

Short Note

Influence of Human Exposure on the Anti-Predator Response of Harbor Seals (*Phoca vitulina*)

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Human encroachment upon wildlife habitat makes human disturbance a pressing issue in conservation (e.g., Gill et al., 1996; St Clair et al., 2010). Although many interactions with humans do not result in wildlife mortality, animals typically perceive human activities as a predation risk and respond to anthropogenic disturbance stimuli by engaging in anti-predatory behaviors such as fleeing, increased vigilance, and shifts in habitat choice (Frid & Dill, 2002). However, fleeing from a threat can also lead to fitness costs such as energy loss and time diverted away from essential activities. Thus, an animal's response to a perceived threat presumably aims to optimize the trade-off between the perceived advantage of avoiding predation and the costs of unnecessarily engaging in predator aversion behavior (Frid & Dill, 2002).

Repeated exposure to nonlethal human stimuli over time can make wildlife tolerant to anthropogenic activities that would otherwise cause a costly change of behavior (Bejder et al., 2009). While this process of habituation to human activity is often assumed to be a beneficial response and is sometimes deliberately encouraged as a technique to improve education, study, and the efficiency of wildlife viewing tours (Nisbet, 2000; Bejder et al., 2009; Knight, 2009), it may also negatively affect the fitness of animals by increasing their predation risk from natural predators (Baudains & Lloyd, 2007; Mcleery, 2009; Higham & Shelton, 2011).

Marine mammals are increasingly exposed to humans (Martínez et al., 2007). In the highly populated Salish Sea off British Columbia (Canada) and Washington State (USA), harbor seals (*Phoca vitulina*) are the most abundant and widespread marine mammal species (Jeffries et al., 2000). There are more than 300 known harbor seal haul-out sites in the Salish Sea, some of which are

located within easily accessible state parks or on protected or private land (Jeffries et al., 2000). The factors influencing when harbor seals haul out appear to be site-specific but include season, tide level, time of day, air temperature, wind speed, precipitation, and risk of terrestrial predation (Pauli & Terhune, 1987; Huber et al., 2001; Nordstrom, 2002; Reder et al., 2003; Hayward et al., 2005). Despite their healthy population status, harbor seals in the Salish Sea are still highly vulnerable to human activity and will flush into the water from a haul-out site in response to motorized or nonmotorized (e.g., kayaks) boat traffic or noise (Suryan & Harvey, 1999; Johnson & Acevedo-Gutiérrez, 2007; Cates & Acevedo-Gutiérrez, 2017).

Harbor seals in the Salish Sea are also vulnerable to natural predators such as killer whales (*Orcinus orca*; London, 2006), coyotes (*Canis latrans*; Steiger et al., 1989), and occasionally bald eagles (*Haliaeetus leucocephalus*; Hayward, 2009). Bald eagles are attracted to seal haulouts to feed on dead seal pups or placentas (Calambokidis & Steiger, 1985). They also opportunistically attack and prey on vulnerable live seal pups (Hayward, 2009; Lambourn et al., 2010) and frequently disturb harbor seals, causing both adults and pups to act alert or flush into the water (Suryan & Harvey, 1999). This flushing behavior is consistent with the anti-predatory response of harbor seals to other threats (Terhune, 1985).

Harbor seals in the Salish Sea appear to have an increased tolerance to vessels in areas of high disturbance (Cates & Acevedo-Gutiérrez, 2017); however, it is unknown how these differences in tolerance to humans affect their behavioral response to natural predators. Due to their healthy population status, the numerous and varied locations of their haul-out sites, and their known

anti-predator response to bald eagles, harbor seals in the Salish Sea are an ideal means to answer questions about the effects of human exposure on wildlife. To examine the hypothesis that exposure to humans reduces anti-predator response in harbor seals, we compared the alert and flushing behavior of seals in response to bald eagle activity at sites with three different levels of vessel traffic.

We observed harbor seals at six known haul-out sites in the San Juan Islands and southern Puget Sound in Washington State (Jeffries et al., 2000; Figure 1). Human exposure levels (i.e., vessel traffic) were determined based on preliminary observations and prior knowledge of the study area. Differences in vessel traffic between sites were later confirmed through statistical analyses. We collected data on two low human-exposure sites: Gertrude Island ($47^{\circ} 1' 57''$ N, $122^{\circ} 39' 40''$ W) and Smith Island ($48^{\circ} 19' 24''$ N, $122^{\circ} 49' 18''$ W); two medium human-exposure sites: Peapod Rocks ($48^{\circ} 38' 30''$ N, $122^{\circ} 44' 49''$ W) and Williamson Rocks ($48^{\circ} 26' 58''$ N, $122^{\circ} 42' 21''$ W); and two high human-exposure sites: Eagle Island ($47^{\circ} 11' 13''$ N, $122^{\circ} 41' 46''$ W) and Spindle Rock ($48^{\circ} 35' 17''$ N, $122^{\circ} 48' 3''$ W). We observed harbor seals at one haul-out site per day on weekdays from June through September 2012 for approximately 4 h/d.

Observations at Gertrude and Eagle Islands were taken from concealed viewing platforms located on McNeil Island > 100 m from the harbor seals. From these land-based platforms, seals were viewed with a spotting scope (Fujinon Field Scope Super Ed 80; 20 to 60X zoom). Observations for all other sites were conducted from a 5.8-m inflatable boat anchored within view of the haulout approximately 200 m away. We enforced a minimum adjustment period of 30 min before collecting behavioral observations at these sites to reduce any stress or alterations in behavior that might have been caused by our approach. During boat-based observations, seals were viewed with binoculars (STEINER Commander Military, Northbrook, IL, USA; 7×50 C). All observations were conducted by the same observer and were focused within the lower portion of the tide cycle when haul-out use is highest (Jeffries et al., 2000). We recorded the number of boats/h within 500 m from each site to estimate the level of human exposure. Boat distances were estimated using a laser range-finder (± 1 m per yard up to 500 m) and known distances to land-based reference points from the haul-out site

We monitored the baseline behaviors (i.e., behavior in the absence of a disturbance stimulus)

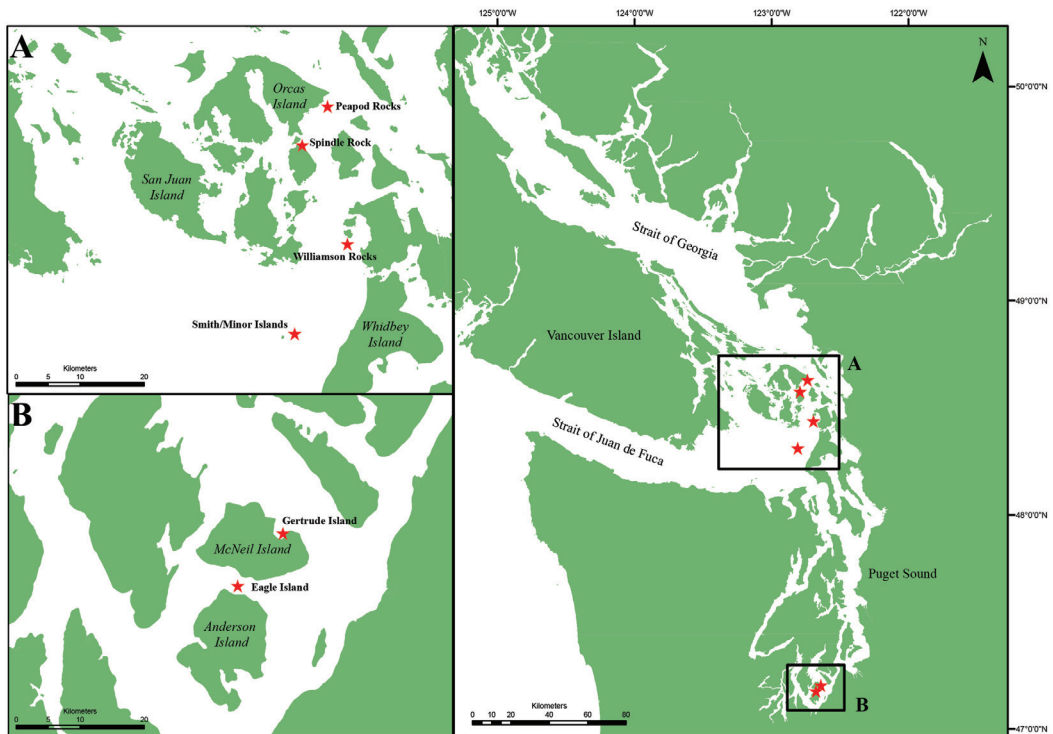


Figure 1. Location of the six harbor seal haul-out sites within the San Juan Islands (A) and southern Puget Sound (B) regions of the Salish Sea in Washington State (USA)

of the entire haul-out site at 15-min intervals using instantaneous scan-sampling to determine how many seals showed alert or flush behaviors (Martin & Bateson, 2007; Table 1). During the baseline intervals, we also recorded the total number of seals hauled out and the total number of pups. Baseline measurements were not taken if a disturbance stimulus occurred within 2 min of the count. We used instantaneous scan-sampling to determine the behavioral response of seals to five different bald eagle behaviors (Table 1). To account for the rate of interaction between eagles and seals (i.e., eagle activity), we recorded seal responses to any of the five eagle behaviors and, henceforth, refer to them as an “interaction,” regardless of actual seal response. If more than one eagle behavior occurred during a scan (e.g., land and scavenge), the response of seals was analyzed as one interaction.

All data were analyzed using Generalized Linear Mixed Effect Models (GLMMs)—flexible, powerful tests that are useful for analyzing non-normal data and which allow for the inclusion of both fixed and random effects (Bolker et al., 2008; Zuur et al., 2009). The model of best fit was determined using the lowest AICc value. To account for uncertainty in model selection, we averaged all models with $\Delta\text{AICc} < 2$ and presented the resulting parameter estimates and relative importance of the model-averaged variables (Burnham et al., 2011; Symonds & Moussalli, 2011). All models were fit using the *lme4* package in program *R* and were averaged using the *MuMIn* package.

To assess differences of human exposure between sites, we grouped the sites into three categories based on *a priori* predictions. We ran a GLMM to assess whether the categories were statistically different using boats/h as the response

variable, human exposure as a fixed factor with three levels (low, medium, and high), and site as a random factor. We used a Gaussian distribution and an identity link function, which are appropriate for continuous data.

In the model for harbor seal baseline behavior, we tested the fixed effect of human exposure (low, medium, and low) as well as the random effects of haul-out site and total number of seals on the proportion of harbor seals exhibiting alert behaviors (flushing behavior was too infrequent at baseline intervals to use for comparison). Because the response variables were binary, we used a binomial distribution with a logit link function.

To account for variation in harbor seal exposure to eagles, we assessed the level of eagle activity at each haul-out site using the observed rate of interaction between eagles and seals (i.e., interactions/h). We divided the sites into our predicted low and high levels of overall eagle activity and ran a GLMM to assess whether the categories were statistically different. We used the total number of interactions/h as a response variable, overall eagle activity as a fixed factor with two levels (low and high), and site as a random factor. We used the Gaussian distribution and an identity link. Because of the variation, we also used the level of eagle activity as a covariate in our anti-predatory response models. Odds ratios were calculated using the exponent of the model averaged regression estimates and associated 95% confidence intervals.

We used two models to examine the behavioral response of harbor seals to bald eagles. To determine if seals became more vigilant, we examined the proportion of seals exhibiting alert behaviors in the absence of a flushing event. To investigate escape response, we examined the

Table 1. Ethograms of bald eagle (*Haliaeetus leucocephalus*) and harbor seal (*Phoca vitulina*) behaviors

<i>Eagle behavior</i>	Distinguishing characteristics
Glide	Eagle glides or soars (i.e., wings do not flap) directly above the haulout
Powered flight	Eagle has directed flight (i.e., wings flapping) directly above the haulout
Land	Eagle lands or is landed on haul-out site (on ground or perched in tree)
Scavenge	Eagle consumes afterbirth or dead seal
Attack	Eagle attempts to injure or kill live seal
<i>Seal behavior</i>	Distinguishing characteristics
No reaction	Animal does not visibly react to disturbance
Alert	Animal's head is raised and looking in the direction of the disturbance, animal is surveying its surroundings, or animal changes its position on the beach
Flush	Animal flushes into the water from hauled-out position

Table 2. Generalized Liner Mixed Model (GLMM) results for comparing level of human exposure, level of eagle activity, and harbor seal baseline behaviors across six haul-out sites in the Salish Sea

Model ^a	df	AICc	ΔAICc	Weight
<i>Human exposure</i>				
traffic ~ exposure + (site)	5	215.8	0.00	0.999
traffic ~ (site)	3	230.7	14.91	0.001
<i>Eagle activity</i>				
interactions ~ activity + (site)	4	284.0	0.00	0.953
interactions ~ (site)	3	290.0	6.03	0.047
<i>Baseline behaviors</i>				
alert ~ (seals) + (site)	3	1,574.8	0.00	0.747
alert ~ traffic + (site) + (seals)	5	1,577.0	2.17	0.253

^aRandom variables are indicated by parentheses.

presence or absence of flushing (i.e., > 1 harbor seal flush). Presence or absence of flushing was used instead of a proportion of hauled-out seals that entered the water because flushing is frequently an “all-or-none” response in harbor seals (Terhune & Brilliant, 1996). Both models included the fixed effects of human exposure and eagle activity. Given that all observations took place during pupping season and the fact that southern Puget Sound and the San Juan Islands have different birthing peaks (Huber et al., 2012), we also included the proportion of pups (i.e., total number of pups divided by total number of seals) as a fixed factor to represent time from peak pupping. Finally, both models included the random effects of haul-out site, total number of seals, and the daily rate of interaction between seals and eagles. Because the response variables were binary (i.e., no reaction vs alert, or no flushing vs flushing), we used a binomial distribution with a logit link function. Results are expressed as mean ± SE

We completed 162 h of observations with approximately 25 h at each of the six sites. GLMMs confirmed the grouping of sites into three levels of human exposure: low (0.26 ± 0.12 boats/h, mean ± SE, $n = 2$), medium (1.56 ± 0.38 boats/h, $n = 2$), and high (6.07 ± 0.73 boats/h, $n = 2$ sites; Table 2). GLMMs also confirmed the grouping of sites into two levels of eagle activity (Table 2). Sites with high levels of eagle activity included Eagle, Gertrude, and Smith (3.96 ± 1.07 interactions/h, $n = 3$), and sites with low levels of eagle activity included Peapod, Williamson, and Spindle (0.29 ± 0.16 interaction/h, $n = 3$).

Harbor seals were more alert to eagles at sites with lower levels of human exposure and when higher percentages of pups were present as

supported by the highest weighted model, including the fixed factors of human exposure and proportion of pups (Figure 2; Table 3). The proportion of pups was the most important of the model-averaged variables, which is consistent with eagles’ preference to feed on placentas and dead pups (Hayward, 2009; Table 4). Human exposure was the second most important model-averaged

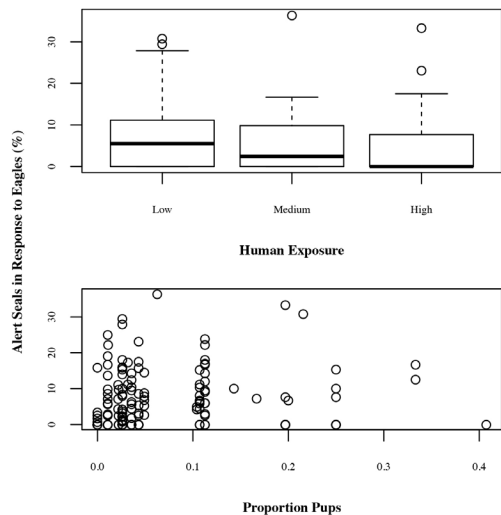


Figure 2. Proportion of harbor seals (*Phoca vitulina*) exhibiting alert behaviors in response to bald eagles (*Haliaeetus leucocephalus*) at six sites in the Salish Sea relative to low, medium, and high exposure to vessel traffic (top) and to the proportion of pups present at the haul-out site (bottom). Outliers (values > 1.5 × interquartile range) on top panel are shown as open circles.

Table 3. GLMM results for harbor seal anti-predatory behavioral response to bald eagle interactions (alert or flush) in the Salish Sea. Responses are shown relative to the level of human exposure (traffic), the level of eagle activity (eagles), the proportion of pups present (pups), seal numbers (seals), haul-out site (site), and total eagle interactions per day (int/day).

Model ^a	df	AICc	ΔAICc	Weight
<i>Proportion of alert seals in response to eagles</i>				
response ~ traffic + pups + (site)+(seals)+(int/day)	7	623.7	0.00	0.226
response ~ eagles + pups + (site)+(seals)+(int/day)	6	623.9	0.19	0.205
response ~ traffic + eagles + pups + (site) + (seals) + (int/day)	8	624.2	0.47	0.179
response ~ pups + (site)+(seals)+(int/day)	5	625.1	1.40	0.112
response ~ traffic + (site) + (seals)+(int/day)	6	625.3	1.62	0.100
response ~ (site)+(seals) + (int/day)	4	625.6	1.88	0.088
response ~ eagles + (site)+(seals) + (int/day)	5	626.6	2.89	0.053
response ~ traffic + eagles + (site) + (seals) + (int/day)	7	627.3	3.66	0.036
<i>Presence/absence of flushing in response to eagles</i>				
response ~ eagles + (site)+(seals)+(int/day)	5	112.0	0.00	0.327
response ~ (site)+(seals)+(int/day)	4	112.9	0.87	0.212
response ~ traffic + (site)+(seals)+(int/day)	6	113.9	1.85	0.130
response ~ eagles + pups + (site)+(seals)+(int/day)	6	113.9	1.88	0.127
response ~ pups + (site)+(seals)+(int/day)	5	115.0	2.99	0.073
response ~ traffic + eagles + (site)+(seals)+(int/day)	7	115.6	3.53	0.056
response ~ traffic + pups + (site)+(seals)+(int/day)	7	115.8	3.73	0.051
response ~ traffic + eagles + pups + (site)+(seals)+(int/day)	8	117.2	5.14	0.025

^aRandom variables are indicated by parentheses.

variable for harbor seal alert response toward eagles (Table 4). Seals at our low human-exposure sites were 2.11 times (95% CI: 1.03 to 4.32) more likely to show alert behaviors in response to eagles compared to seals at our high human-exposure sites, which suggests a decrease in vigilance of harbor seals to bald eagles at sites with high levels of human exposure (Figure 2). Furthermore, we did not observe differences in seal baseline behaviors (Table 2); this suggests that the increased alert behaviors of seals in response to eagles at our low human-exposure sites cannot simply be attributed to natural variation in vigilance among sites.

Differences in harbor seal alertness at study sites that exhibited varying levels of boat traffic suggest habituation to humans could be occurring. Without longitudinal data, we were unable to definitively test for the process of habituation; however, we believe that a transfer of habituation from human to eagle stimuli offers the most parsimonious explanation for why seals at haulouts with higher human exposure also showed less

vigilance for eagles. This hypothesis is consistent with several previous studies on the impacts of human activity. For example, fox squirrels (*Sciurus niger*) in urban areas showed decreased anti-predator behaviors in response to playback of predator calls when compared to squirrels in suburban or rural areas (McCleery, 2009). Similarly, slower escape responses and increased mortality in chicks of the white-fronted plover (*Charadrius marginatus*) at sites with high levels of human recreation were hypothesized to be the result of habituation to human presence and increased predation by domestic dogs (Baudains & Lloyd, 2007). Finally, rangers at Kruger National Park in South Africa have noted that tourism in the park, particularly related to roads and high levels of traffic, has led to an increased vulnerability to predation in a variety of resident species (Freitag-Ronaldson et al., 2003).

The level of eagle activity was the most important variable explaining flushing behavior in response to eagles (Table 3). Models for flushing

Table 4. Model-averaged parameter estimates, standard error (SE), and relative importance of variables explaining harbor seal anti-predatory behavioral response to bald eagle interactions (alert behaviors) in the Salish Sea; values based on Table 3 averaged models.

Parameter	Estimate	SE	Relative importance
(Intercept)	-3.770	0.417	--
Pups	3.330	1.530	0.79
Traffic (Low)*	0.747	0.366	0.55
Traffic (Medium)	0.329	0.601	--
Eagles (Low)^	-0.779	0.505	0.42

*Traffic (High) was the reference category.

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behavior could not be averaged due to nonconvergence, most likely driven by the small number of actual flushing events witnessed. Nevertheless, all flushing events ($n = 17$) occurred at the three sites with high levels of eagle activity. We believe that the importance of eagle activity was driven by eagles providing stronger threat stimuli during intermittent moments of intensity, such as close approaches during placenta scavenging or birthing events, which were only observed at sites with high eagle activity. This is consistent with predictions of the risk-disturbance hypothesis, which suggests that fleeing (or flushing in the case of harbor seals) is more likely to occur when a stimulus approaches more directly (Frid & Dill, 2002). Interestingly, multiple eagle-related flushing events occurred at low human-exposure sites without a placenta scavenging or pupping event taking place; whereas the one unique flushing event we observed at a high human-exposure site involved a close approach of an eagle following a seal birth. These observations suggest that seals at the low human-exposure sites were more likely to flush in response to weaker disturbance stimuli than those at high human-exposure sites. Had we directly observed close approaches or pupping events at all sites, we may have detected an effect of human exposure in addition to eagle activity. Future studies should incorporate a measure of behavioral intensity (such as speed of approach or distance between predator and prey) in addition to frequency of interaction.

The transfer of habituation hypothesis assumes a generalized threat response from the prey. In other words, one would not expect an animal capable of predator-specific responses to reduce their reaction to a recognized high-risk threat. Harbor seals are capable of responding to visual, auditory, and spatial cues, all of which are important aspects of predator recognition (Schusterman, 1982; Renouf & Gaborko, 1988). Harbor seals are able

to distinguish between predators as evidenced by their stronger behavioral responses to mammal-eating transient killer whale acoustics compared to salmon-eating residents (Deecke et al., 2002).

Harbor seals may even possess a threat image of potential predators as evidenced by an experimental study in which seal numbers declined at haulouts in the presence of a black bear model but were unaffected by a control object of similar size and color (Nordstrom, 2002). We believe, however, that the relatively low risk of mortality associated with vessel traffic and eagle interactions might help to explain the generalized behavioral response in our study. Given the healthy population status and the preference of eagles to target primarily vulnerable pups for predation, harbor seals in the Salish Sea are likely faced with weak selection for eagle predation. The idea that the transfer of habituation is more likely to occur when the risk of mortality is low is consistent with the results of McCleery (2009).

Furthermore, like other wildlife, harbor seals have evolved to react to generalized threat stimuli (e.g., loud noises or quickly approaching objects). This reaction allows them to respond to potential threats even if they are relatively new in their evolutionary history—power boats, for example (Frid & Dill, 2002). This reaction may also influence their response to opportunistic predators, such as bald eagles, that only pose a threat to vulnerable individuals at specific times of the year (Hayward et al., 2010). When faced with continuous, nonlethal threat stimuli at our high human-exposure sites, however, the negative energetic costs of anti-predator behavior may eventually cross a threshold and outweigh the benefit, thus tipping the scale of the trade-off balance toward a reduced response (i.e., habituation).

Mechanisms other than habituation might also explain the reduced vigilance at our high human-exposure sites. Higher tolerance of harbor seals at a given haul-out site may be the result of

permanent displacement of less tolerant individuals; however, this is unlikely. Evidence from tagging suggests that harbor seals in the Salish Sea exhibit high site fidelity (e.g., Suryan & Harvey, 1998; Hardee, 2008). Another possibility is that constant flushing in response to boat traffic at the high human-exposure sites may have weakened those seals and made them less willing and less able to respond to milder threats. This explanation also seems unlikely given the relatively low energetic cost associated with flushing and the healthy status of harbor seals in the Salish Sea. Considering that bald eagles are more likely to prey on premature or newborn pups, it is possible that the age structure of pups at our haul-out sites affected the response of seals to bald eagles. To further clarify this effect, future studies should estimate the age category of pups.

The likelihood that increased tolerance to humans can lead to an increased risk of natural predation makes it crucial to better understand interactions between human activities and various predator-prey relationships. Our results provide suggestive evidence of an effect of human exposure on harbor seal anti-predatory response. Although harbor seal populations in the Salish Sea appear to be healthy (Department of Fisheries and Oceans Canada [DFO], 2010), it is unknown how a transfer of habituation might affect less healthy or less resilient species. Furthermore, habituation to humans might add an additional level of vulnerability for prey species facing novel predator situations such as an invasive or introduced predator (e.g., Berger et al., 2007), a predator experiencing a rapid population recovery (e.g., Grier, 1982), or a shift in prey choice for a generalist predator (e.g., Rutz & Bijlsma, 2006). Given the tendency for recreation and ecotourism industries to perceive habituation as a desirable process, the transfer of habituation hypothesis warrants further investigation. Additional long-term studies are needed to test the hypothesis of habituation as a low-impact activity. In the absence of those studies, managers may need to limit wildlife viewing in areas where the focal species is under threat of predation or facing a novel predation threat.

Acknowledgments

We thank S. Jeffries and D. Lambourn of Washington Fish and Wildlife for providing access to haul-out sites. J. Bower and B. Miner provided support and feedback throughout the study. Shannon Point Marine Center, D. Senner, A. Hulbert, C. Moore, and E. D'Agnesse assisted with data collection in the field. This manuscript was improved by comments from J. Gaydos. This project was funded by Western Washington

University and the Anacortes Kiwanis Society. Activities were conducted under NMFS Permit No. 16621-00 awarded to Alejandro Acevedo-Gutiérrez by the National Oceanic and Atmospheric Administration.

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