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Short Note

Directional Orientation of Harbor (*Phoca vitulina*) and Gray (*Halichoerus grypus*) Seals at Haul-out Locations in New York City

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Resting is an important behavioral and metabolic function for all animals. Relaxed immobility is typically reserved for recovery and thermoregulation, and the resting metabolic rate (RMR) comprises the largest daily activity budget for humans. However, an individual's RMR is variably influenced by the type and duration of physical exertion (Speakman & Selman, 2003). Daily energetic demands, such as foraging (Williams et al., 2004), locomotion (Williams et al., 2000), migration (Villegas-Amtmann et al., 2015), and thermoregulation (Rosen et al., 2007), are costly and, therefore, extensive periods of rest are necessary to restore/balance physical and metabolic functioning (Seibel & Drazen, 2007). These extensive periods of rest constitute a significant portion of an individual's circadian cycle and serve as both a necessary behavioral and physiological activity. However, the extensive period for rest creates a window for vulnerability to environmental threats.

For marine mammals like pinnipeds that haul out on land in communal aggregations for rest (Schneider & Payne, 1983; Calambokidis et al., 1987; Cunningham et al., 2009; London et al., 2012), a typical and constant threat is predation (Glass et al., 2021). For example, Nordstrom (2002) found that Pacific harbor seals (*Phoca vitulina richardii*) collectively select isolated haul-out sites to reduce exposure to potential terrestrial predators. In another antipredator strategy, Kingsley & Stirling (1991) found that hauled out ringed seals (*Phoca hispida*) are often oriented downwind and toward their breathing holes for a hastier escape from terrestrial predators such as polar bears (*Ursus maritimus*). Subsequently, in the same study, bearded seals (*Erignathus barbatus*) were found to haul out on the edges of large ice holes, floating ice edges, and near ice flows, where they were similarly positioned downwind and oriented toward the water (Kingsley & Stirling, 1991). Thus, the behavior of bearded seals here indicated that the safety of the individual is compromised during on-land resting periods where they are exposed to external stimuli that pose threats during their recovery.

Directional orientation in a social aggregation may also alert conspecifics to potential threats and reduce risk. This is especially true for animals in a metabolically needed resting state (e.g., pinnipeds) as they must survey proximal habitat and distal landscapes for indicators of increased danger (Schakner & Blumstein, 2013) while also using as little energy as possible since the behavioral goal is restorative in nature. Often, the tradeoff in a group is between collective or individual vigilance and population density (Roberts, 1996). Da Silva & Terhune (1988) found that larger aggregations of harbor seals (*Phoca vitulina*) increased safety as group vigilance increases with population size. Similarly, at the Anholt seal reserve in Denmark, Andersen et al. (2012) found similar anti-predator responses (e.g., alert distance, flight initiation distance, flee distance, flight duration) in harbor seals to staged anthropogenic threats and also noted that general group alertness increased with population size.

As species that typically haul out for significant periods, both harbor and gray (*Halichoerus grypus*) seals commonly aggregate in social groups at overlapping global locations (Stanley et al., 1996; Klimova et al., 2014). During these haul-out periods, the local population density may fluctuate because of the tides (Pauli & Terhune, 1987b), access (Payne & Selzer, 1989), and other environmental conditions such as temperature, precipitation, and cloud cover (Pauli & Terhune, 1987a). However, while hauled out, individuals continue to remain observant of their surroundings. Terhune (1985) observed a haul-out location near Saint John, New Brunswick, and found that harbor seals were readily vigilant; however, they decreased time spent on scanning the surroundings as their population size increased.

Pinnipeds routinely haul out at locations across the tri-state area of New York, New Jersey, and Connecticut between mid-autumn and mid-spring, which constitutes a general field season for observations between October and April (Payne & Selzer, 1989). Around New York City (NYC), sightings of harbor and gray seals are often accidental as they utilize the rivers and channels between urban landmasses and often haul out at random locations either individually or in very small groups. While these sightings are often by chance, there are select known locations within NYC that are reliable haul-out locations for seals, and the seasonal populations of harbor and gray seals are found within these urban waterways for nearly 7 mo of the year (Woo & Biolsi, 2018). Notably, NYC has an environment full of stimuli that are both threatening (relevant) and nonthreatening (irrelevant), thus providing opportunities to observe vigilance behaviors in these pinniped species. These populations are especially important to study as they are small in their overall seasonal numbers relative to other haul-out locations (e.g., eastern Long Island), yet they are exposed to large amounts of dynamic natural and anthropogenic stimuli from the immediate environment; therefore, one would expect a very high vigilance level at these NYC haul-out locations. While the effects of anthropogenic factors are not fully understood for these populations, observed directional orientation when they are hauled out may serve as a measure of vigilance that may be correlated to other environmental factors of these urban resting areas.

We documented the directional orientation of harbor and gray seals that were hauled out on Swinburne Island in NYC. Herein, we examine whether seals collectively favored orienting in the same direction or in other compass directions. We then considered whether group size and directional orientation were positively or negatively correlated or simply unrelated.

We conducted our boat-based observations at Hoffman and Swinburne Islands (40° 33' 56.9232" N, 74° 3' 0.0468" W), two artificially constructed islands in close proximity that are located in the lower Hudson River delta between the NYC boroughs of Staten Island and Brooklyn. Both islands were constructed of dredged sand from the NYC harbor and encircled with large irregularly shaped boulders. Hoffman Island, which is the larger and northern island, typically is not a haul-out location for seals, though they may be readily seen in the water surrounding the island. By contrast, Swinburne Island to the south of Hoffman Island is a reliable haul-out location for seals as they are typically found along the eastern side and within the small bay on the north side of the island (see Figure 1).

At Swinburne Island, we conducted our observations with no interaction or introduction of experimental treatments. Our observation period lasted for 1 h, which constituted ½ h before and ½ h after peak low tide. Our vessel was a 10.6-m Duffy Express Cruiser (built in the year 2000 by the Atlantic Boat Company, Brooklin, ME, USA) with a Yanmar 6CXM ETE 420HP engine (Yanmar, Osaka, Japan). While the underwater topography was relatively shallow during peak low tide, we were able to approach the island from the west within 100 m. Most observations were conducted at this distance as it also left the hauled-out populations relatively undisturbed.

During our initial observations of seals in the field, we used a Nikon D5000 digital single lens reflex camera (12.3 MP; Nikon USA, Melville, NY, USA) with a Tamron SP A011 150-600 mm telephoto lens (Tamron USA, Inc., Commack, NY, USA). With this apparatus, we were able to conduct our observations and capture various digital photographs (.jpg) at different distances from Swinburne Island with combinations of optical and digital zoom. These photographs were then downloaded onto an Apple Mac-Mini (3.0GHz dual-core Intel Core i7 processor; Apple Inc., Cupertino, CA, USA) and subsequently stored in the Dropbox™ (Dropbox, Inc., San Francisco, CA, USA) cloud.

From the 2014 to 2019 field seasons, we identified 58 potentially useful days with digital photographs that we could review for directional orientation. However, we eventually used 34 panoramic photographs within our initial range as these images provided the best resolution for counting individuals and measuring their cardinal direction. To avoid counting the same animal more than once on a given observation, we only used one image per day for analysis.

We measured the directional orientation as based on the cardinal direction (e.g., N, E, W, S) that each individual's head was facing, irrespective of

Figure 1. Three panels demonstrating observation site: location of Swinburne Island (left); overhead view of Swinburne Island (center); and easterly view of Swinburne Island's western shoreline with large freight in the background traveling through the major shipping lane to New York City harbor (right).

the angular posture of its body and its general orientation to water or land. Using the nearest neighbor as a fixed point, we then measured whether a specific seal was also facing the same compass direction as the closest individual. Seals were also identified by likely age (adult vs juvenile based on relative size) and species (harbor vs gray seal). We measured the cardinal direction of both adults and juveniles, and whether both groups also faced the same compass direction. Similarly, we measured the cardinal direction of harbor and gray seals, and whether they subsequently faced the same cardinal direction.

The cardinal direction provided four defined points for orientation direction. However, when considering the direction for analysis, we recorded whether the majority of seals in each frame were facing the same or different direction. Therefore, we identified four categorical measures for orientation: (1) same direction forward, (2) 90º to the left, (3) 90º to the right, and (4) opposite 180º. In each photographic frame, we considered the same direction forward where there were the greatest numbers of seals that were oriented in the alike positional bearing. For directional orientation of all individuals and orientation compared to nearest neighbor, we used a nonparametric chi-squared goodness of fit test. For each identified group (i.e., adult, juvenile, harbor, and gray), we also used a nonparametric chi-squared goodness of fit test. To compare orientation direction between groups, we used a nonparametric chi-squared test of independence for comparisons between adults and juveniles, and between harbor and gray seals. Lastly, we employed a two-tailed, nonparametric Spearman's rho correlation to examine any correlations between population size and orientation direction. We analyzed all data using IBM® *SPSS® Statistics*, Version 22, for Mac OS X (Armonk, NY, USA). In addition, we reported all significance levels at $p < 0.05$.

The results showed a significant difference in directional orientation ($\chi^2(3, N = 416) = 123.54$; $p < 0.05$) where all seals ($N = 416$) overwhelmingly oriented themselves in the same direction ($n = 197$; 47.36%; Figure 2). However, orientation to 90º left ($n = 87$; 20.91%) and 90º right ($n = 86$; 20.67%) were nearly identical, while they oriented least often in the opposite 180º direction ($n = 46$; 11.06%). When compared to their nearest neighbor ($N = 316$; Figure 3a), seals also significantly oriented ($\chi^2(3, N = 316) = 30.46$; $p < 0.05$) in the same direction ($n = 120$; 37.97%). Orientation to 90º left ($n = 72$; 22.78%) and 90º right ($n = 62$; 21.84%) was also fairly similar. Seals oriented in the opposite direction the least often ($n = 55$; 17.41%).

Adult seals ($N = 393$; Figure 3b) showed a similar trend where they significantly oriented ($\chi^2(3, N = 393) = 109.01$; $p < 0.05$) to the same direction ($n = 184$; 46.82%). Directional orientation in adults reflects a similar trend from the overall population of seals that were sampled as there was nearly equal distribution between orientation to 90º left ($n = 83$; 21.12%) and 90º right ($n = 81$; 20.61%). Adult seals also oriented themselves in the opposite direction least often ($n = 45$; 11.45%). Juveniles ($N = 23$; Figure 3b) also showed a similar trend in directional orientation where they significantly oriented ($\chi^2(3, N = 23) = 13.70$; $p < 0.05$) in the same direction ($n = 13$; 56.52%). Like adults, juveniles also oriented nearly evenly to 90º left ($n = 4$; 17.39%) and 90º right ($n = 5$; 21.74%), and least often in the opposite direction ($n = 1$; 4.35%). Both adult and juvenile orientation trends were fairly similar overall ($\chi^2(3, N = 416) = 1.58$; $p = 0.66$).

When examining orientation based on species, harbor seals ($N = 403$; Figure 3c) showed a significant difference for directional orientation ($\chi^2(3, N = 403) = 112.62$; $p < 0.05$) and faced the same direction as other individuals ($n = 183$; 46.90%) most often. Harbor seals showed equal probability for

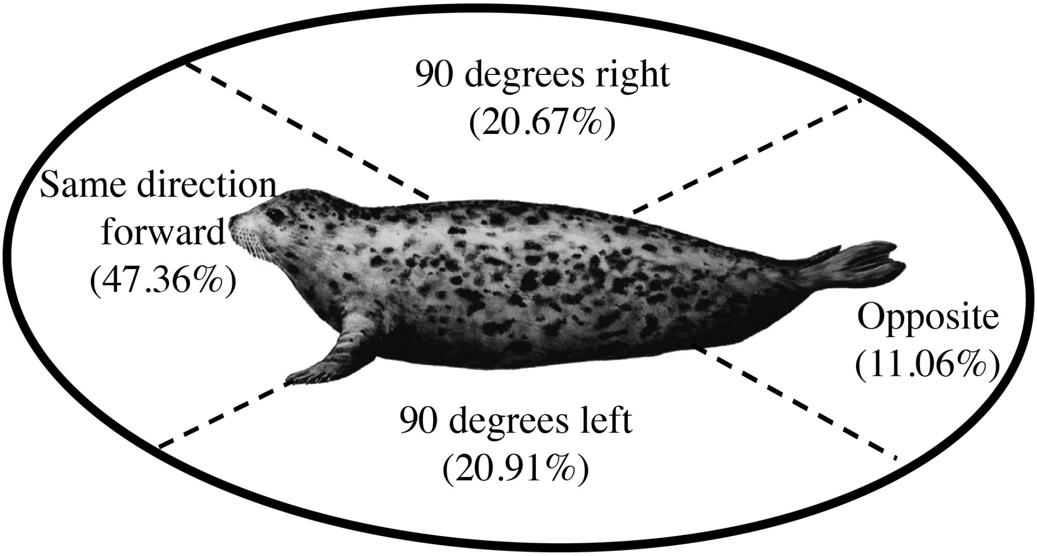

Figure 2. Individuals collectively and significantly oriented to the same forward direction most often. This was followed by similar directional behavior to 90° left and 90° right. Seals oriented least often in the opposite 180° direction.

orientation in both the 90° left (n = 84; 20.84%) and 90° right (n = 84; 20.84%) directions, and they oriented least often in the opposite direction (n = 46; 11.41%). While there were dramatically fewer gray seals (N = 13; Figure 3c), there was no significance in orientation ($\chi^2(3, N = 13) = 4.77; p = 0.92$), yet they seemed to orient mostly in the same direction (n = 8; 61.54%). The anomaly between significance and percentage may likely be the result of a low sample size for statistical analysis at these haul-out sites. Gray seals showed similar orientation to 90° left (n = 3; 23.08%) and 90° right (n = 2; 15.38%), and no gray seals were found to orient in the opposite directions. Both harbor and gray seals revealed similar trends in their directional orientation ($\chi^2(3, N = 416) = 2.27; p = 0.52$).

Lastly, no correlation between population size and orientation direction was detected ($\varrho(414) = 0.044; p = 0.371$).

The seals at Swinburne Island clearly demonstrated collective orientation in the same positional direction most often, indicating a potentially deliberate preference for orienting in the same direction as their conspecifics on any given day. Orientation behavior to either the right or left was similar, indicating no preference for specific compass direction, while seals orienting in the opposite direction as their conspecifics was observed least often. This orientation trend was also observed in comparisons between adults and juveniles, and between harbor and gray seals, which indicated collective orientation among these pinniped species overall and that this was not dependent on other individual-level factors. However, there seemed to be no correlation between population size and directional orientation, further suggesting that group size does not influence orientation directionality. Despite Terhune (1985) observing a correlation between population size and orientation, the division of directional orientation in our NYC sample appears to be maintained across all group sizes.

In haul-out aggregations, similar directional orientation may also suggest that conspecifics may initially attune to specific directional stimuli and that others may orient to the same direction based on the social facilitation of movement (Evans & Marler, 1994) and not based on perceived environmental context or the exchange information. While we did not specifically identify the stimulus in the most preferred direction, their willingness to position their bodies and align their gaze accordingly provides evidence that social facilitation during rest is potentially quite powerful. In addition, the nearly equal distribution to either the left or right orientation further suggests that peripheral stimuli is still important but perhaps is on a lower tier of consideration. Social facilitation of foraging has been observed in cetaceans, such as humpback whales (*Megaptera novaeangliae*; Wiley et al., 2011), and in pinnipeds, such as the Antarctic fur seal (*Arctocephalus gazella*; Hooker et al., 2015). This is likely the first documentation of social facilitation at rest for these populations of seals.

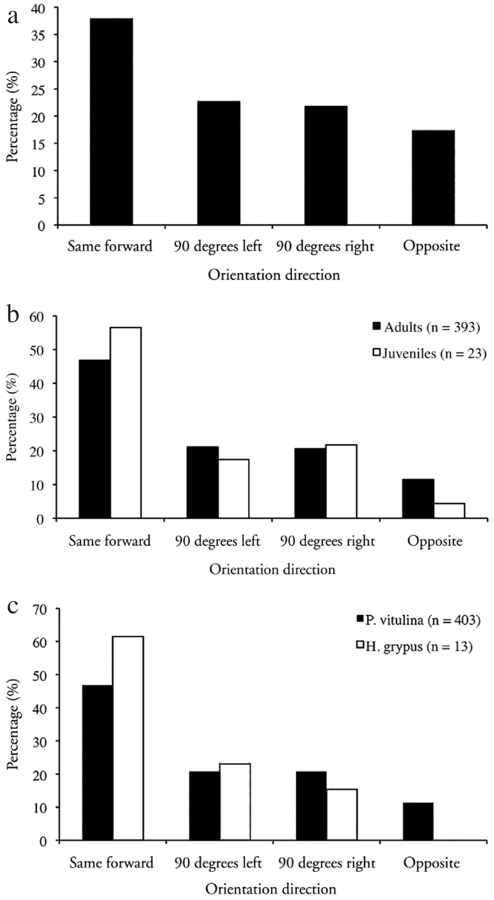

Figure 3. (a) When compared to the closest neighbor, individuals significantly oriented in the same forward direction most often, followed by orientation to the 90° left and 90° right directions, and least often in the opposite 180° direction; (b) in comparison between adults to juveniles, both groups followed a similar trend to orient in the same forward direction, followed by directional orientation to 90° left and 90° right, and subsequently with individuals oriented least often in the opposite 180° direction; and (c) lastly, when harbor seals (*Phoca vitulina*) were compared to gray seals (*Halichoerus grypus*), both species also demonstrated the observed trend to orient in the same forward direction most often, followed by orientation to the 90° left and 90° right directions, and least often in the 180° direction.

We found no correlation between directional orientation and population size, noting that vigilance in this case appears to neither favor larger nor smaller group sizes. With similar sample sizes, our results are in contrast to Da Silva & Terhune (1988), who found that harbor seals reduce vigilance for predators as group size increases. In this study, vigilance may be important for detecting salient movements in the environment or other visual information that may also be potentially indicative of threat. However, as shown by the observations of individuals that oriented in all compass directions, increased group size is unlikely to be as important for improved detection (Roberts, 1996). It is often associated that while a larger population may increase the probability of detection, smaller population sizes may be actively engaged in vigilance (Delm, 1990). However, irrespective of larger or smaller population sizes, one likely explanation is that to engage in active vigilance, it would be necessary to trade off engagement in other behaviors such as feeding (Lima & Bednekoff, 1999). Passive vigilance may still be just as effective if individuals favor other strategies like social facilitation.

To mitigate potential risks to safety, vigilance is paramount; therefore, its presence or absence is a critical behavior for the perception of and subsequent response to potential threat. In surveying the immediate environment, gaze or directional orientation of the head may be a successful strategy as these outward signals suggest that there may be a stimulus of concern to warrant attention (Beauchamp, 2015). These signals can be actively or passively observed and reacted upon by conspecifics to increase the likelihood of predator avoidance. Often, gaze-following is more easily measured in controlled laboratory studies (Kaminski et al., 2005). In bottlenose dolphins (*Tursiops truncatus*), individuals that were tested in laboratory settings were able to recognize and respond to human gaze (Tschudin et al., 2001; Pack & Herman, 2004). Similarly, South African fur seals (*Arctocephalus pusillus*) also used head and eye gazes to follow experimenter-pointed cues in a controlled laboratory environment (Scheumann & Call, 2004). It is likely that eye gaze is a way for individuals to communicate (actively or passively) if they have determined a stimulus to be relevant (i.e., a perceived threat which warrants behavioral change; Stankowich & Blumstein, 2005) or irrelevant (no perceived threat and consequently unlikely to disrupt their rest; Speakman et al., 2020). In this way, gaze-following may offer implications of social cognition and decision-making (Shepherd, 2010), which are important behaviors for communicating within social aggregations. Ideally, further *in situ* and laboratory exploration may help elucidate any potential connection between orientation and social communication during vigilance.

In an urban environment such as NYC, seals must contend with both marine predators and anthropogenic threats while hauled out. This is an ecosystem where the interaction between collective vigilance, safety, and reliance on conspecifics is paramount. For example, Speakman et al. (2020) found that Australian fur seals (*Arctocephalus* *pusillus doriferus*) were more alert to vessels, which included both recreational and commercial boats, at high-traffic areas compared to baseline levels of vigilance. Similarly, disturbances by smaller crafts, such as smaller motor boats, yachts, kayaks, and canoes, seemed to increase alertness in harbor seals that were hauled out in Métis Bay in the Saint Lawrence Estuary (Henry & Hammill, 2001). Thus, in the urban environment, both harbor (Farrer & Acevedo-Gutiérrez, 2010) and gray (Strong & Morris, 2010) seals remain vigilant to both natural and artificial stressors (Wright et al., 2007) but must clearly contend with the challenges derived from anthropogenic activity. For seasonally returning individuals, it is then important for them to learn about the components of their environment and readily adapt when circumstances change as they do frequently in urban habitats. Therefore, future investigations on the impacts of anthropogenic activity on the social behavior of urban populations would provide baseline information on the interaction between seals and their immediate environment.

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Literature Cited

Andersen, S. M., Teilmann, J., Dietz, R., Schmidt, N. M., & Miller, L. A. (2012). Behavioural responses of harbour seals to human-induced disturbances. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *22*(1), 113-121. https://doi.org/10.1002/aqc.1244

Beauchamp, G. (2015). *Animal vigilance: Monitoring predators and competitors*. Academic Press. https://doi.org/10.1016/B978-0-12-801983-2.00008-5

Calambokidis, J., Taylor, B. L., Carter, S. D., Steiger, G. H., Dawson, P. K., & Antrim, L. D. (1987). Distribution and haul-out behavior of harbor seals in Glacier Bay, Alaska. *Canadian Journal of Zoology*, *65*(6), 1391-1396. https://doi.org/10.1139/z87-219

Cunningham, L., Baxter, J. M., Boyd, I. L., Duck, C. D., Lonergan, M., Moss, S. E., & McConnell, B. (2009). Harbour seal movements and haul-out patterns: Implications for monitoring and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *19*(4), 398-407. https://doi.org/10.1002/aqc.983

Da Silva, J., & Terhune, J. M. (1988). Harbour seal grouping as an anti-predator strategy. *Animal Behaviour*, *36*(5), 1309-1316. https://doi.org/10.1016/S0003-3472(88)80199-4

Delm, M. M. (1990). Vigilance for predators: Detection and dilution effects. *Behavioral Ecology and Sociobiology*, *26*(5), 337-342. https://doi.org/10.1007/BF00171099

Evans, C. S., & Marler, P. (1994). Food calling and audience effects in male chickens, *Gallus gallus*: Their relationships to food availability, courtship and social facilitation. *Animal Behaviour*, *47*(5), 1159-1170. https://doi.org/10.1006/anbe.1994.1154

Farrer, J., & Acevedo-Gutiérrez, A. (2010). Use of haul-out sites by harbor seals (*Phoca vitulina*) in Bellingham: Implications for future development. *Northwestern Naturalist*, *91*(1), 74-79. https://www.jsor.org/stable/40856460; https://doi.org/10.1898/NWN08-46.1

Glass, T. W., Breed, G. A., Robards, M. D., Williams, C. T., & Kielland, K. (2021). Trade-off between predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted mesocarnivore. *Animal Behaviour*, *175*, 163-174. https://doi.org/10.1016/j.anbehav.2021.02.017

Henry, E., & Hammill, M. O. (2001). Impact of small boats on the haulout activity of harbour seals (*Phoca vitulina*) in Métis Bay, Saint Lawrence Estuary, Quebec, Canada. *Aquatic Mammals*, *27*(2), 140-148.

Hooker, S. K., Barychka, T., Jessopp, M. J., & Staniland, I. J. (2015). Images as proximity sensors: The incidence of conspecific foraging in Antarctic fur seals. *Animal Biotelemetry*, *3*(1), 1-11. https://doi.org/10.1186/s40317-015-0083-2

Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour*, *69*(1), 11-18. https://doi.org/10.1016/j.anbehav.2004.05.008

Kingsley, M. C., & Stirling, I. (1991). Haul-out behaviour of ringed and bearded seals in relation to defence against surface predators. *Canadian Journal of Zoology*, *69*(7), 1857-1861. https://doi.org/10.1139/z91-257

Klimova, A., Phillips, C. D., Fietz, K., Olsen, M. T., Harwood, J., Amos, W., & Hoffman, J. I. (2014). Global population structure and demographic history of the grey seal. *Molecular Ecology*, *23*(16), 3999-4017. https://doi.org/10.1111/mec.12850

Lima, S. L., & Bednekoff, P. A. (1999). Back to the basics of antipredatory vigilance: Can nonvigilant animals detect attack? *Animal Behaviour*, *58*(3), 537-543. https://doi.org/10.1006/anbe.1999.1182

London, J. M., Ver Hoef, J. M., Jeffries, S. J., Lance, M. M., & Boveng, P. L. (2012). Haul-out behavior of harbor seals (*Phoca vitulina*) in Hood Canal, Washington. *PLOS ONE*, *7*(6), e38180. https://doi.org/10.1371/journal.pone.0038180

Nordstrom, C. A. (2002). Haul-out selection by Pacific harbor seals (*Phoca vitulina richardii*): Isolation and perceived predation risk. *Marine Mammal Science*, *18*(1), 194-205. https://doi.org/10.1111/j.1748-7692.2002.tb01028.x

Pack, A. A., & Herman, L. M. (2004). Bottlenosed dolphins (*Tursiops truncatus*) comprehend the referent of both static and dynamic human gazing and pointing in an object-choice task. *Journal of Comparative Psychology*, *118*(2), 160-171. https://doi.org/10.1037/0735-7036.118.2.160

Pauli, B. D., & Terhune, J. M. (1987a). Meteorological influences on harbour seal haul-out. *Aquatic Mammals*, *13*(3), 114-118.

Pauli, B. D., & Terhune, J. M. (1987b). Tidal and temporal interaction on harbour seal haul-out patterns. *Aquatic Mammals*, *13*(3), 93-95.

Payne, P. M., & Selzer, L. A. (1989). The distribution, abundance and selected prey of the harbor seal, *Phoca vitulina concolor*, in southern New England. *Marine Mammal Science*, *5*(2), 173-192. https://doi.org/10.1111/j.1748-7692.1989.tb00331.x

Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour*, *51*(5), 1077-1086. https://doi.org/10.1006/anbe.1996.0109

Rosen, D. A. S., Winship, A. J., & Hoopes, L. A. (2007). Thermal and digestive constraints to foraging behaviour in marine mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1487), 2151-2168. https://doi.org/10.1098/rstb.2007.2108

Schakner, Z. A., & Blumstein, D. T. (2013). Behavioral biology of marine mammal deterrents: A review and prospectus. *Biological Conservation*, *167*, 380-389. https://doi.org/10.1016/j.biocon.2013.08.024

Scheumann, M., & Call, J. (2004). The use of experimenter-given cues by South African fur seals (*Arctocephalus pusillus*). *Animal Cognition*, *7*(4), 224-230. https://doi.org/10.1007/s10071-004-0216-0

Schneider, D. C., & Payne, P. M. (1983). Factors affecting haul-out of harbor seals at a site in southeastern Massachusetts. *Journal of Mammalogy*, *64*(3), 518-520. https://doi.org/10.2307/1380370

Seibel, B. A., & Drazen, J. C. (2007). The rate of metabolism in marine animals: Environmental constraints, ecological demands and energetic opportunities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1487), 2061-2078. https://doi.org/10.1098/rstb.2007.2101

Shepherd, S. V. (2010). Following gaze: Gaze-following behavior as a window into social cognition. *Frontiers in Integrative Neuroscience*, *4*, 5. https://doi.org/10.3389/fnint.2010.00005

Speakman, C. N., Johnstone, C. P., & Robb, K. (2020). Increased alertness behavior in Australian fur seals (*Arctocephalus pusillus doriferus*) at a high vessel traffic haul-out site. *Marine Mammal Science*, *36*(2), 486-499. https://doi.org/10.1111/mms.12654

Speakman, J. R., & Selman, C. (2003). Physical activity and resting metabolic rate. *Proceedings of the Nutrition Society*, *62*(3), 621-634. https://doi.org/10.1079/PNS2003282

Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2627-2634. https://doi.org/10.1098/rspb.2005.3251

Stanley, H. F., Casey, S., Carnahan, J. M., Goodman, S., Harwood, J., & Wayne, R. K. (1996). Worldwide patterns of mitochondrial DNA differentiation in the harbor seal (*Phoca vitulina*). *Molecular Biology and Evolution*, *13*(2), 368-382. https://doi.org/10.1093/oxfordjournals.molbev.a025596

Strong, P., & Morris, S. R. (2010). Grey seal (*Halichoerus grypus*) disturbance, ecotourism and the Pembrokeshire Marine Code around Ramsey Island. *Journal of Ecotourism*, *9*(2), 117-132. https://doi.org/10.1080/14724040903019869

Terhune, J. M. (1985). Scanning behavior of harbor seals on haul-out sites. *Journal of Mammalogy*, *66*(2), 392-395. https://doi.org/10.2307/1381258

Tschudin, A., Call, J., Dunbar, R. I., Harris, G., & van der Elst, C. (2001). Comprehension of signs by dolphins (*Tursiops truncatus*). *Journal of Comparative Psychology*, *115*(1), 100-105. https://doi.org/10.1037/0735-7036.115.1.100

Villegas-Amtmann, S., Schwarz, L. K., Sumich, J. L., & Costa, D. P. (2015). A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere*, *6*(10), 1-19. https://doi.org/10.1890/ES15-00146.1

Wiley, D., Ware, C., Bocconcelli, A., Cholewiak, D., Friedlaender, A., Thompson, M., & Weinrich, M. (2011). Underwater components of humpback whale bubble-net feeding behaviour. *Behaviour*, *148*(5/6), 575-602.

Williams, T. M., Fuiman, L. A., Horning, M., & Davis, R. W. (2004). The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: Pricing by the stroke. *Journal of Experimental Biology*, *207*(6), 973-982. https://doi.org/10.1242/jeb.00822

Williams, T. M., Davis, R. W., Fuiman, L. A., Francis, J., Le Boeuf, B. J., Horning, M., Calambokidis, J., & Croll, D. A. (2000). Sink or swim: Strategies for cost-efficient diving by marine mammals. *Science*, *288*(5463), 133-136. https://doi.org/10.1126/science.288.5463.133

Woo, K. L., & Biolsi, K. L. (2018). *In situ* observations of pinnipeds in New York City, 2011-2017. *Aquatic Mammals*, *44*(3), 244-249. https://doi.org/10.1578/AM.44.3.2018.244

Wright, A. J., Soto, N. A., Baldwin, A. L., Bateson, M., Beale, C. M., Clark, C., Deak, T., Edwards, E. F., Fernández, A., Godinho, A., Hatch, L. T., Kakuschke, A., Lusseau, D., Martineau, D., Romero, M. L., Weilgart, L. S., Wintle, B. A., Notarbartolo di Sciara, G., & Martin, V. (2007). Do marine mammals experience stress related to anthropogenic noise? *International Journal of Comparative Psychology*, *20*(2), 274-316. https://doi.org/10.46867/IJCP.2007.20.02.01