df = 3, P < 0.001). The shallow-diving penguins had longer surface intervals following a bout of dives before 9:00 a.m. compared with other times of the day, whereas the deeper-diving penguins rested for longer periods between bouts of dives in the afternoon compared with the morning (Table 2).

3.5 | Vulnerable time at sea

During a single dive, the shallow-diving penguins swam within the top 2 m for 1–38 consecutive seconds (Mdn = 2 s) and the deeper-diving penguins spent 1–23 consecutive seconds (Mdn = 1 s) in this depth range. The sustained time within the top 2 m occurred throughout the day.

There was a significant difference in vulnerability across the day (χ^2 = 53.244, df = 11, P < 0.001) and between the shallow and deep divers (χ^2 = 96.596, df = 1, P < 0.001). The shallower-diving penguins were more vulnerable to potential interactions with watercraft each

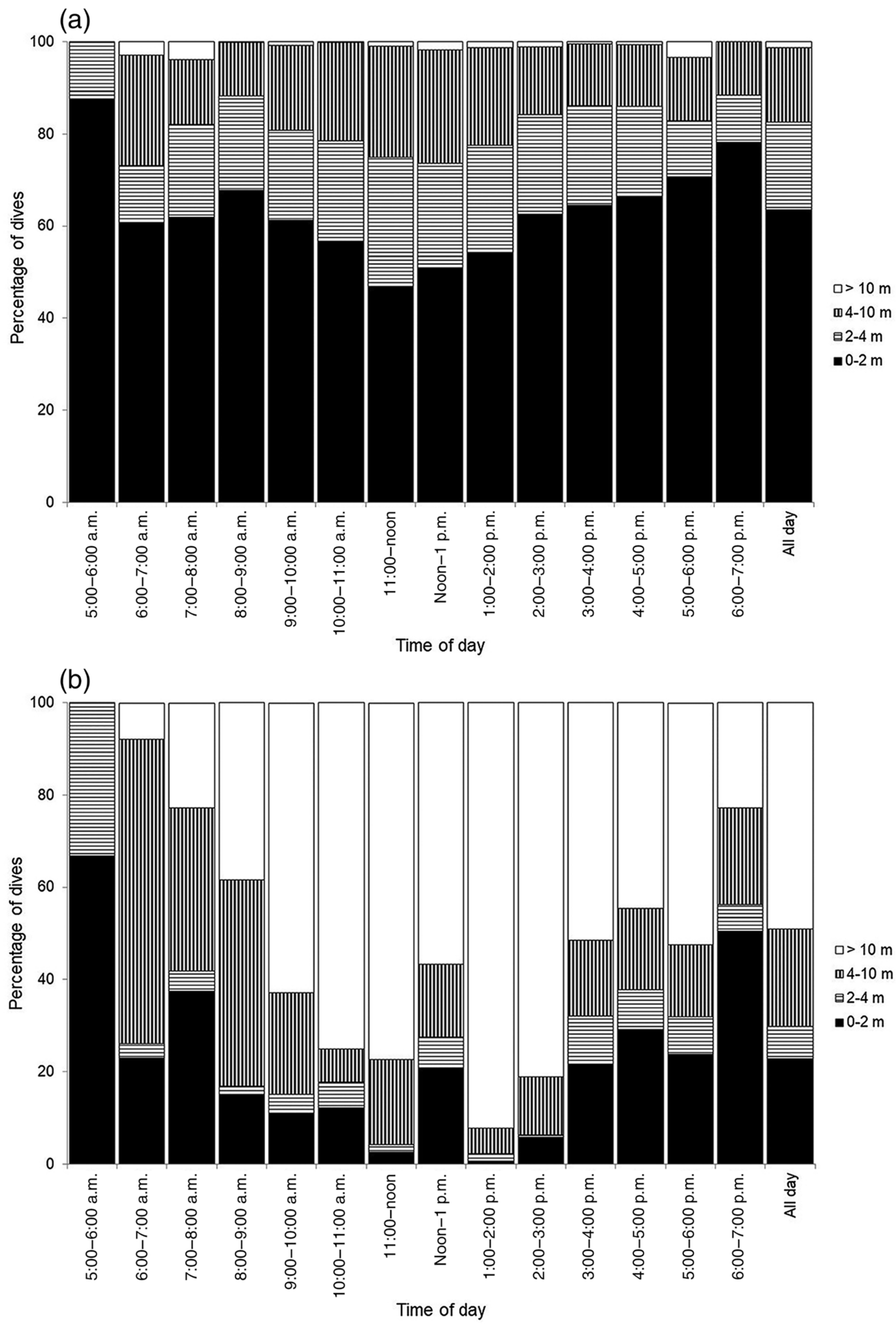

FIGURE 4 The percentage of all dives each hour, and for the whole day, to each depth category for (a) shallow-diving and (b) deep-diving little penguins

hour, being present in the vulnerable zone for more than two-thirds of each hour (Figure 7), and for an average of 613 ± 33 min day^{-1}. However, the deeper-diving penguins were vulnerable for at least one-third of each hour (Figure 7), and for an average of 320 ± 65 min day^{-1}. Time of day affected vulnerability for the shallow-diving birds only, decreasing in the middle of the day (Figure 7).

3.6 | Seasonality of trauma

There was a difference in the rate of mortality due to physical trauma between seasons (χ^2 = 21.6, df = 3, P < 0.001). The highest rate of mortality occurred in summer (53% of trauma cases), and then in spring (24% of cases) (Figure 8), whereas the lowest rates occurred in winter (9%) and autumn (13%). However, summer was the only season that had a significantly different proportion of deaths (Table 3).

4 | DISCUSSION

These findings confirm that little penguins' diving behaviour predisposes them to risk of injury or disturbance by watercraft regardless of the foraging depths they use. All penguins were in the water at a time of day that coincided with recreational boat use in the

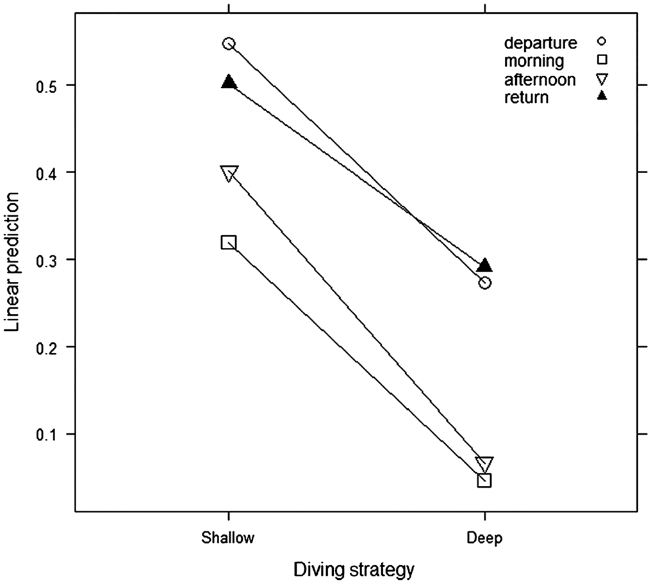

FIGURE 5 An interaction plot based on the least-squares means of the proportion of travelling dives during departure, morning, afternoon, and return for shallow and deep-diving little penguins

TABLE 1 Pairwise contrasts of the proportion of travelling dives throughout the day for shallow and deep-diving penguins using least-squares means

	Shallow		Deep	
Time of day contrast	*t*	*P*	*t*	*P*
Departure and morning	4.106	0.0004	3.089	0.0130
Departure and afternoon	2.811	0.0288	3.005	0.0166
Departure and return	0.820	0.8447	−0.244	0.9948
Morning and afternoon	−1.578	0.3945	−0.297	0.9908
Morning and return	−3.285	0.0071	−3.333	0.0061
Afternoon and return	−1.934	0.2190	−3.266	0.0075

Departure: 5:00–09:00 a.m.; morning: 9:00 a.m.–noon; afternoon: noon–4:00 p.m.; return: 4:00–6:00 p.m.

local areas, as determined by surveys of recreational boat usage (Ryan et al., 2015; Sumner et al., 2008; Sumner & Williamson, 1999). All the penguins swam within the top 2 m, either during travelling, shallow dives, or the ascent and descent phases of a deeper dive. They all spent short periods of time on the surface after a dive and extended periods of time on the surface throughout the day. However, it is assumed that the biggest risk to the birds is when they are on the surface or in the top 2 m. This is because typical watercraft used in the areas that the penguins forage during chick rearing, i.e. Cockburn Sound, west side of Garden Island, Warnbro Sound and Comet Bay (Figure 1; B. L. Cannell, unpublished data), have a draft range of 0.3–1.7 m. Therefore, the shallow-diving penguins are more than twice as vulnerable as deeper-diving penguins to interactions with watercraft throughout their day at sea. This study represents the first published research estimating the potential impacts of vessel strike on little penguins, based on their travelling and foraging behaviour.

Management options to attempt to reduce collisions with marine fauna globally have included recommended or obligatory routes, speed restrictions, and the development of marine protected areas (e.g. Hazel et al., 2007; Laist & Shaw, 2006; Tyne et al., 2015). Although the Penguin Island colony is located within a gazetted marine park, there are a few restrictions on motorized watercraft in some of the areas the penguins use within the park. Even if the restrictions were adhered to, these are unlikely to solve the problem. Although motorized watercraft are restricted to travelling at 8 kn (~4.1 m s^{-1}) immediately surrounding Penguin Island, (State Law Publisher, 2016), windsurfers and kite surfers do not have to comply with such restrictions. Furthermore, these, as well as high-speed motorized watercraft, can also use the majority of the bays outside the marine park, as do the penguins. Regardless of the type of watercraft used in the coastal areas, they are all likely to travel faster than penguins, whose estimated travelling speed is 1.1–1.8 m s^{-1} and top speed is 3.3 m s^{-1} (Bethge et al., 1997; Kato et al., 2006). This means that the penguins may not be able to swim fast enough to avoid oncoming watercraft. As travelling penguins are not visible while underwater and, in this study, remain submerged for up to 18 s, they may not be detected by a watercraft operator. Therefore, they can be unknowingly struck, as happens for even large marine fauna, such as turtles, manatees, dolphins, and even whales (e.g. Hazel et al., 2007; Laist et al., 2001; Parks et al., 2011).

Apart from travelling dives, all the penguins performed dives with undulations within the top 2 m of the water column. Undulations within a dive are likely to indicate a chase, and perhaps capture of prey (Simeone & Wilson, 2003), and the shallow-diving penguins had a greater proportion of such dives in the top 2 m than the deep-diving penguins. Even in the middle of the day, when all the penguins tended to dive deeper, almost half of the dives by the shallow-diving penguins were in the top 2 m. As little penguins from Penguin Island headed predominantly downwards and chased prey close to the sea bed (Ropert-Coudert, Kato, Wilson, & Cannell, 2006), it is likely that the shallow-diving penguins, in particular, largely confined themselves to foraging in shallow waters. In the study area, shallow waters (<4 m) extend up to 4 km from the coastline (Figure 1). Some of these shallow waters are also adjacent to existing boat ramps or launching areas (Figure 1); thus, boating activity is likely to be concentrated in these areas. In fact, the time of peak departures from, and arrivals at, boat ramps (i.e. 6:00–10:00 a.m. and noon–3:00 p.m. respectively; Ryan et al., 2015) coincides with penguin foraging activity. The situation near boat ramps is even more problematic for shallow-diving penguins. Not only are they more vulnerable to collisions in the morning during peak departures, but penguins foraging in shallow waters near boat ramps would not be able to dive deeper to safety, and hence would be more vulnerable to collisions with watercraft than the deeper-foraging penguins.

Proximity to boating not only threatens the penguins' safety, it may also compromise their capacity to feed and, ultimately, their breeding success, as has been identified for other waterbirds

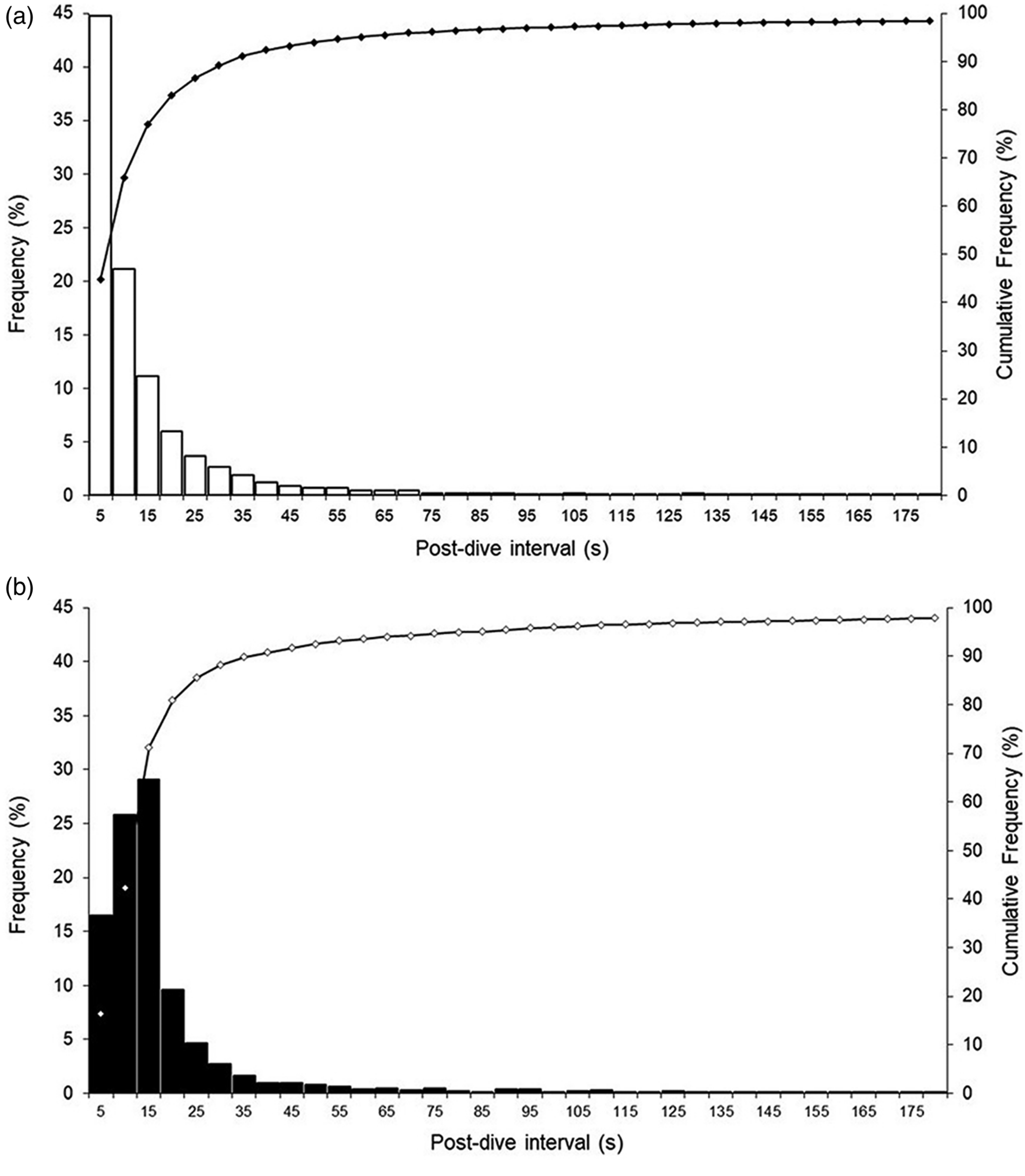

FIGURE 6 The frequency distribution and cumulative frequency of post-dive intervals for (a) shallow-diving and (b) deep-diving little penguins

(Bellefleur et al., 2009; Knapton, Petrie, & Herring, 2000). Following a dive, the penguins spend a recovery time on the surface during which they replenish their supplies of oxygen (Butler & Stephenson, 1987) and prepare the oxygen load for the next dive (Wilson, 2003). The duration of time spent on the surface is greater following a bout of dives. But anecdotal evidence from observations of little penguins at sea suggests that they dive as boats approach (Watterson, 2001; R. Donaldson, April 2004, personal communication). Thus, boat traffic could affect the recovery of the penguins' oxygen stores, which in turn could impact their ability to dive repetitively (Walton, Ruxton, &

TABLE 2 Back-transformed least-square mean (*SE*) duration of post-bout surface intervals (seconds) for shallow and deep-diving penguins, with the *t*-value (*P*-value) of pairwise contrasts between blocks of times for each diving strategy. Note that only significant contrasts have been tabulated

Time of day	Shallow	Deep
Departure	143.5 (17.4)	108.8 (17.0)
Morning	89.2 (10.6)	85.7 (15.6)
Afternoon	73.4 (6.6)	154.0 (26.9)
Return	86.2 (9.3)	109.2 (18.2)
Time of day contrast		
Departure and morning	3.148 (0.010)	
Departure and afternoon	5.153 (0.001)	
Departure and return	3.578 (0.0022)	
Morning and afternoon		−2.596 (0.0483)

Departure: 5:00–09:00 a.m.; morning: 9:00 a.m.–noon; afternoon: noon–4:00 p.m.; return: 4:00–6:00 p.m.

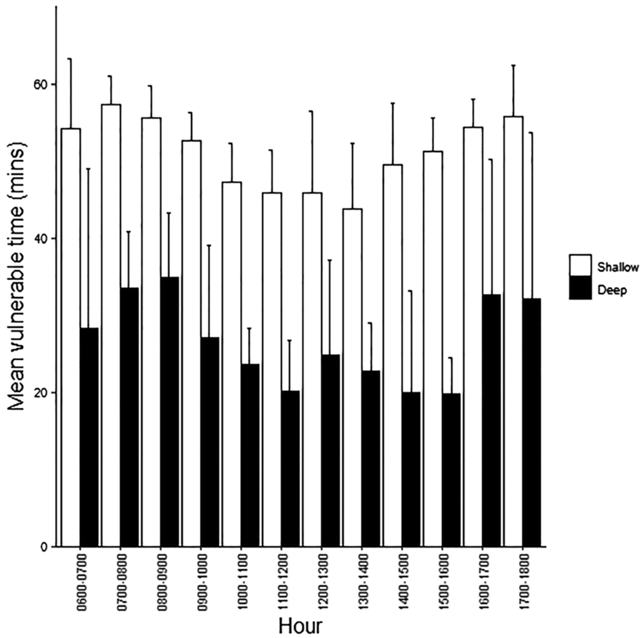

FIGURE 7 The average total minutes per hour that shallow and deep-diving little penguins were in a vulnerable position for collisions with watercraft (i.e. on the surface and within the top 2m)

Monaghan, 1998), and hence their ability to catch sufficient prey to maintain themselves and feed their chicks. Furthermore, the gut motility of penguins, and hence digestion, is greater when they are on the surface (Peters, 2004; Ropert-Coudert et al., 2004), and adult penguins empty their entire stomach contents within approximately 4 hr of ingestion (Wilson, Ryan, & Wilson, 1989 and references within). Although this has not been confirmed for little penguins, it is possible that prey caught by chick-rearing penguins at the beginning of the day may be used for the maintenance of the individual, whereas those caught in the afternoon are for chicks. Thus, interruption on the surface can slow down digestion, potentially leaving less time to acquire food for chicks. Additionally, as there is an afternoon peak in the return to boat ramps near Penguin Island, then there is likely an increased interruption of penguin activity on the surface in the early afternoon. This may reduce the amount of food that penguins can bring back to their chicks. The deeper-diving penguins had a greater frequency of longer recovery periods following both individual dives (11–15 s) and bouts of dives in the afternoon; thus, they potentially had a greater risk of having their recovery/anticipatory time interrupted. In addition to these relatively short periods on the surface, all the penguins spent long periods on the surface, particularly during times of relative diving inactivity in the early morning and late afternoon. Both shallow and deep-diving penguins are therefore vulnerable to interactions with watercraft, whether this be from (a) interruption of their surface recovery time and oxygen replenishment, (b) impacts on digestion, or (c) collisions while they are on the surface.

There is little doubt that penguins can potentially be impacted by watercraft in a wide range of situations, but can they successfully avoid the watercraft? Just over a quarter of the dead penguins found over 9 years had injuries likely to be caused by watercraft, and it is clear that these interactions can be fatal. It is not possible to determine the absolute numbers of penguins likely to be affected by watercraft, given that it is estimated that 1–60% of penguins that die at sea are likely to be found (Dann, 1991). However, using the long-term average of the proportion of nestboxes used for breeding within different seasons (penguins from Penguin Island rear chicks anytime from June to January; B. L. Cannell, unpublished data), and multiplying this by recent population estimates (Cannell et al., 2011), then there would be an average of 300 chick-rearing penguins using the local waters each day in winter, 380 in spring, 16 in summer, and 10 in autumn. This equates to 5,120–9,808 ‘vulnerable minutes per day’ in summer (i.e. 16 penguins × 320 min to 16 × 613 min) and 121,600–232,940 min in spring (i.e. 380 × 320 min to 380 × 613 min). The number of boats surveyed using nearby boat ramps in 2013 ranged from approximately 450 to 2,000 per month in spring, 1,500 to 2,500 in autumn (March and April only), and 1,600 to 2,700 per month in summer (Ryan et al., 2015). Even though there are more boats in summer but many fewer apparent vulnerable minutes per day, why is the mortality rate due to injury much higher in summer? The answer is linked to the penguins' annual cycle. In WA, the penguins moult over a 2 to 3-week period during the summer months. Thus, during the summer the penguins are generally either building up fat reserves for moulting or have completed their annual moult and have departed the colony for a month or longer. During both pre and post-moult, the penguins can forage further from the island. So, their range extends from some 30 km north and south of the colony during chick rearing to 200 km or more at other stages within the annual cycle (B. L. Cannell, unpublished data). However, regardless of the distance travelled from the colony, the penguins have been observed to primarily remain within 10 km of the coast (B. L.

FIGURE 8 Dorsal laceration on a little penguin. This type of injury is typical of those due to watercraft injury (for further information, see Cannell et al., 2016)

TABLE 3 Critical values for the differences in proportions of mortality due to trauma in summer, autumn, winter and spring

	Proportion difference	Critical value	Significant
Summer versus autumn	0.4	0.251	Yes
Summer versus winter	0.44	0.240	Yes
Summer versus spring	0.29	0.274	Yes
Autumn versus winter	0.04	0.184	No
Autumn versus spring	0.11	0.227	No
Winter versus spring	0.15	0.214	No

Cannell, unpublished data). Therefore, the number of boats that they are potentially exposed to also increases, especially considering (a) the presence of marinas, harbours, 30 boat ramps, and moorings within the extended range (Department of Transport, http://www.transport.wa.gov.au/imarine/boating-facilities.asp), and (b) recreational boaters with larger watercraft cover more expansive areas (Sumner et al., 2008). It is likely that the probability of collisions or other negative impacts will increase with the increasing boat usage in the south-west region (Department of Transport, 2011; Sumner et al., 2008), and thus effective management strategies must be developed.

Which areas should the management strategies target? It is possible to determine the areas within a 30 km radius of the colony that were likely to be used by the penguins during this study, based on (a) the number of travelling dives, (b) the depths of other dives, (c) the evidence that little penguins tend to feed near or at the sea bed (Kato et al., 2006; Ropert-Coudert, Kato, et al., 2006), or presumably other raised structures such as reefs, and (d) known foraging areas used by the penguins from this colony in other studies (B. L. Cannell, unpublished data). For example, the deeper-diving penguins exhibited few typical travelling dives throughout the day but were diving mainly to depths greater than 10 m from early morning. As Warnbro Sound is close to the colony and up to 19 m deep, it is likely that these penguins were foraging in this area, potentially for the majority of the day. Similarly, the shallow-diving penguins made fewer than 40 dives per hour before 8:00 a.m.; only approximately half of these were classified as travelling dives, and some of the hourly maximum dives executed by the shallow-diving penguins were to depths of 12 m or more during these hours. It is likely, therefore, that these penguins were foraging within Warnbro Sound in the morning. However, the shallow-diving penguins did execute many more travelling dives throughout the day, and their maximum depth each hour typically ranged within 5 to 15 m. Outside Warnbro Sound, such depth profiles are found within Cockburn Sound, west of Garden Island, and within Comet Bay (Figure 1). Therefore, it is likely the shallow-diving penguins travelled and foraged in at least one of these areas for the majority of the day. However, during the incubation stage, the home range of the penguins increases (B. L. Cannell, unpublished data). It is also likely to increase during the pre and post-moult phases, which occur during the summer, when mortality due to watercraft injury was the highest. It is thus clear that effective management strategies across a larger area than currently covered are necessary to minimize the risk to penguins.

From our results, the risk profile to a penguin differs depending on its diving behaviour, but does this alter how we manage the areas that the penguins utilize? The northern end of Comet Bay and all but a small section of Warnbro Sound lie within the boundary of the Shoalwater Islands Marine Park (Figure 1), so these areas have fairly comprehensive management objectives and strategies. However, all forms of commercial and recreational fishing, and motorized boating (including water skiing, jet-skiing, windsurfing, and kite surfing) are allowed in the majority of the park (Department of Environment and Conservation, 2007). With increasing pressure on the coast, it is imperative that we develop dynamic management strategies that are flexible enough to incorporate changes both spatially and temporally, if needed, as more information on little penguin ecology is obtained. For example, it may be necessary to have different management zones for shallow and deep waters within the coastal bays used by the penguins, to have variable speed limits in specific areas based on time of day (i.e. slower in the afternoon as the penguins return to the colony), and to alter the area of the management zone based on the annual stage of the resident penguins' cycle. Equally, the depth that the penguins utilize may be impacted by prevailing environmental variables such as water temperature and the depth of thermoclines, which can influence the type and location of prey (e.g. Ropert-Coudert, Kato, & Chiaradia, 2009). Furthermore, it is essential to identify foraging hotspots and the home range of juvenile and adult penguins, and to determine if these change within and between years. As such, different management strategies may be necessary dependent on penguin life stage, and the strategies may have to adapt based on a suite of environmental criteria. Additionally, it is essential that the strategies also include various methods to educate the general public about little penguin ecology. This is because the policing of applicable regulations cannot cover the penguins' entire foraging habitat all the time. These strategies must be aligned in both the state and local government agencies to ensure that the recreational needs of the people are matched with the conservation needs of the little penguins from Penguin Island. Importantly, to avoid serious impact on the penguin population, it will be necessary to consider the implications of additional structures, such as boat ramps, within the penguins' home range using robust methods such as decision-support tools.

However, such potential conflict between people and penguins is not only restricted to the Penguin Island colony. A second nearby colony, located on Garden Island (Figure 1), lies within the busiest embayment in WA (Department of Environment, 2005) and is accessed by a range of watercraft from small recreational boats to large commercial ships. Furthermore, many little penguin colonies across southern Australia and New Zealand are also located close to urban areas with access to boating, and the rate of boat ownership, at least in Australia, has increased since 2012 (http://www.roymorgan.com/findings/7109-high-tide-boat-ownership-rising-in-australia-201701170931). Therefore, the Penguin Island colony is used to highlight (a) that recreational watercraft activity can be deleterious to little penguins, and (b) that the diving behaviour of the penguins should be taken into consideration when producing management plans or assessing development proposals such as boat ramps, marinas, and ports. As such, effective dynamic management strategies must necessarily be colony specific and must be based on the colony's home range and foraging habitat. They must also include proactive monitoring of environmental variables and regular programmes to search for dead penguins within the colony's home range. Differences in diving strategies between genders or life stage must be included to ensure that no particular group is unfavourably impacted by watercraft in their home range. Finally, peak boating activity near boat ramps coincides with penguin foraging behaviour and increased time resting on the surface in the afternoon. Therefore, alternative locations for boat ramps outside a colony's foraging range should be considered to ensure that vessel strikes on penguins are minimized whilst addressing the growth in recreational boating.

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The authors declare there are no conflicts of interest.

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