RESEARCH ARTICLE

Behavioral responses of Australian fur seals to boat approaches at a breeding colony

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Abstract

In Australia, a multi-million-dollar industry is based on viewing the Australian fur seal (*Arctocephalus pusillus doriferus*), predominantly through boat visits to breeding colonies. Regulation of boat approaches varies by site and no systematic investigations have been performed to inform management guidelines. To investigate possible effects of disturbance, experimental boat approaches were made to a colony at Kanowna Island in northern Bass Strait and seal responses were monitored using instantaneous scan sampling. Colony attendance (individuals remaining ashore) was found to be influenced by approach distance and time of day, but was not affected by environmental variables or season, whereas onshore resting behavior was influenced by approach distance, time of day, ambient temperature and wind direction. Onshore resting behavior decreased following experimental boat approaches to 75 m, but changes in abundance of individuals ashore were not observed at this distance. In contrast, approaches to 25 m elicited a strong response, with a steep decline in the number of individuals ashore. This response was strongest when approaches occurred in the morning, with a decline of approximately 47% of individuals, compared to a decline of 21% during afternoon approaches. With regard to onshore resting behavior, afternoon approaches to 75 m led to minimal response. The remaining three combinations of approach distance and time of day had a similar pattern of reductions in the proportion of individuals engaging in onshore resting behavior. The strongest response was again seen during approaches to 25 m conducted in the morning. These behavior changes suggest that unrestricted boat-based ecotourism at Australian fur seal colonies has the potential to increase energy expenditure and reduce the number of seals ashore. Increasing minimum approach distances to ≥75 m and/or restricting visits to afternoons may minimize these impacts at Kanowna

Island during the post-molt and non-breeding seasons. As several studies have demonstrated considerable intra-species variation in seal responses to boat approaches, research at other colonies is needed before these findings can be generalized to the remainder of the Australian fur seal population.

Introduction

Despite their association with the marine environment, pinnipeds must haul-out on land or ice to rest, evade marine predators, and molt. In addition, they give birth and nurse their young ashore (Gentry and Kooyman 1986; Riedman 1990). While ashore, seals utilize sight, smell and hearing to detect potential above-water threats and to perceive the level of risk these threats present to their survival (Frid and Dill 2002; Nordstrom 2002). When a perceived above-water threat is detected, and individuals deem this threat to be significant, seals will respond by fleeing to the relative safety of the water (Cowling et al. 2015). In gregarious pinnipeds, individuals often detect threats and perceive risk based on the responses of their neighbors, leading to large-scale cascading responses in densely occupied areas that can result in injuries and have significant impacts on colony attendance (Barton et al. 1998; Jay et al. 1998; Stirling 1972).

Pinniped-based ecotourism activities make use of seal haul-out behavior to observe individuals in their natural habitat (Kirkwood et al. 2003). Although the purpose of ecotourism is to give patrons the opportunity to observe animals in the wild engaging in typical behaviors (Orams 1995), ecotourism-based human interactions may instead alter pinniped behavior by initiating responses indicative of predation risk (Frid and Dill 2002). Such responses can interrupt vital activities, increase energy expenditure, reduce breeding success and even cause injury or death (Boren et al. 2002; Marmion 1997; Shaughnessy et al. 2008).

Various environmental factors have the potential to influence a seal's ability to detect threat stimuli and, thus, may also affect responses to anthropogenic disturbance. Wind strength and direction can greatly affect both olfactory and auditory detection of a potential threat (Riedman 1990). Also, sea conditions may influence the willingness of individuals to return to the water, potentially confounding any response to boat-based disturbance. In addition, distance, speed and direction of anthropogenic approach can be important factors in perceived risk, further influencing a seal's response (Frid and Dill 2002; Shaughnessy et al. 2008).

The Australian fur seal (*Arctocephalus pusillus doriferus*) is one of the world's least abundant fur seals and is endemic to Bass Strait, southeastern Australia (Kirkwood et al. 2010). Ecotourism operators visit Australian fur seals at numerous locations, including haul-out sites (where few pup births occur) and breeding colonies (Kirkwood et al. 2003). Previous research on Australian fur seals at haul-outs has indicated that seals there are particularly sensitive to both land- and boat-based approaches (Burleigh et al. 2008; Shaughnessy et al. 2008). When on land, the seals perceive threats by

sight, sound and smell, and generally respond by becoming alert (changing posture and looking toward the threat) and moving to the water (Kirkwood and Dickie 2006; Shaughnessy et al. 2008). Responses may be more pronounced at breeding colonies than at haul-outs, as haul-outs contain mainly adult/sub-adult male and juvenile seals, whereas colonies are densely populated with adult females and pups, groups that are particularly sensitive to disturbance (Barton et al. 1998; Boren et al. 2002; Holcomb et al. 2009). In addition, in colonies where seals have access to higher elevations individuals might perceive their distance to water as greater than seals on flat terrain, and thus sense a greater threat from the boat's approach. They may also detect the boat from a greater distance. Research on New Zealand fur seals has indicated that early detection of a threat tends to moderate responses (Boren 2001).

Despite a multi-million-dollar ecotourism industry based on visits to Australian fur seal breeding colonies (Kirkwood et al. 2003), descriptive and observational data have suggested a heightened response to above-water threats in this species. However, only limited conclusions can be drawn from such data. At the time of undertaking this study management guidelines at Australian fur seal breeding colonies varied by site and season, with minimum approach regulations ranging widely from 30 m (year-round, Seal Rocks) to between 50 m (non-breeding season, Kanowna Island) and 200 m (breeding season, Kanowna Island). These guidelines are largely based on anecdotal evidence. Needlessly strict guidelines may harm ecotour businesses, while unrestricted access could negatively affect seal populations. A recent study on the effects of boat-based approaches on New Zealand fur seals highlighted the ability of evidence-based studies to inform mitigation guidelines (Cowling et al. 2015). However, before evidence-based mitigation guidelines can be proposed for Australian fur seals, controlled studies, which account for potential confounding factors, must be conducted to assess species-specific responses to boat approaches. Therefore, the aims of the present study were to determine seal attendance and behavior in relation to controlled boat approaches at a breeding colony while accounting for potentially confounding environmental variables.

Methods

Study sites and field procedures

This study was conducted at an Australian fur seal breeding colony on Kanowna Island (39°10'S, 146°18'E; Fig. 1) in northern Bass Strait. The island is a granite outcrop with steep cliffs and tussock grass vegetation. The fur seal colony has an annual pup production of approximately 3000 (Gibbens and Arnould 2009; Kirkwood et al. 2005) and is dispersed around two main breeding areas, the larger Main Colony (north-western coast) and the smaller East Colony (east coast). Pups are born from early November to mid-December, molt their natal coat in March and are suckled through to October, with breeding females present at the colony year-round.
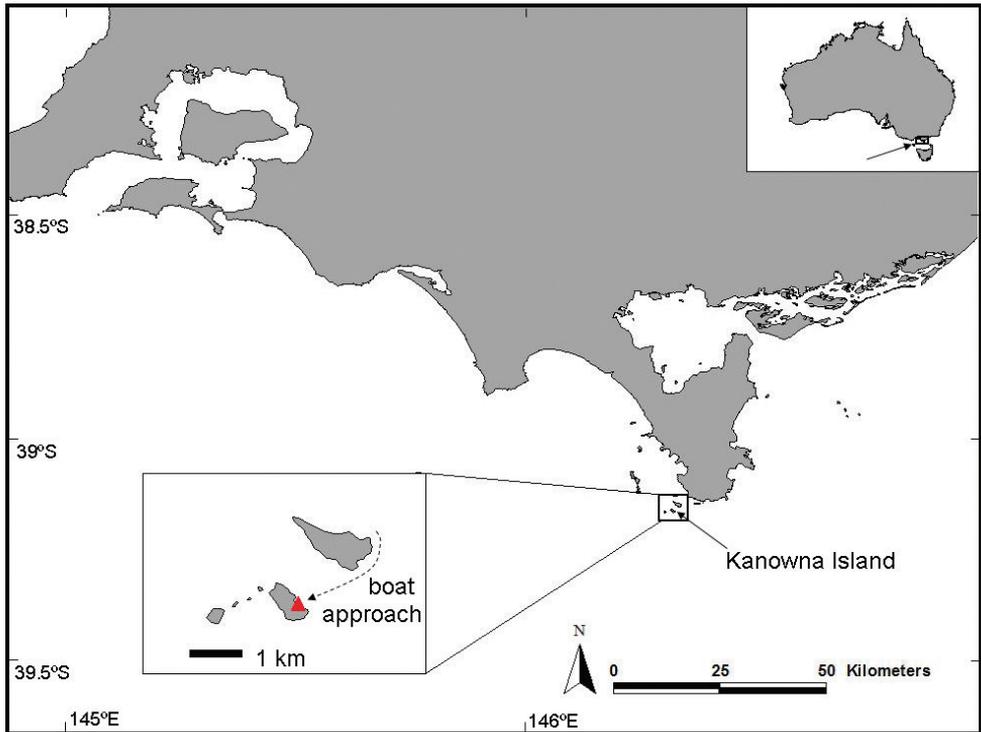
Figure 1. Location of study site at East Colony (red triangle) and direction of boat approach. Kanowna Island, northern Bass Strait.

Terrestrial access to Kanowna Island is restricted to researchers and National Park rangers (several visits a year) and the waters adjacent to the island are within a designated marine park. The then current management guidelines prohibited boats from approaching the island to less than 50 m in the post-molt period (March-October) and less than 200 m during the breeding/post-breeding period (November-February, Patkin 2005). A single commercial ecotour operator conducts 10 or less visits per year to the Main Colony, and the waters surrounding the island are infrequently used by recreational boats and fishing charters (both colonies may be exposed to these infrequent visits). Research-related boat landings occur around 10 times per year, along either the west coast or adjacent to the East Colony, with researchers occupying a plateau-area field camp away from the seals for several months each year.

Experimental boat approaches were conducted at the East Colony. The study area comprised a single stretch of smooth granite shelf where seals haul-out less than12 m from the water's edge. The shelf slopes upward toward the island's interior, with seals resting 1 to 10 m above sea level. The site had a concealed vantage point at the northern end, 14 m above the study area's highest point, from which an observer had an unobstructed view of all seals present. Two digital video cameras (GZ-MG630 and GZ-MG680, JVC, Yokosuka, Japan) were placed at this vantage point to record colony

Table 1. Description of boats used in experimental approaches to the Kanowna Island Australian fur seal colony and the number of approaches conducted by each.

Boat	Length (m)	Engine (# × hp)	# of approaches
Cellana	5.4	2 × 60	4
Sea Eagle	8.0	2 × 150	1
Prom Adventurer	10.0	2 × 250	33

attendance and seal behavior for 30 min prior to, 15 min during and 60 min after each experimental boat approach. The number of seals descending from the hinterland of the East Colony (a portion of the island's elevated interior approximately 10–200 m from the shore that the seals access using two narrow paths) was counted by an observer during the same sampling periods.

Experimental approaches were conducted by three boats ranging in length from 5.4 to 10 m, with the majority (87%) conducted by the 10 m vessel (Table 1). The experimental approach procedures were developed based on a mix of the then current regulatory guidelines and the approach technique at other non-naive colonies/haulouts in the region. Logistic constraints limited this study to two approach distances, initially set at 25 m and 50 m from the shoreline, 50 m being the then current minimum approach protocol. A pilot study revealed strong responses at 50 m and, consequently, the distances were changed to 25m and 75 m. Thus, the experimental distances bracketed the current management guidelines. On each approach, the boat moved at a speed of 25 kn (50 km·h^{-1}) from an out-of-sight point, came into sight 1.5 km offshore toward the study area, slowed to 5 kn (10 km·h^{-1}) at 500 m and proceeded to one of the two approach distances (selected at random), where it remained for 15 min then departed on the same path. A handheld range finder (accuracy ± 0.91 m, Bushnell Yardage Pro Sport 450, Overland Park, KS USA) onboard each boat ensured approach distances were accurate. Time of day, meteorological conditions including ambient temperature, wind speed and wind direction (onshore or offshore) and sea state (i.e. calm, choppy, rough) were recorded for each approach. Wind speed and direction were subsequently transformed to a linear vector where values below 0 represented the speed of offshore wind and values above 0 represent the speed of onshore winds, hereafter referred to as direction-adjusted wind speed.

Seals in the study area were left for greater than 4 h to recover/redistribute between approaches and a maximum of two approaches was conducted per day (one in the morning between 08:00–11:00; one in the afternoon between 13:00–16:00). On average, there were 3.4 ± 0.9 days between experimental approach days. Approaches were conducted during two sampling periods: summer post-breeding (January-February), when most adult and sub-adult males have dispersed and the colony is occupied primarily by 2–3-month-old pups, adult females and juveniles; and winter post-molt (May-August), when the colony comprises mainly 6–7-month-old pups, adult females and juveniles (Warneke and Shaughnessy 1985).

Data collection

Digital video recording enabled observations of a large number of individuals simultaneously. Videos were analyzed using instantaneous scan sampling (Altmann 1974; Boren et al. 2002) at 5-min intervals pre-approach, at 1-min intervals while the boat was at the designated approach distance (to maximise our ability to detect rapid behavioural changes occurring during the peak disturbance times), and at 5-min intervals for 60 min post-approach (26 scans per boat approach). Boat arrival was defined as T= 00; thus, boat departure occurred at T= 15 and the end of the sampling period at T= 75. During 11 trials, observations ended prematurely due to events such as inclement weather, an unrelated boat within sight of the colony or equipment failure.

During each instantaneous scan, the age/sex, posture and behavior of each individual within the study area was recorded. Age/sex classes comprised adult males, adult females, sub-adult males, juveniles and pups, and were based upon Goldsworthy and Shaughnessy (1994), with classes differentiated based on size, head and snout shape, shoulder development and pelage (Table 2). The ethogram used to classify behavior was modified from that used by Boren et al. (2002) for instantaneous scan samples at colonies of New Zealand fur seals (*A. forsteri*). Seals were classified into one of five behavior classes: *At Rest*, *Comfort*, *Active*, *Mother-pup* or *Interaction* (Table 3). Due to the rare occurrence of *Interaction* behaviors (less than 1 per scan), these were included in the *Active* category. To quantify colony-wide behavioral responses to vessel approaches, the above behavior classes were incorporated into one of two categories, *Resting* (including *At Rest*, *Comfort*, and *Mother-pup*) or *Active* (Boren et al. 2002).

Pre-approach age/sex composition, attendance and behavior were calculated from the averaged pre-approach scans for each trial. Due to the variation in attendance numbers between trials, for inter-trial comparisons all data were converted into a proportion of pre-approach attendance. For the same reason, the number of *Resting* seals ashore (versus *Active*) was also converted into a proportion of the number of seals ashore at baseline for inter-trial comparisons. Recovery time was measured at the colony level based upon the time it took for the study area to return to pre-approach numbers and activity levels (as a proportion of pre-approach numbers). The use of pre-approach attendance numbers to measure recovery assumes that the same number of seals that entered the water in response to approach returned to the study area however because we do not have information on individual identity of seals we only make our inferences at the colony level and do not assume that the same seals present pre-disturbance are those returning post-disturbance. Studies on other pinnipeds indicate that adult females exhibit extremely high site fidelity and generally do return to the same area following a benign disturbance (Kovacs and Innes 1990; Lidgard 1996). Accordingly, and as individuals that fled could not be tracked individually, it was assumed that they remained in the water until they returned to the study area. Additionally, the proportion of seals that remained ashore during each scan that were in the *Resting* category (versus the *Active* category) were analyzed. This provided activity level data that only took into account the seals that remained ashore during each scan as a further measure of colony recovery.

Table 2. Age sex classifications used for Australian fur seals derived from Goldsworthy and Shaughnessy (1994).

Age/sex class	Description
Adult males	Mature males, possessing well-developed chests, manes and shoulders.
Sub-adult males	Males, similar in size or slightly larger than adult females but distinguished from them by shoulder development, larger head and pointed snout.
Adult females	Mid-sized animals with smaller, sleeker heads than males and lacking shoulder development.
Juveniles	Smaller than adult females and sub-adult males but larger than molted pups, and with more defined muzzles and muscle tone.
Pups	Seals <1 year old, with black natal pelage until March/April, then molting to silver-grey juvenile-type pelage.

Table 3. Ethogram of seal behavior modified from Boren et al. (2002).

Behavior[1]	Definition
Resting	Lying with head down, lying or sitting with head arched in "skypointing" position, usually with eyes closed
Comfort	Grooming, scratching, shifting position, flipper-waving and other thermoregulatory behaviors
Mother-Pup	In pups, suckling; in females, nursing and/or sniffing, caressing a suckling pup
Active	Lying or sitting with head up and aware, alert or moving
Interaction	Interaction with another animal (excluding mother-pup pairs), noted if aggressive.

[1]Classes are mutually exclusive and are listed hierarchically, *e.g.*, a resting seal also engaged in a comfort behavior would rank 'Comfort', an adult female nursing a pup and engaging in a comfort behavior would rank 'Mother-Pup'.

In addition to the seals within the study area, the movements of individuals between the hinterland above it and the shoreline were monitored to determine whether seals up to 100 m inland detected and were disturbed by experimental boat approaches. Seals accessed the hinterland via two narrow pathways that were easily visible from the observation point.

Statistical analysis

Behavioral observations were correlated temporally, while also being nested into individual boat approaches (i.e. multiple serial observations per boat approach). There was no expectation that the response of seals to boat approaches should show a linear response. To account for this nested structure and the expected non-linear response, data were analyzed using Generalized Additive Mixed-effect Models (GAMMs). GAMMs were fitted to investigate the response of the number of animals ashore (Poisson error distribution with log link) and the proportion of resting individuals ashore (binomial error distribution with log link) by treating each instantaneous scan sample as a single observation in time. Experimental (boat approach distance and time of day, time since disturbance) and environmental (breeding cycle period, ambient temperature, direction adjusted wind speed, sea state) fixed predictor variables were included in the models, with a random effect of unique boat approaches. Behavioural scans (attendance and activity level) were included as response variables.

Within these models, smoothing splines (thin plate regression splines) were fitted to the time since disturbance and ambient temperature at the time of observation. Degree of smoothness was calculated via Generalised Cross Validation following (Wood 2006). The interaction between time of day, approach distance and the time since disturbance was modelled using splines fitted to the time since disturbance split by experimental factors such that individual splines were fitted for each of the four unique factor combinations of time of day (AM or PM) and approach distance (25 m or 75 m). Additional environmental variables were treated as factors (sea state and season) or linear with second-degree polynomial (direction adjusted wind speed) covariates. Residual temporal correlations between observations were accounted for (to the best of our ability) using an auto-regressive correlation structure of the order 1 [corAR1(form= ~time|ApproachTrial. no)] within the GAMM models. The most appropriate model - with or without correlation structure - was selected for via AIC. The most parsimonious models were identified using a backwards step-wise AIC based model selection. All models were fitted using the mgcv package (v 1.8–7; Wood 2006) in the R statistical framework.

To investigate the differences in baseline attendance and activity level during periods exclusive of boat approaches paired and student *t*-tests were used, following assessments for normality and transformation of data where necessary. Non-parametric data were compared using Mann-Whitney *U* tests or Wilcoxon signed-ranked tests. Unless otherwise noted, all references to proportional change regarding behavioral data were quantified relative to pre-approach values. Data are presented as the mean ± one standard error (SE) and results are considered significant at $P < 0.05$.

Results

The effects of boat approach on colony attendance

In the summer post-breeding period, a mean of 110.0 ± 12.7 seals were present in the study area prior to approaches, comprising 33.1 ± 1.9% pups, 38.8 ± 1.9% adult females, and 28.1 ± 1.4% other seals (primarily juveniles, occasional sub-adult males and rare adult males; Fig. 2). In the winter post-molt period, 146.9 ± 8.5 seals were present pre-approach, comprising 74.0 ± 2.3% pups, 23.5 ± 2.0% adult females, and 2.5 ± 0.4% other seals (Fig. 2). During the summer post-breeding period, the number of seals present pre-approach was lower during the afternoon than in the morning (t_6 = 2.627, $P = 0.039$). Time of day had no effect on pre-approach seal numbers during the winter post-molt period (t_6 = -2.194, $P = 0.071$).

Thirty-eight experimental boat approaches were conducted (18 to 25 m and 20 to 75 m). Approaches occurred between January and September with approaches ranging between 1 and 44 days apart (average: 6.2 d). Model selection on GAMMs fitted to assess the response of colony attendance to boat disturbance resulted in a final model showing the influence of approach distance and time of day to colony attendance, but no effect from the environmental variables or season (Table 4). Approach distance

Table 4. Summary results for GAMMs assessing the number of individuals ashore and the proportion of individuals resting in response to boat approaches and weather conditions. Results shown here are for the most parsimonious models selected via AIC-based model selection.

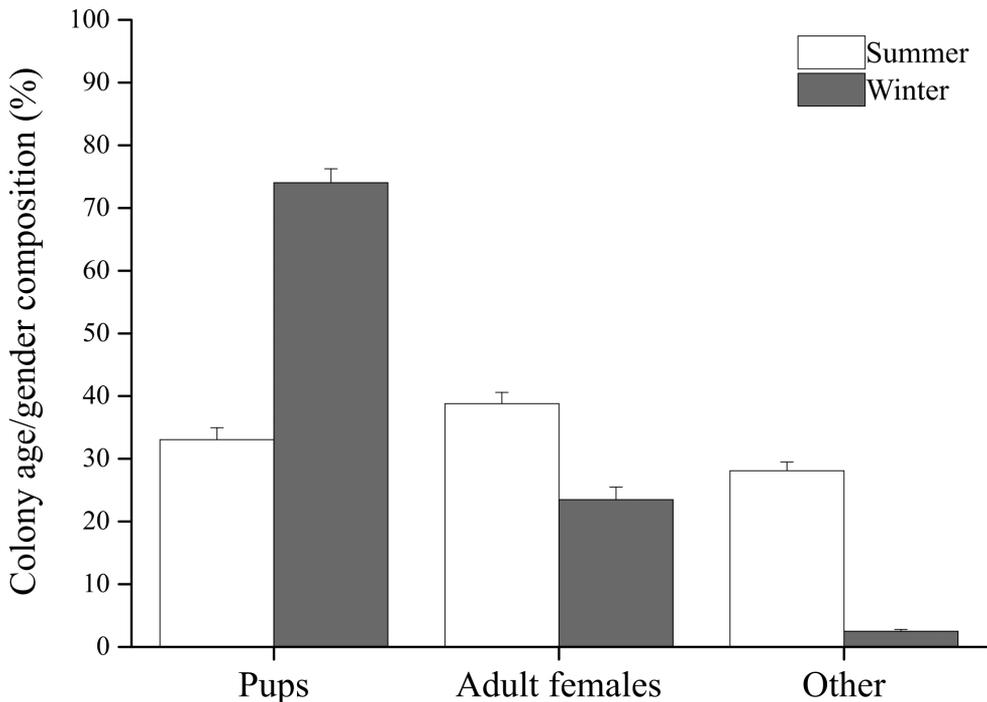| Predictor variables	Parametric coefficients			Approximate significance of smooth terms	
	Est	SE	*t*	edf	*F*
Number of individuals ashore					
Intercept	4.24	0.16	25.11		
AM_25m				7.52	8.48
AM_75m				2.19	1.84
PM_25m				7.05	4.47
PM_75m				1.00	0.22
Proportion of individuals resting					
Intercept	4.166	0.18	22.85		
Direction adjusted wind speed	-0.11	0.05	-2.08		
Temperature				3.0	5.20
AM_25m				7.3	10.85
AM_75m				6.5	17.25
PM_25m				7.9	13.58
PM_75m				1.0	4.06

Figure 2. Age and sex composition of the Kanowna Island Australian fur seal colony during the boat approach trials in the summer post-breeding period (Jan-Feb) and winter post-moult period (May-Aug). *Other* category includes juveniles, sub-adult males and adult males.
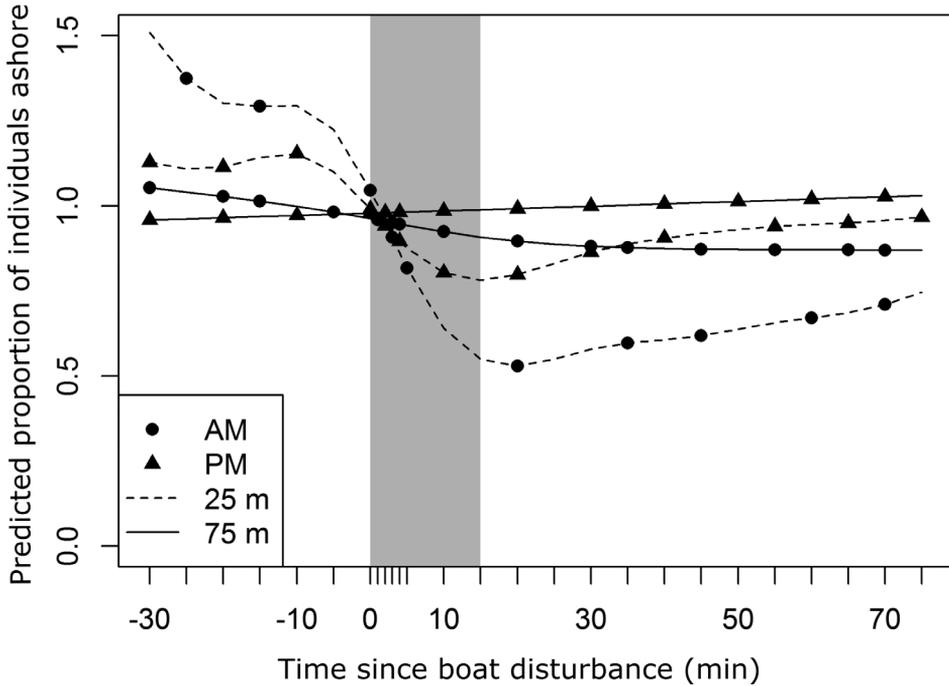
Figure 3. The GAMM predicted change in the number Australian fur seals ashore at the Kanowna Island study area in response to experimental boat approaches. Values are shown as proportions of individuals ashore centered on the count taken when the boat arrived at its' prescribed distance. Dashed lines represent 25m approaches. Solid lines represent 75-m approaches. Triangles show approaches conducted in the morning (08:00–11:00) and circles show approaches conducted in the afternoon (13:00–16:00). The grey shading shows the period the boat stayed at either 25 m or 75 m. Tick lines on the x-axis show time points where observations were recorded.

provided the strongest influence on colony attendance to boat approaches (Fig. 3, Table 4). Experimental boat approaches to 75 m showed no change in the trend in abundance of individuals ashore, with there being either a slight but steady decrease (in the morning) or increase (in the afternoon) in numbers through the observation period (Fig. 3, Table 4). In contrast, approaches to 25 m elicited a strong response, with a steep decline in the number of individuals ashore beginning shortly before the boat arrived at the 25 m point and continuing until the boat had left (Fig. 3, Table 4). This response was strongest when approaches occurred in the morning, with a decline of approximately 47% of individuals from the beginning of the boat's arrival until it left, compared to a decline of 21% when the approach was conducted in the afternoon.

There were sudden increases in the number of seals descending from the hinterland to the shore during eight (21.1%) experimental boat approaches, six in summer and two in winter (Descents by approach type and time of day: 25 m/AM = 1, 25 m/PM =2, 75 m/AM = 5). This suggests that seals distant from the shoreline study area occasionally detected the presence of the boat and perceived it as a threat.
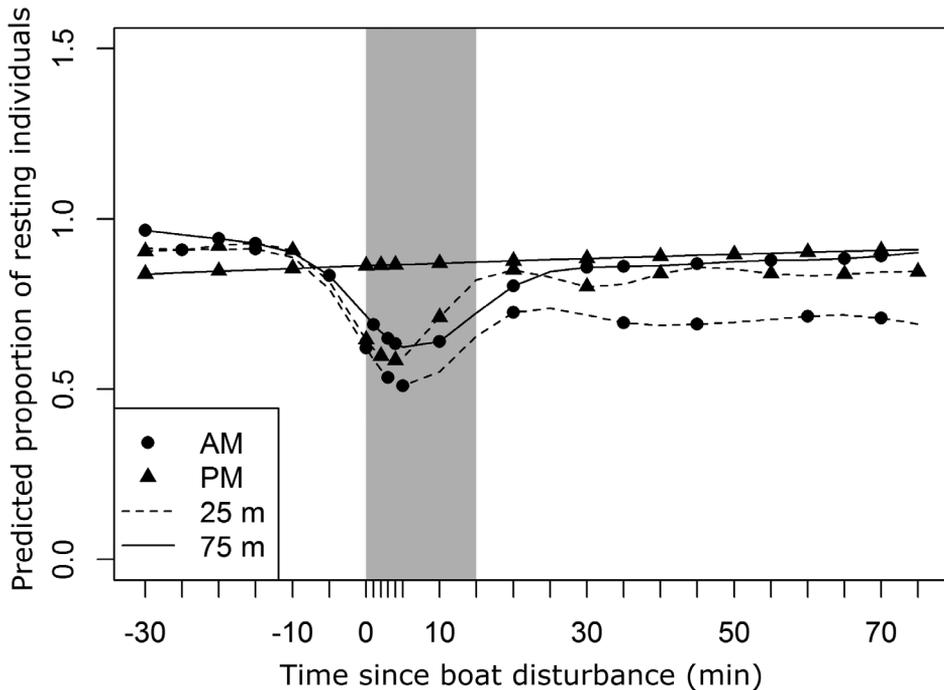
Figure 4. The GAMM predicted change in the proportion of Australian fur seals resting at the Kanowna Island study area in response to experimental boat approaches. Dashed lines represent 25-m approaches. Solid lines represent 75-m approaches. Triangles show approaches conducted in the morning (08:00–11:00) and circles show approaches conducted in the afternoon (13:00–16:00). The grey shading shows the period the boat stayed at either 25 m or 75 m. Tick lines on the x-axis show time points where observations were recorded.

Behavioral responses to boat approach

During the summer post-breeding period, prior to boat approaches, seals in the study area were engaged in the following behaviors: 60.2 ± 2.9% *Resting*, 17.8 ± 1.7% *Comfort*, 11.5 ± 0.9% *Mother-pup* and 10.0 ± 1.0% *Active*. In the winter post-molt period, prior to boat approaches, the proportions were 70.7 ± 1.9% *Resting*, 7.4 ± 0.6% *Comfort*, 12.8 ± 1.2% *Mother-pup* and 9.0 ± 1.1% *Active*.

Model selection on GAMMs fitted to investigate the influence of boat disturbance to the proportions of resting individuals ashore resulted in a final model demonstrating the influence of approach distance and time of day on colony attendance, as well as that of ambient temperature and direction adjusted wind speed (Table 4). Approaches conducted in the afternoon to 75 m showed an almost flat response with regard to the proportion of individuals resting during boat approaches (Fig. 4). The remaining three combinations of approach distance and time of day had a similar pattern in terms of the proportion of individuals resting, with reductions in the behaviours of individuals remaining ashore beginning between 5 and 10 min prior to the boat's arrival at the prescribed distance and continuing until approximately 5 min after arrival (Fig. 4).
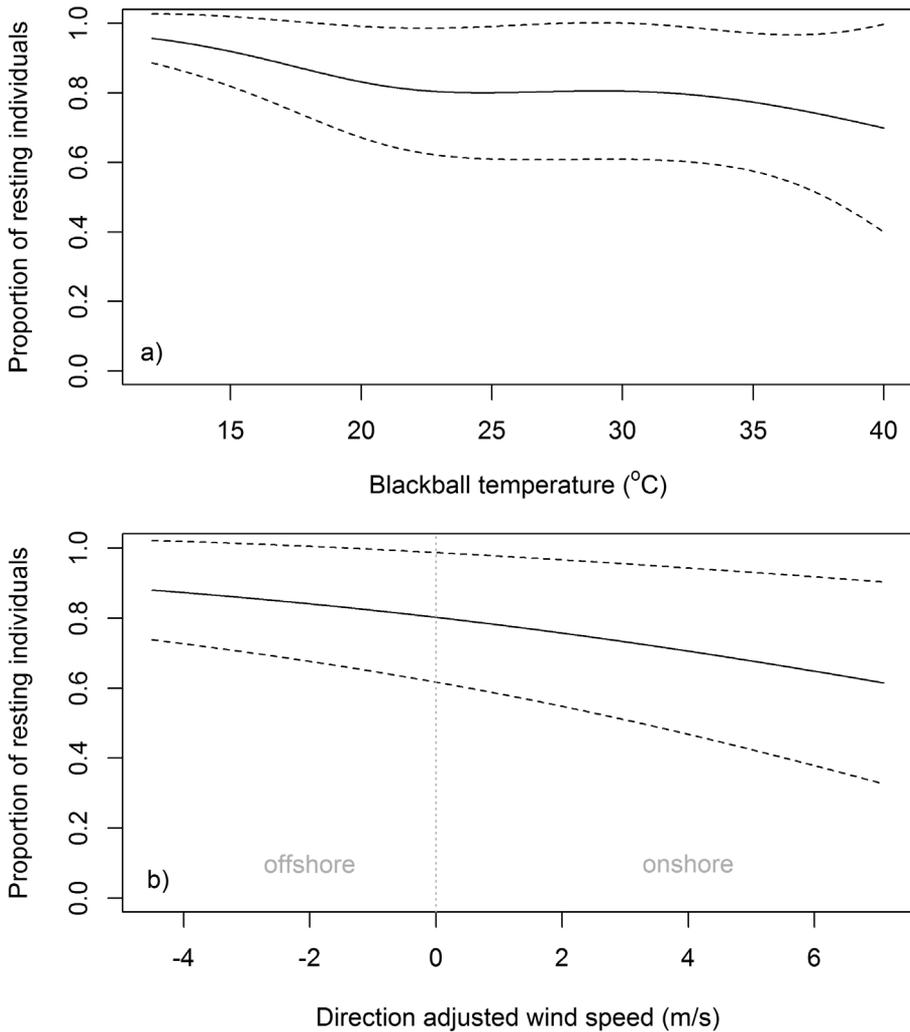
Figure 5. The GAMM predicted change in the proportion of Australian fur seals resting at the Kanowna Island study area in response to environmental conditions. **a** Blackball temperature **b** Direction adjusted wind speed.

The strongest response, determined by the steepness of decline during the disturbance period, was again seen during approaches to 25 m conducted in the morning, where the proportion of individuals remaining ashore who were resting did not recover by the conclusion of the recording period, as evidenced by the numbers of resting individuals not returning to pre-disturbance levels during the monitoring period (Fig. 4).

Weather was also found to have an effect on the proportion of individuals resting with fewer individuals resting as the temperature increased (Fig. 5a, Table 4). There was also a slight linear reduction in the proportion of individuals resting as winds turned onshore and increased in speed (Fig. 5b, Table 4).

Discussion

Australian fur seals at the Kanowna Island colony responded to experimental boat approaches to both 75 and 25 m by becoming more active ashore and responded to 25 m approaches by fleeing to the water. Of the factors examined in the present study, proximity of approach had the greatest influence on the ability of seals to detect a boat and perceive it to be a threat. Time of day also influenced the strength of responses (determined by the steepness of decline during the disturbance period) to boat approaches, while environmental factors (temperature, wind speed/direction) were only observed to affect baseline resting behavior.

Australian fur seals, like other fur seals, are thought to rely on olfaction or auditory stimuli as principle means of detecting threats when they are on land (Riedman 1990; Shaughnessy et al. 1999). This is because they are short-sighted when out of water and cannot focus on objects in the distance (Hanke et al. 2006). The results of the present study, in which individuals were disturbed by boats up to 75 m away, suggest initial detection was by olfaction or audition. However, although individuals ashore displayed increased alert behaviors, when boats remained at 75 m this did not translate into animals leaving the colony. In contrast, when boats approached to 25 m, departures occurred. As such, it appears that while olfaction/auditory stimuli play a role in the initial detection of a potential threat, individuals may not respond further until a threat is perceived to be imminent (Tripovich et al. 2012).

The most severe response Australian fur seals exhibited to boat approaches was to flee toward the water; during approaches to 25 m, this caused dramatic changes in colony attendance. The periods fur seals spend ashore at colonies are particularly important for resting, evading predators, molting, breeding and rearing young (Gentry and Kooyman 1986; Riedman 1990). Fleeing behaviors in themselves expend energy, and time spent in the water as a result of flight responses can also be energetically costly due to active movement, being alert for predators and maintaining body temperature (Donohue et al. 2000). The actual energetic costs related to fleeing behaviors in this species are difficult to determine, but could result in the need for additional rest time ashore and/or greater caloric intake.

Fleeing responses to boat approaches may have even greater implications for adult females and pups, which are of particular concern because they are bound to breeding colonies and may be more energetically constrained than other age classes (Barton et al. 1998; Boren et al. 2002; Riedman 1990). Pups are also at risk of being trampled or falling from cliffs as a result of stampedes (Mattlin 1978). In addition, if they flee into the water they would incur high energetic costs and experience greater risk of predation, as they are small and have limited swimming and diving capabilities (Donohue et al. 2000; Shaughnessy et al. 1999). The separation of mother-pup pairs and resulting interruptions to suckling behavior also have serious implications for pup survival (Boren 2001; Kovacs and Innes 1990).

Although boat approaches to 75 m did not significantly impact seal attendance, the observation that approaches to 75 m resulted in significant behavioral changes still has substantial implications. Many seals remaining ashore changed posture and stayed alert

for the entire duration of the boat's visit, investing more time and potentially more energy into vigilance behavior (Amo et al. 2006; Lidgard 1996) than they did before the boat arrived. Thus, events that appear to cause low-level disturbance without large-scale changes in attendance at Australian fur seal colonies could influence a seal's energy budget. Further investigation of the physiological impacts of disturbance on this species is warranted.

Time of day was also found to influence seal responses to boat disturbance, with individuals showing stronger responses to disturbance during morning approaches. It is possible that the weaker response observed in the afternoon was biased by afternoon trials being preceded by a morning approach, which may have habituated the seals present for the earlier approach or displaced sensitive seals to another location at the colony (Nordstrom 2002). Two approaches occurred on the same day for 80.0% of trials. Further investigation into decreased sensitivity with repeated disturbance, as well as potential temporal and density-dependent responses, is needed to fully explain these results. In relation to vessel approaches, greater caution or greater approach distances may be required at the first approach compared with latter approaches.

While colony-level responses to boat approaches were not found to differ between seasons, ambient temperature did have an effect on baseline resting behavior, with individuals more likely to be resting at cooler temperatures. However, no effect was identified with regard to the number of individuals remaining ashore during boat approaches, suggesting that temperature did not influence individual responses to threat stimuli. Cowling et al. (2015) identified a seasonal influence on seal response to such stimuli, with the proportion of New Zealand fur seals at rest decreasing during summer months. However, Cowling et al. (2015) did not measure ambient conditions directly but rather used time of year as a proxy for weather so it is not clear whether their results were temperature-related or due to other factors, such as breeding cycle. Further studies on the influence of temperature on fur seal behavior, particularly in terms of resting behavior and disturbance, is needed to clarify these relationships.

For many pinniped species, colonies are not restricted to the immediate shoreline and can often extend considerable distances and/or elevations inland (Stevens and Boness 2003). Seals resting inland may be less likely to detect an approaching boat and, because proximity to the water provides a level of security for some seals (van Polanen Petel 2005), they may perceive a higher threat level and, consequently, respond more severely than seals near the water's edge. Hence, disturbances that affect animals inland at colonies may result in extra energy expenditure due to the greater distances animals must travel to get to water, and may cause injury and even death if stampeding animals fall over cliffs or into crevasses (Mattlin 1978).

In the present study, the number of seals descending from the hinterland above the study area increased during 21.1% of experimental approaches. Three stampedes also occurred there as a result of boat approaches. During one such stampede (the final of the three) in the non-breeding season, two pups were observed to fall >10 m from a cliff and land on rock shelves below. Two of these stampedes occurred during afternoon approaches to 25 m, while one occurred during a morning approach to 75 m. Similar events were observed at a New Zealand fur seal colony due to land-based research activities, with stampedes causing several pups to be trampled to death and another pup

dying as a result of falling 10 m off a cliff (Mattlin 1978). Direct injuries or mortalities to pups resulting from boat approaches have not been observed in Australian fur seals or other pinniped species (Boren et al. 2002; Burleigh et al. 2008; Nordstrom 2002; Shaughnessy et al. 2008). Due to the relative rarity of these events, we were unable to determine which approach distance or environmental factors (e.g. wind direction) influenced hinterland stampedes. Nonetheless, these findings do suggest that guidelines at the time of this study allowing 50-m approach distances at Kanowna Island would be unlikely to entirely preclude such events. It is possible that limiting approaches to ≥75 m and to afternoons could minimise hinterland stampedes but further research would be needed to confirm this. While the infrequency of these events suggests they are unlikely to have population-level effects, such disturbance impacts are in violation of state and federal regulations protecting marine mammals (IUCN 2007; Patkin 2005). Thus, the terrain of colony and haul-out sites, particularly seal use of hinterland/elevated regions, should be taken into consideration when developing management guidelines. Haul-out sites or low-lying colonies with limited access to such areas may not need to be managed as stringently as colonies with greater variation in terrain.

There were several limitations to this study. In addition to inter-specific variation among pinnipeds, several previous studies demonstrated a high degree of intra-species variation due to factors including age/sex class present, site type, density ashore and previous exposure to humans (Barton et al. 1998; Boren et al. 2002; Shaughnessy et al. 2008). Hence, developing appropriate management guidelines is challenging without extensive species-specific investigation. As this study was conducted at a single site, interpretation of data with regard to site structure, terrain, population density and previous exposure to vessel traffic must be made with caution, limiting the generalizability of these findings to other breeding sites. In addition, analysis based on boat size and vessel-related noise could not be conducted due to logistical constraints.

Furthermore, colony attendance and onshore behaviour were treated as independent predictor variables within two separate GAMMs. There exists the possibility that different behavioral phenotypes within the population meant that only a certain class of individuals remained onshore during boat approaches – the bold individuals – as such these data may not be truly independent. Model complexity (nested data structure with non-linear responses) excluded us from examining these data using multivariate methods. Therefore, data should be interpreted with the understanding that onshore behavioural responses represent the subset of the population that remained onshore and that this subset may not be a truly random sample of the population as a whole.

In summary, the findings of the present study reveal distinct gradients of response to the approach of boats at an Australian fur seal colony influenced by both approach distance and time of day. These results suggest that unrestricted boat-based ecotourism at colonies, particularly approaches to <75 m, may have implications for energy expenditure and reproductive success in the Australian fur seal. Current guidelines, implemented following this study, now limit boat approaches to 100 m at Kanowna Island from March through October now making them unlikely to affect behaviour at this colony. However, this study was limited to a single colony and further research will be needed to generalize these results to other sites.

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