

**THE EFFECT OF HUMAN EXPOSURE ON THE ANTI-PREDATORY RESPONSE OF  
HARBOR SEALS (*PHOCA VITUNLINA*)**

By

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Accepted in Partial Completion  
of the requirements for the Degree  
Master of Science

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MASTER'S THESIS

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A Thesis

Presented to

The Faculty of

Western Washington University

In Partial Fulfillment

Of the Requirements for the Degree

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## ABSTRACT

Increased exposure to anthropogenic activities often results in animals developing higher tolerance to activities that would otherwise disturb them. Although this response is sometimes viewed as a beneficial survival mechanism, habituation to human activities may lead to negative consequences, such as decreased predator aversion. Due to their healthy population status, the numerous and varied locations of their haul-out sites and their anti-predatory response to bald eagles, harbor seals in the Salish Sea are an ideal study system to answer questions concerning the effects of human exposure on wildlife. To examine my hypothesis that increased human exposure reduces anti-predatory response in harbor seals, I used instantaneous scan-sampling techniques to compare the behavioral responses of seals to bald eagles and to humans at six haul-out sites with varying levels of exposure to anthropogenic activities. Sites were classified as high exposure ( $6.07 \pm \text{SE } 0.73 \text{ boats} \cdot \text{h}^{-1}$ ,  $n=2$  sites), medium exposure ( $1.56 \pm \text{SE } 0.38 \text{ boats} \cdot \text{h}^{-1}$ ,  $n=2$  sites), and low exposure ( $0.26 \pm \text{SE } 0.12 \text{ boats} \cdot \text{h}^{-1}$ ,  $n=2$  sites). Based on generalized linear mixed-effects models (GLMM), the presence of harbor seal anti-predatory response to bald eagles was significantly related to human exposure but not to eagle exposure. Seals showed an anti-predatory response to eagles more often at low-exposure sites (77.17%,  $n=127$  events) than at medium- (60.0%,  $n=15$  events) or high- (45.45%,  $n=33$  events) exposure sites. Also based on GLMMs, human exposure significantly influenced harbor seal response to boat traffic. Seals reacted to passing boats more often at low-exposure sites (100%,  $n=10$  events) than at medium- (77.8%,  $n=72$  events) or high- (83.2%,  $n=208$  events) exposure sites. This study provides the first empirical evidence outside of an urban setting to support the hypothesis that increased interactions with humans can lead to a reduction in overall predator aversion. This finding highlights the potential impact that increased human exposure can have on the predation risk of

wildlife populations and disputes the traditionally accepted view of habituation as having little-to-no impact on the animals involved.

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## INTRODUCTION

### **Human Disturbance of Wildlife**

Human disturbance of wildlife is one of the most pressing issues today in conservation biology due to a rise in the recreational use and human development of important wildlife habitats (Gill et al. 1996; St. Clair et al. 2010). Human disturbance can be defined as any anthropogenic stimulus that causes a deviation in an animal's typical behavior (Suryan & Harvey 1999; Frid & Dill 2002). The effects of human disturbance have been well documented for a number of species and include modifications to home range size, habitat use, foraging behavior, reproductive success, body condition, disease susceptibility, sex ratio, daily activity period, social development, mating system, and social structure (Galicia & Baldassarre 1997; de la Torre et al. 2000; Lacy & Martins 2003; Constantine et al. 2004; Müllner et al. 2004; Bejder et al. 2006; Bejder et al. 2009; French et al. 2011).

Although many interactions with humans do not result in wildlife mortality, animals typically perceive human activities as a predation risk (Frid & Dill 2002). Consequently, animals respond to anthropogenic disturbance stimuli by engaging in anti-predatory behaviors such as fleeing, increased vigilance, and shifts in habitat choice (Frid & Dill 2002). There is strong selection pressure for anti-predatory behavior in animals given that failure to react to a potential threat could result in death; however, fleeing from a threat also leads to fitness costs, such as energy loss and time diverted away from essential activities like feeding and reproduction (Ydenberg & Dill 1986; Frid & Dill 2002). Thus, an animal's response to a perceived threat presumably aims to optimize this trade-off between the risk of predation and the costs of unnecessarily engaging in predator aversion behavior.

Over time, repeated exposure to human stimuli can cause animals to develop an increased tolerance to anthropogenic activities (Bejder et al. 2009). This process, known as habituation, leads to a reduction in specific behavioral responses from the exposed animals. Habituation of wildlife to humans is often misinterpreted as a beneficial response and is sometimes actually deliberately encouraged (Nisbet 2000; Bejder et al. 2009). Even within the realm of research, scientists have historically utilized the idea of habituation in hopes of observing the behavior of wild animals (Pusey et al. 2008). However, in reality there could be serious consequences to the fitness of the animals involved (Woodford et al. 2002; Müllner et al. 2004; Bejder et al. 2009; Higham & Shelton 2011). For example, increased exposure to humans may result in an increased disease risk for apes (Woodford et al. 2002) and potential habituation of Hector's dolphins (*Cephalorhynchus hector*) to boat traffic in New Zealand has led to an increased risk of ship strike mortalities (Stone & Yoshinaga 2000).

Another important negative consequence of habituation to humans may be an increased risk of natural predation. For instance, slower escape responses and increased mortality in chicks of the white-fronted plover (*Charadrius marginatus*) at sites with high levels of human recreation are hypothesized to be the result of habituation to human presence (Baudains & Lloyd 2007). Furthermore, fox squirrels (*Sciurus niger*) in urban areas showed decreased anti-predatory behaviors in response to experimental predator acoustics when compared to squirrels in suburban or rural areas (McCleery 2009). The potential link of increased tolerance to predation risk makes it crucial that we gain a better understanding of the interactions between human activities and various predator-prey relationships. Nevertheless, studies that examine the response of animals to natural predators relative to the level of anthropogenic exposure are limited.

Marine mammals in particular are experiencing increased exposure to human activities and disturbance due to a steady rise in human populations in coastal areas: worldwide, at least 41% of humans live  $\leq 100$  km from the seacoast and this percentage is rapidly rising (Martínez et al. 2007). As with other wildlife, marine mammals living in regions with high levels of exposure to humans have an increased tolerance to human activities (Schusterman 1982; Suryan & Harvey 1999; Boren et al. 2002; Blackwell et al. 2004; Bejder et al. 2009). New Zealand fur seals (*Arctocephalus forsteri*), for example, show decreased “avoidance” and “aggression” behaviors towards humans at sites with high levels of tourist activity when compared to sites with low levels of tourist activity (Boren et al. 2002). This thesis addresses the hypothesis that the response of marine mammals to natural predators decreases with increased exposure to human activity, a hypothesis that has not previously been examined.

### **Study species: harbor seal (*Phoca vitulina*)**

#### **Harbor seals and anthropogenic disturbance**

Harbor seals are one of the most widespread and abundant pinniped species worldwide (Burns 2009). They are also the most abundant marine mammal and the only non-migratory resident pinniped in the Salish Sea, the inland waters of the North American Pacific Northwest (Jeffries et al. 2000) that includes both Washington State, USA, and British Columbia, Canada. According to National Marine Fisheries Service (NMFS) stock assessment reports (SARs), harbor seals living in the Salish Sea belong to the Washington Inland Waters Stock (NOAA 2010). Pupping season in the Salish Sea varies slightly by geographical region, but takes place within the summer months (June-September) for the San Juan Islands and Southern Puget Sound (Jeffries et al. 2000). Currently, the Washington Inland Waters stock is not listed as “depleted”

under the MMPA or “endangered” under the ESA, and is viewed as an abundant and healthy stock (Jeffries et al. 2003; NOAA 2010).

Despite their healthy population status, harbor seals in the Salish Sea are still highly vulnerable to human activity. Common sources of anthropogenic disturbances to harbor seals include boat traffic, noise, industrial development, and harassment by human individuals or ecotourists (Suryan & Harvey 1999; Johnson & Acevedo-Gutiérrez 2007; Patterson & Acevedo-Gutiérrez 2008; Farrer & Acevedo-Gutiérrez 2010; Acevedo-Gutiérrez & Cendejas-Zarelli 2011). Given the prevalence of harbor seals in the highly developed northern hemisphere, interactions between harbor seals and humans are likely to increase along with rising coastal human populations. Pinnipeds, including harbor seals, breed and haul-out in coastal colonies with certain spatial and temporal predictability that makes them easily accessible by vessels and humans, often resulting in disturbance (Tershy et al. 1997; Engelhard et al. 2001; Hayward et al. 2005). The factors influencing when seals haul-out appear to be site-specific, but include season, tide level, time of day, air temperature, wind speed, and precipitation (Pauli & Terhune 1987; Huber et al. 2001; Reder et al. 2003; Hayward et al. 2005). Human disturbance, however, is another important factor that can affect harbor seal haul-out behavior (Grigg et al. 2002).

When disturbed by humans, harbor seals that are hauled-out typically flush into the water (Terhune & Almon 1983; Allen et al. 1984; Johnson & Acevedo-Gutiérrez 2007). The primary disadvantage of flushing behavior is energy loss, which can be especially costly when hauling-out is imperative, such as during pupping or molting seasons (Suryan & Harvey 1999). Over longer periods of time, disturbance may result in seals hauling-out at times of day when disturbance is low (Grigg et al. 2002), avoiding areas of high disturbance (Montgomery et al. 2007), or abandoning a haul-out site (Newby 1973). Not surprisingly, tolerance to potential

disturbances is related to the level of human activities. For instance, harbor seals appear to tolerate closer boat approaches in areas of high traffic (Suryan & Harvey 1999). However, we do not know how exposure to varying levels of human activity affects the response of harbor seals to non-human predators.

### **Harbor seals and bald eagles**

In the Salish Sea, harbor seals are vulnerable to natural predators such as killer whales (*Orcinus orca*), coyotes (*Canis latrans*), and eagles (*Accipitridae*; Steiger et al. 1989; London 2006; Hayward 2009). Bald eagles (*Haliaeetus leucocephalus*) in particular frequently occupy the same habitat as harbor seals, and the presence of bald eagles is positively correlated with the number of harbor seals hauled-out (Hayward et al. 2010). Eagles primarily feed on dead seal pups or afterbirth, but they also attack and prey on live seal pups (Hayward 2009; Lambourn et al. 2010). Evidence of the extent to which bald eagles prey on harbor seal pups is limited; however, predation of bald eagles on other marine mammal offspring has been previously reported. For instance, puncture wounds on carcasses and sightings of eagles carrying pups in their talons suggest that adult bald eagles may frequently feed on live sea otter pups at Amchitka Island, Alaska (Sherrod et al. 1975). Due to the high numbers of both bald eagles and harbor seals in the Salish Sea, predation on harbor seal pups may actually be a more common occurrence than the present lack of data suggests (Hayward 2009). Further, bald eagles are a frequent cause of disturbance to harbor seals in the region and adult harbor seals, as well as pups, will often act alert or flush into the water in response to low flying bald eagles (Suryan & Harvey

1999; K. Cates pers. comm.<sup>1</sup>; S. Jeffries, pers. comm.<sup>2</sup>; Hayward, pers. comm.<sup>3</sup>). This seal behavior is consistent with the anti-predatory response of harbor seals to other terrestrial threats (Terhune 1985) and makes it clear that bald eagles elicit anti-predatory behaviors in harbor seals.

Given the healthy status of the Washington Inland Waters Stock of harbor seals (Jeffries et al. 2003; NOAA 2010), bald eagles are not likely having a strong impact on the survival of harbor seal populations. However, there may be cause for concern in the future. Not only does the highest concentration of bald eagles in Washington State occur in the Salish Sea, but population counts show a 187% increase since the late 1970s (Bower 2009; Hayward 2009). Furthermore, many major food sources of bald eagles are declining, and the diets of these birds are dependent on prey availability (Grubb & Hensel 1978; Nehlson et al. 1991; Bower 2009). Bald eagles shift their diet over seasonal (short) and historical (long) periods of time as a result of this generalist feeding strategy (Todd et al. 1982; Collins et al. 2005). Thus, the cumulative effect of growing eagle populations, declining food sources, and local harbor seal abundance could potentially give rise to a shift in prey choice toward harbor seal pups (Hayward, pers. comm.<sup>3</sup>). Nevertheless, there is still extremely limited information about predator-prey interactions between these two species.

Due to their healthy population status, the numerous and varied locations of their haul-out sites and their anti-predatory response to bald eagles, harbor seals in the Salish Sea are an ideal study system to answer questions concerning the effects of human exposure on wildlife. To test my hypothesis that exposure to human activities affects anti-predatory response in harbor seals, I

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<sup>1</sup> Kelly Cates, Western Washington University, 516 High St, Bellingham, WA 98225, September 2011.

<sup>2</sup> Steve Jeffries, Washington State Fish and Wildlife, 7801 Phillips Road SW, Lakewood, WA 98498, July 2011.

<sup>3</sup> James Hayward, Andrews University, Berrien Springs, MI 49104, February 2012

compared the anti-predatory behaviors of harbor seals at sites with varying levels of human activities. The primary objective was to compare the behavioral response to bald eagles, a natural predator. A secondary objective was to compare the behavioral response to potential anthropogenic disturbances. For both objectives, I predicted that seals exposed to high levels of anthropogenic activities would be less likely to react to a potential threat than seals with less exposure to anthropogenic activities.

## METHODS

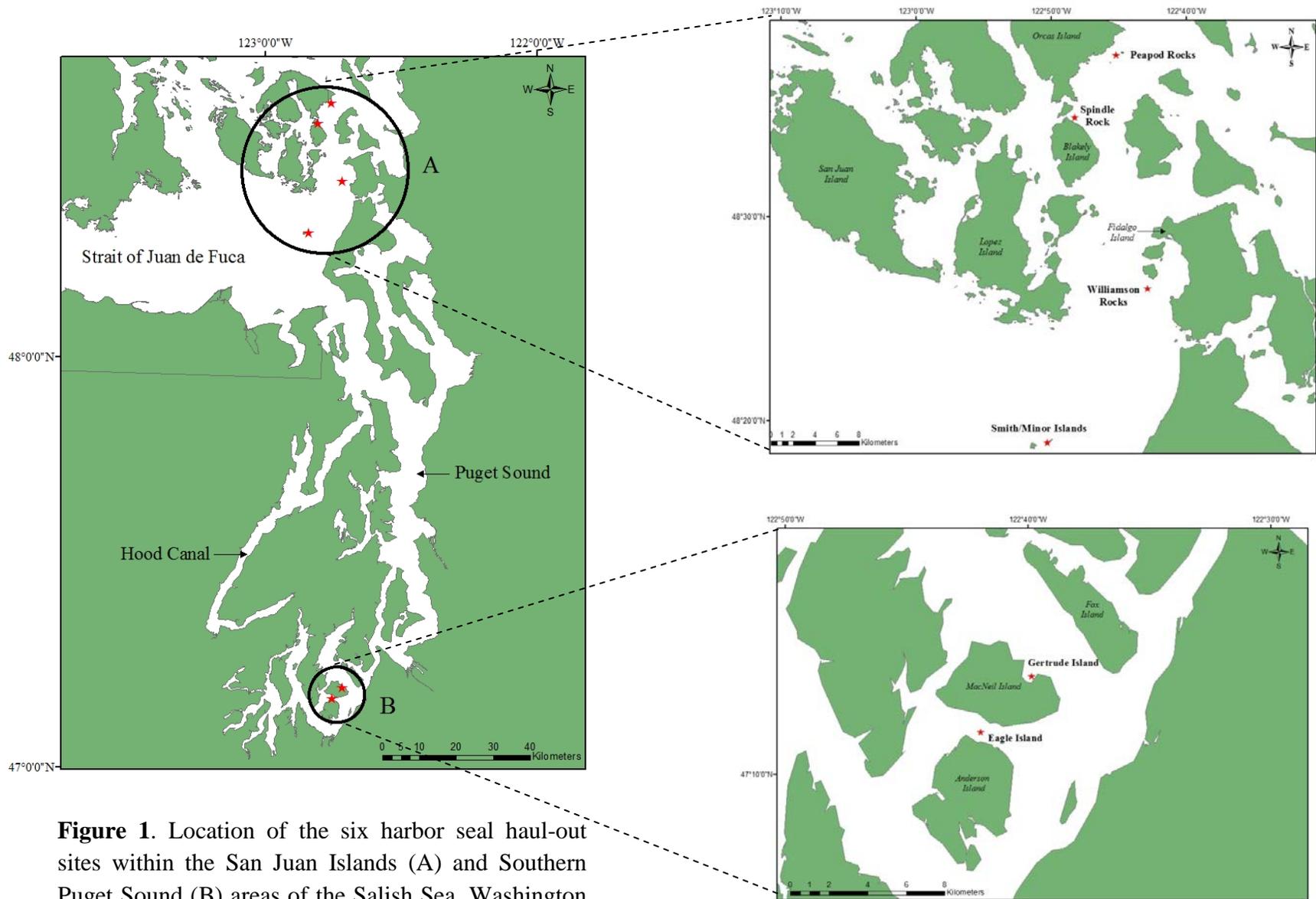
### Study sites

All study sites were located within two main regions of the Salish Sea: Puget Sound and the San Juan Islands (Figure 1). Puget Sound is a body of water extending from Deception Pass to Olympia with connections to both the Strait of Juan de Fuca and the Pacific Ocean. The San Juan Islands are an archipelago including a multitude of smaller waterways situated north of the Strait of Juan de Fuca. In Puget Sound and the San Juan Islands, there are >150 harbor seal haul-out sites, some of which are located in state parks and some of which are on private land (Jeffries et al. 2000). The high numbers and varied locations of haul-outs in these two areas are ideal for selecting sites that span a wide range of exposure to humans.

Low-exposure sites included Gertrude Island and Smith Island (Figure 1). Gertrude Island (47° 12' 57'' N, 122° 39' 40'' W) is located in southern Puget Sound and is situated within the boundary of the McNeil Island Corrections Center. Due to strict security monitoring, boat traffic and foot traffic is virtually non-existent at this haul-out site (S. Jeffries, pers. comm.<sup>4</sup>). The Department of Corrections maintains a 100-yd security limit, and boats that are not associated with the facility are restricted from entering Still Harbor, where the haul-out is located. Gertrude Island is the largest harbor seal haul-out in southern Puget Sound and is an important pupping, breeding, and molting site for >500 seals (Jeffries et al. 2000; Lambourn et al. 2010). Furthermore, bald eagles were noted scavenging dead pups in the area in the early

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<sup>4</sup> Steve Jeffries, Washington State Fish and Wildlife, 7801 Phillips Road SW, Lakewood, WA 98498, July 2011



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

1990s, and are common throughout pupping season (Lambourn et al. 2010).

The second low-exposure site, Smith Island, is located within Island County in northern Puget Sound and is part of the San Juan Islands National Wildlife Refuge (Murphy et al. 2010). Smith Island is connected to Minor Island at low tide, and hundreds of harbor seals haul-out on the spit of land connecting the two sites (48° 19' 24'' N, 122° 49' 18'' W). Both islands are closed to the public year-round and the United States Fish and Wildlife Service (USFWS) prohibits any boating activity within a 200-yd buffer zone surrounding the islands. Furthermore, Smith and Minor Islands are relatively isolated from other islands in the San Juan Archipelago and are situated outside of most major boating paths (Gene McKeen, pers. comm.<sup>5</sup>). The protected status and relative difficulty of access to Smith and Minor Islands result in minimal human disturbance in the area. There is also a known bald eagle presence at the site and numbers have been increasing in recent years (Murphy et al. 2010).

Medium-exposure sites included Peapod Rocks and Williamson Rocks, both of which are located in the San Juan Islands (Figure 1). Peapod Rocks are split into North, South, and Middle Peapod and are located on the east side of Orcas Island. My observations were restricted to Middle (48° 38' 23'' N, 122° 45' 8'' W) and North Peapod Rocks (48° 38' 30'' N, 122° 44' 49'' W). Williamson Rocks (48° 26' 58'' N, 122° 42' 21'' W) is located just outside the southern entrance to Burrows Bay in Island County, WA. Like Smith and Minor Islands, both Peapod Rocks and Williamson Rocks are part of the San Juan Islands National Wildlife Refuge (Public Lands Information Center 2011). They are also closed to the public and all visitors are asked to remain 200 yd from shore; however, these two sites do not experience the same level of isolation

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<sup>5</sup> Gene McKeen, Shannon Point Marine Center, 1900 Shannon Point Road, Anacortes, WA 98221, April 2011

as Smith Island. Peapod Rocks is tucked away from most major boating paths, but tend to serve as a popular area for recreational fishing boats (L. Hubbert, pers. comm.<sup>6</sup>). Similarly, Burrows Bay is home to Skyline Marina, which greatly increases boat traffic near Williamson Rocks.

High-exposure sites included Eagle Island and Spindle Rock (Figure 1). Eagle Island (47° 11' 13'' N, 122° 41' 46'' W) is located in southern Puget Sound on the southwest side of MacNeil Island. As a designated state marine park, this island serves as an attraction spot for human recreation and ecotourism. It is also located within Balch Passage, a heavily trafficked area and one of the primary channels used to access Southern Puget Sound (Lambourn et al. 2010). Spindle Rock, located off the north end of Blakely Island in the San Juan Islands (48° 35' 17'' N, 122° 48' 3'' W), is also subject to increased boat traffic due to its highly exposed location in a key channel for transiting recreation and fishing boats (L. Hubbert, pers. comm.<sup>6</sup>).

### **Observer location**

All observations at Gertrude and Eagle Island were taken from a land-based position because there was access to a concealed viewing location >100 m from the seals. Specifically, Gertrude Island observations were collected from an elevated blind located on MacNeil Island near the southeast side of Still Harbor, approximately 175 m from the seals. Eagle Island observations were collected from a small cliff on the northwest side of MacNeil Island, approximately 600 m from the harbor seals. Because of these large distances, behavioral observations were conducted using a spotting scope (Fujinon Field Scope Super Ed 80; 20-60X zoom).

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<sup>6</sup> *Leroy Hubbert, Blakely Island Field Station, 1 University Drive, Blakely Island, WA 98222, November 2011*

Observations for all other sites were conducted from a 19' inflatable boat anchored within view of the haul-out. Once a distance of 500 m from a haul-out site was reached, I reduced the engine speed to an idle pace and approached the haul-out slowly at an angle roughly parallel to the harbor seals. At nearly all sites, I anchored approximately 200 m away from the seals. The only exception was Williamson Rocks, where, due to the location of the seals and the topography of the ocean floor, I was restricted to an anchoring position approximately 100 m from the seals. All distances to the harbor seals were estimated using a laser range finder (Leica Rangemaster CRF 1000;  $\pm 1$  m/yd up to 500 m/yd or  $\pm 2$  m/yd up to 900 m/yd) and all behavioral observations were conducted using binoculars (STEINER Commander Military; 7x50 C).

After approaching a site via boat, I allowed a minimum adjustment period of 30 min before collecting behavioral observations to reduce any stress or alterations in behavior that might have been caused by our approach. There was no adjustment period for the land-based sites because the harbor seals were unaware of our presence. Due to anchoring restrictions and the spread of seals across large haul-out areas, observations for my boat-based sites were usually centered on a segregated area of observable seals. Given the topography of the sites, I was able to observe all seal reactions and numbers, making it possible to compare data between sites with different viewing platforms. All activities were conducted under NMFS Permit No. 16621-00 awarded to Alejandro Acevedo-Gutiérrez by the Office of Protected Resources of NOAA.

### **Quantifying human exposure**

I estimated the level of human exposure by using counts of boat traffic within 500 m of the haul-out sites. Boat distances were estimated using a laser range finder, as well as utilizing

known distances to land-based reference points from the haul-out site. Reference points were determined *a priori* using Google Maps. Eagle Island, for example, is located approximately 200 m from Anderson Island on the opposite side of Balch Passage from MacNeil Island; therefore, any boat passing between the two islands fell within the 500 m limit.

Human exposure data were collected concurrently with behavioral observations. Weather permitting, observations were conducted Monday-Friday from June–September 2012. I visited only one site per day, with the exception of the two land-based sites, and the schedule of visits was dependent on a number of factors. Observations at Gertrude and Eagle were planned around WDFW visitations and ferry schedules to MacNeil Island. I attempted to rotate through the remaining four sites sequentially and centered my observations around mean lower low water. On days where access to the sites at low tide was not feasible, I collected data at Smith Island or Peapod Rocks where seals would still be visible at higher tides, and trips to Smith Island were prioritized on days with  $<10 \text{ km} \cdot \text{h}^{-1}$  of wind for safety reasons.

## **Behavioral observations**

### **Baseline measurements**

Once the 30-min adjustment period was complete, I monitored the baseline behaviors of the entire haul-out at 15-min intervals using instantaneous scan-sampling to record three behavioral states (Martin & Bateson 2007; Table 1a). During the baseline intervals, I also

**Table 1a.** Ethogram of harbor seal baseline behaviors.

<b>Behavior</b>	<b>Distinguishing characteristics</b>
Rest	Animal's head is on the ground and/or has its eyes closed
Scan	Animal's head is raised (eyes are open) and is surveying its surroundings
Active	Animal is interacting with other seals, vocalizing, or adjusting position on beach

**Table 1b.** Bald eagle behaviors recorded at harbor seal haul-out sites.

<b>Behavior</b>	<b>Distinguishing characteristics</b>
Acoustics	Eagle vocalization within hearing range of the haul-out
Glide	Eagle glides or soars (i.e. wings do not flap) above the haul-out
Powered Flight	Eagle has directed flight (i.e. wings flapping) above the haul-out
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

**Table 1c.** Ethogram of harbor seal behavioral responses to potential disturbances.

<b>Response</b>	<b>Distinguishing characteristics</b>
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 (scan), or animal is shifting its position on the beach (active)
Flush	Animal flushes into the water from hauled-out position

recorded the total number of seals hauled-out, total number of seals in the water and the total number of pups using binoculars or a spotting scope. For sites with >200 seals hauled-out at a time, total counts were collected every 30 min, while behaviors were still monitored every 15 min.

### **Anti-predatory responses**

***Response to bald eagles.*** I recorded bald eagle visitations to the haul-out sites, taking date, time of arrival, duration of visit, and behavior of the eagles during each sighting (Table 1b). I also used instantaneous scan-sampling to determine the behavioral response of the harbor seals during each eagle interaction (Table 1c). Harbor seal responses were noted for each eagle sighting and/or change of a particular eagle behavior (Table 1b). In the event that multiple eagle behaviors occurred simultaneously, the response of the harbor seals was analyzed as one interaction. The effect of specific eagle behaviors was not examined as it fell beyond my study question. I employed *ad libitum* sampling (Martin & Bateson 2007) during moments of extended and intense interactions between the two species, such as pupping events or stillborn births, to gather as much information as possible on the interactions between bald eagles and harbor seals.

***Response to anthropogenic activities.*** I recorded the reaction of harbor seals to three types of potential anthropogenic disturbances. A potential disturbance was defined as boat traffic within 500 m of the haul-out, aerial traffic passing directly above the haul-out site or in the haul-out vicinity, or foot traffic directly on the haul-out site. For each potential disturbance, I noted the onset time and duration of the incident, minimum distance from the haul-out site, and behavioral response of the harbor seals (Table 1c). I used instantaneous scan-sampling (Martin & Bateson 2007) to determine how many seals showed alert or flush behaviors. For potential

disturbances that persisted longer than 2 min, scans of the entire haul-out were taken at 2-min intervals, but only data from the moment of greatest impact (i.e., the time at which the maximum number of seals flushed or showed a visible reaction to the potential disturbance) were used for analyses. All flushing events were recorded, even if the event was triggered by something outside our definition of potential disturbances.

### **Statistical Models**

Data were analyzed using Generalized Linear Mixed Effect Models (GLMMs). GLMMs are flexible, powerful tests that are useful for analyzing non-normal data (such as proportions and counts) and which allow for the inclusion of both fixed and random effects (Faraway 2005; Bolker et al. 2008). Furthermore, they are able to account for correlated variables and are robust to dealing with unbalanced data sets (Breslow & Clayton 1993; Hebbelwhite & Merrill 2008). All data were analyzed using the lme4 package in the program *R* (version 2.13.1; Bates & Maechler 2009).

### **Human exposure**

To assess my categorical grouping of sites into different levels of human exposure, I ran a GLMM using boats  $\cdot h^{-1}$  as my response variable. My parameters included human exposure as a fixed factor with three levels (high, medium, low) and site as a random factor. I used a Gaussian distribution and an identity link function, both of which are most appropriate for continuous data, and the model of best fit was determined using the lowest AIC value (Bolker et al. 2008; Zuur et al. 2009).

## **Eagle exposure**

Following preliminary observations and data exploration, it was clear that there were not only differences in the exposure to humans among sites, but also in the amount of exposure to bald eagles. In order to take this variation into consideration, I divided the sites into high and low categories of eagle exposure and ran a GLMM to assess whether the categories were statistically different. I used the total number of eagle interactions  $\cdot h^{-1}$  as my response variable and my parameters included eagle exposure as a fixed factor with two levels of exposure (high, low) and site as a random factor. I used the Gaussian distribution and an identity link, which are most appropriate for continuous data, and the model of best fit was determined using the lowest AIC value (Bolker et al. 2008; Zuur et al. 2009).

## **Baseline behaviors**

The full baseline model tested the fixed effect of human exposure (low, med, high), as well as the random effects of haul-out site and seal numbers on the response variable. To best compare baseline behaviors to anti-predatory responses, scan and active behaviors were combined into one category: “alert” behavior. Hence, the response variable was the proportion of seals exhibiting alert behavior. Because I used proportion data with the values of my response variable ranging from 0-1, I used a binomial distribution with a logit link function, and the model of best fit was determined using the lowest Akaike Information Criterion (AIC) value (Bolker et al. 2008; Zurr et al. 2009).

## **Anti-predatory responses**

*Response to bald eagles.* To test the behavioral response to bald eagles, I utilized three models. The first model tested for the simple presence or absence of an anti-predatory response (i.e. alert or flush behaviors). The parameters for the model included the fixed effects of human exposure (low, medium, high) and eagle exposure (low, high) as well as the random effects of haul-out site and seal numbers. Because the response variable was binary, I used a binomial distribution with a logit link function, and the final model was determined using the lowest AIC value (Bolker et al. 2008; Zurr et al. 2009).

To further investigate the magnitude of seal responses, the second two sets of models looked at the proportion of seals exhibiting a particular behavior. The response variable for the first model was the proportion of seals that showed flush behaviors, and the response variable for the second model was the proportion of seals that showed alert behaviors. The parameters for both models included the fixed effects of human exposure and eagle exposure as well as the random effects of haul-out site and seal numbers. Alert behaviors were only used as a response variable in the absence of a flushing event. Flushing is a more dramatic and energetically costly behavior than scanning; thus, looking at the proportion of alert seals in response to a potential disturbance without considering whether flushing has occurred may result in a skewed image of anti-predatory response. I used a binomial distribution with a logit link function and determined the model of best fit using the lowest AIC value.

*Response to anthropogenic activities.* To determine harbor seal reaction to anthropogenic activities, I looked at the response to three different types of potential disturbances: boat traffic, air traffic, and foot traffic. No GLMMs were used to test for differences in response to human foot traffic as there were only two instances of foot traffic, both

of which occurred at the same site. To test the behavioral response to boat traffic, I utilized the same three model sets with equivalent response variables and parameters as stated above for bald eagles. Due to a limited number of flushing events ( $n=2$ ), I only compared harbor seal response to air traffic using proportion of alert behaviors. Again, I used a binomial distribution with a logit link function and determined the model of best fit using the lowest AIC value.

## **RESULTS**

### **Human exposure**

Overall, I completed 161.72 hours of human-exposure observations. GLMMs confirmed statistical differences in the categorical grouping of boat traffic into high, medium, and low levels (Tables 2-3). Sites classified as high exposure had  $>5$  boats  $\cdot h^{-1}$  on average, sites classified medium exposure had 1-3 boats  $\cdot h^{-1}$  on average, and sites classified as low exposure had  $<1$  boat  $\cdot h^{-1}$  on average.

### **Eagle exposure**

I observed bald eagles at the haul-out sites on 61.5% of our observation days (n=52). Bald eagles were present at all six of our sites at least once, but were most commonly seen at the sites with low human exposure, Gertrude and Smith, as well as Eagle Island. Bald eagles were seen on 80.0% of observations days for Smith Island (n=10), 75% for Gertrude Island (n=8), 75% for Eagle Island (n=4), 66.7% for Peapod Rocks (n=12), 50% for Spindle Rock (n=8), and 30% for Williamson Rocks (n=10).

Bald eagles were spotted at haul-out sites in both southern Puget Sound and the San Juan Islands from the beginning of the sampling period in June throughout the end of August. No eagles were seen at any of the haul-out sites during the month of September. The peak count for bald eagles (12 individuals) occurred in mid-July. Overall, bald eagle numbers appeared to peak shortly prior to the peak number of pups for the summer, which also occurred in July.

**Table 2.** Comparison of boat traffic at six different harbor seals haul-out sites. Values are expressed as mean  $\pm$  SE.

<b>Site</b>	<b>Total Time (hr)</b>	<b>Mean boats <math>\cdot</math> h<sup>-1</sup></b>
<b>Spindle (High)</b>	16.33	6.4 $\pm$ 1.10
<b>Eagle (High)</b>	27.50	5.6 $\pm$ 0.83
<b>Williamson (Med)</b>	39.00	2.2 $\pm$ 0.70
<b>Peapod (Med)</b>	30.67	1.0 $\pm$ 0.35
<b>Gertrude (Low)</b>	23.60	0.3 $\pm$ 0.24
<b>Smith (Low)</b>	24.62	0.2 $\pm$ 0.10

**Table 3.** Generalized Linear Mixed Model (GLMM) results for boat traffic relative to the level of human exposure (low, medium, high) and haul-out site (Site) from June-September 2012.

<b>Model</b>	<b>Df</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
Traffic ~ Exposure + (1 Site)	5	214.5	0
Traffic ~ (1 Site)	3	230.2	15.7

GLMMs confirmed statistical differences in the grouping of eagle behaviors into high and low categories (Table 4). Eagle, Gertrude, and Smith Islands had a significantly greater number of eagle interactions per day than Peapod, Williamson, or Spindle (Figure 2). Because of this variation in harbor seal exposure to eagles among the different haul-out sites, I included eagle exposure as a fixed factor in my anti-predatory response models.

### **Baseline measurements**

The average number of harbor seals hauled-out across all baseline samples at all sites was  $97.12 \pm \text{SE } 15.88$  ( $n=51$ ) while the average number of pups was  $6.43 \pm \text{SE } 1.26$  ( $n=51$ ); however, the total harbor seal and pup counts varied greatly by site (Table 5).

There was no difference in baseline behaviors among the different levels of human exposure. Based on AIC values, the final model for alert behavior was best described only by the random variables of site and seal numbers (Table 6). Because there was no difference in baseline behaviors at the different levels of human exposure, baseline behavior level was not included as a covariate in any of the anti-predatory response models. The average percentage of seals showing alert behaviors at baseline intervals was similar for all sites and ranged between 8-12% of the total number of seals present.

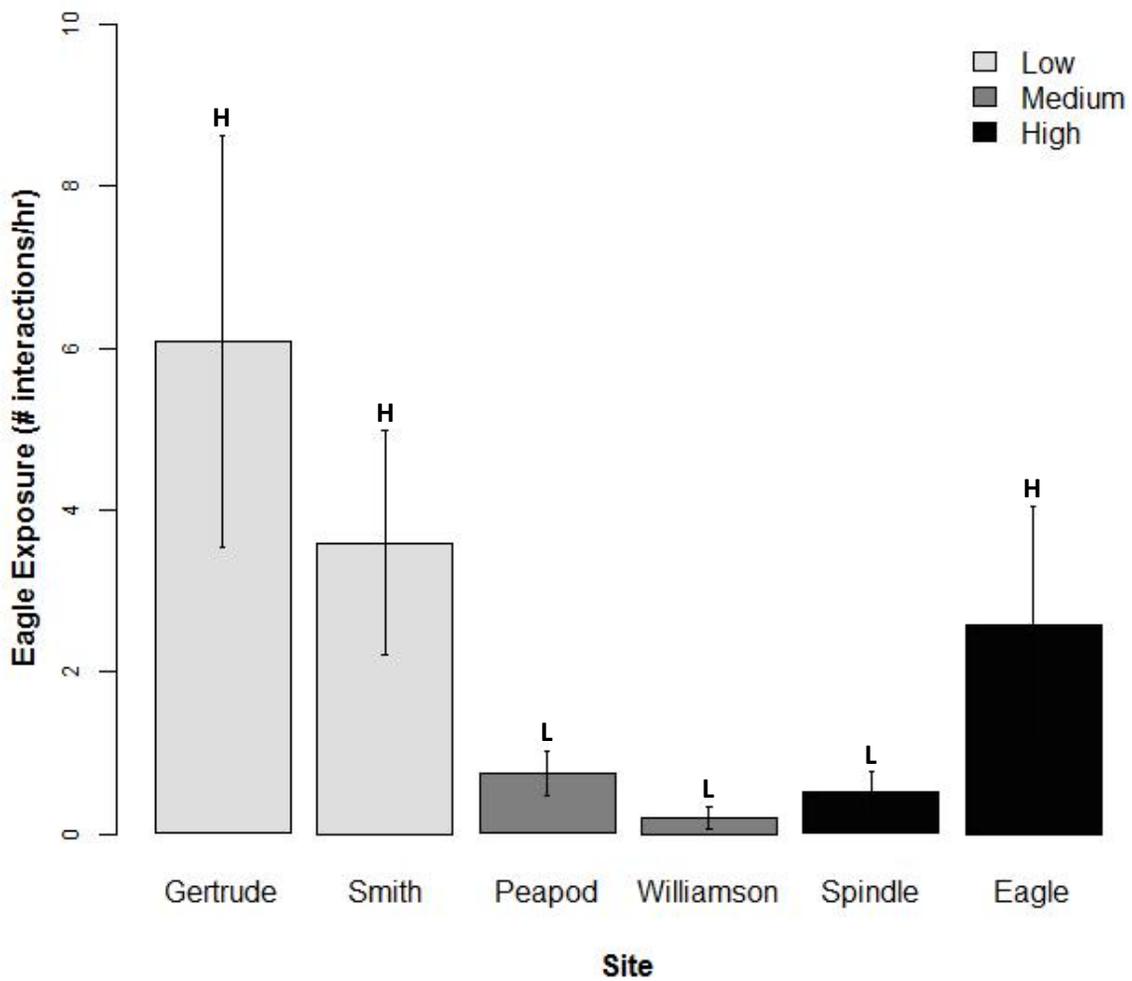
### **Anti-predatory responses**

#### **Response to bald eagles**

As predicted, harbor seal response to bald eagles varied according to the level of human exposure (Table 7). The model of best fit included both human exposure and the random factors of site and seal numbers. Contrarily, the amount of eagle exposure did not have an effect on the

**Table 4.** Generalized Linear Mixed Model (GLMM) results for eagle interactions (per hour) relative to the level of eagle exposure (low, high) and haul-out site (Site) from June-September 2012.

<b>Model</b>	<b>Df</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
Interactions ~ Exposure + (1 Site)	4	283.1	0
Interactions ~ (1 Site)	3	289.5	6.4



**Figure 2.** Average eagle interactions per hour for six different harbor seal haul-out sites. Bar color indicates level of human exposure and error bars represent  $\pm$  SE. Letters indicate the level of eagle exposure (H=High, L=Low).

**Table 5.** Average number of harbor seals hauled out and average number of pups hauled out at six haul-out sites. Averages are based on the max counts per day and values are expressed as mean  $\pm$  SE. N represents the total number of days per site.

<b>Site</b>	<b>Total seals</b>	<b>Pups</b>	<b>N</b>
Eagle	100.8 $\pm$ 11.7	13.5 $\pm$ 3.1	4
Spindle	33.8 $\pm$ 3.2	4.9 $\pm$ 1.6	8
Williamson	25.5 $\pm$ 4.4	1.5 $\pm$ 0.7	10
Peapod	46.6 $\pm$ 11.3	4.4 $\pm$ 1.5	12
Smith	117.1 $\pm$ 21.1	4.4 $\pm$ 1.1	9
Gertrude	301.5 $\pm$ 49.6	15.9 $\pm$ 6.1	8

**Table 6.** Generalized Linear Mixed Model (GLMM) results for the average percentage of seals alert at 15-min baseline intervals relative to the level of human exposure (Traffic), seal numbers (Group), and haul-out site (Site) from June-September 2012.

<b>Model</b>	<b>Df</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
Alert ~ (1 Group) +(1 Site)	3	1574.8	0
Alert ~ Traffic + (1 Site)+ (1 Group)	5	1576.9	2.1

**Table 7.** Generalized Liner Mixed Model (GLMM) results for three different harbor seal responses to bald eagle interactions: presence/absence of an anti-predatory behavioral response, proportion of seals showing flush behavior, and proportion of seals showing alert behavior. Responses are shown relative to the level of human exposure (Traffic), the level of eagle exposure (Eagles), the seal numbers (Group), and haul-out site (Site) from June-September 2012. The model of best fit for each category is indicated by the lowest AIC value.

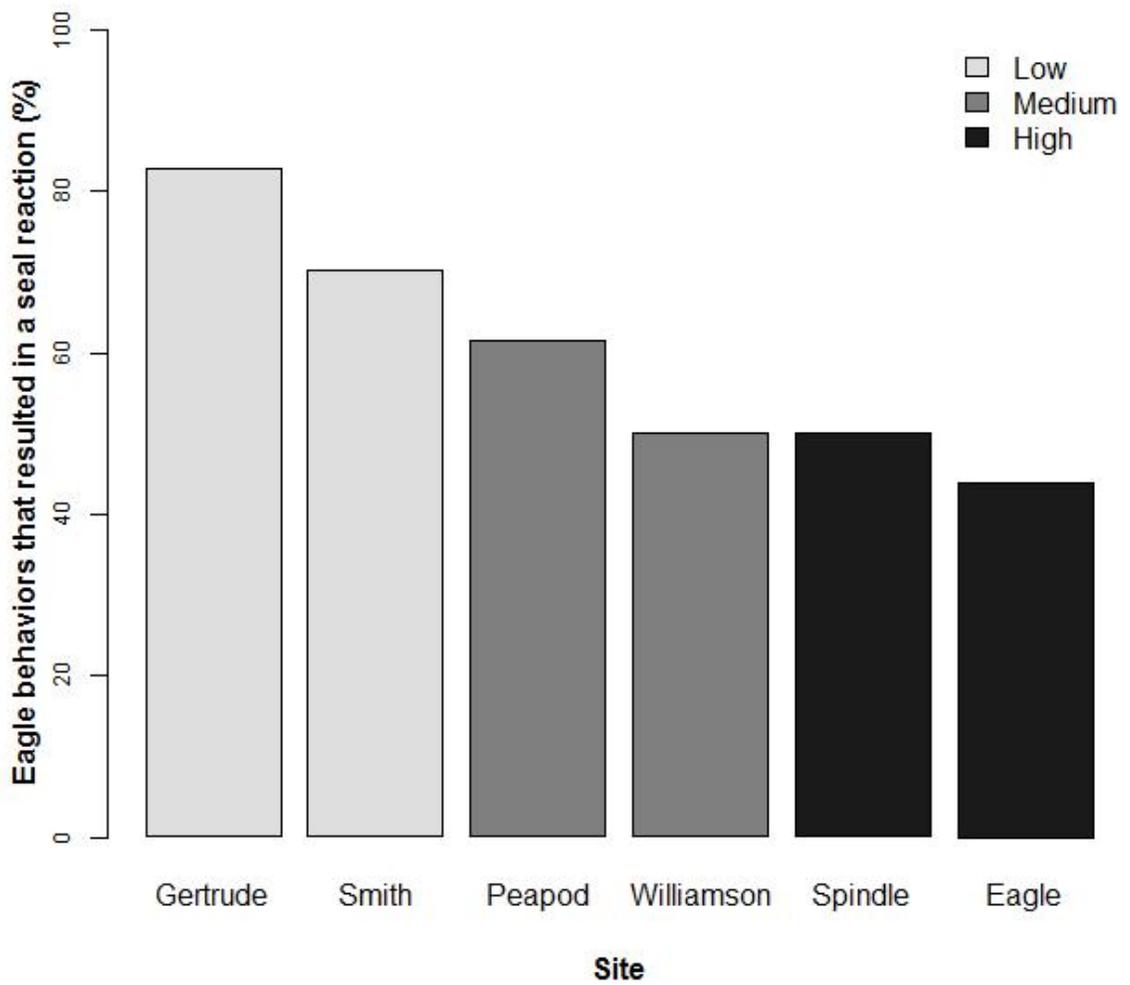
<b>Model</b>	<b>df</b>	<b>AIC</b>	<b>ΔAIC</b>
<b>Presence/Absence of Anti-Predatory Response</b>			
Response ~ Traffic + (1 Site)+(1 Group)	5	211.6	0
Response ~ Traffic + Eagles + (1 Site)+(1 Group)	6	213.6	2
Response ~ (1 Site)+(1 Group)	3	215.1	3.6
Response ~ Eagles + (1 Site)+(1 Group)	4	215.8	4.2
<b>Proportion of Seals Flushing</b>			
Flush ~ Eagles + (1 Site)+(1 Group)	4	347.5	0
Flush ~ Traffic + (1 Site)+(1 Group)	5	365.4	17.8
Flush ~ Traffic + Eagles + (1 Site)+(1 Group)	6	388.4	40.8
Flush ~ (1 Site)+(1 Group)	3	431.4	83.9
<b>Proportion of Seals Alert</b>			
Alert ~ Traffic + (1 Site)+(1 Group)	5	622.8	0
Alert ~ (1 Site)+(1 Group)	3	623.3	0.6
Alert ~ Eagles + (1 Site)+(1 Group)	4	624.2	1.4
Alert ~ Traffic + Eagles + (1 Site)+(1 Group)	6	624.6	1.8

presence of harbor seal anti-predatory response. Harbor seals showed an anti-predatory response (either alert or flush behaviors) to bald eagles at low exposure sites more often than at the medium or high exposure sites (Figure 3). Seals at low exposure sites reacted during 77.17% (n=127) of recordable bald eagle interactions, seals at medium exposure sites reacted during 60.0% (n=15) of interactions, and seals at high exposure sites reacted during 45.45% (n=33) of interactions.

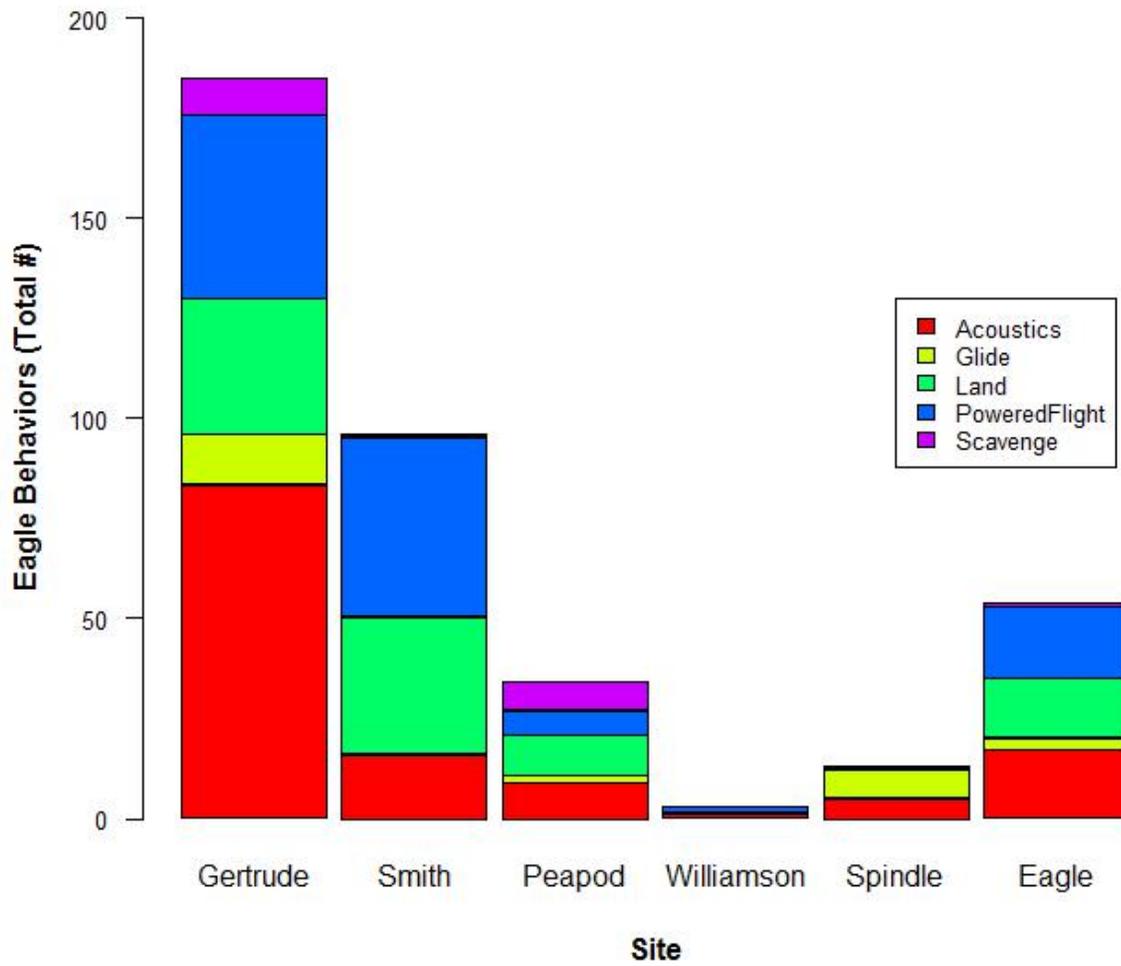
Based on AIC values, the level of human exposure was not included in the model of best fit for differences in the proportion of seals that flushed in response to eagles (Table 7). The final model included the fixed factor of eagle exposure and the random variables of haul-out site and seal numbers. All 18 flushing events in response to eagles took place at the sites with high exposure to eagles. Harbor seals flushed in response to 20.0% of eagle interactions (n=70) at Gertrude, 5.3% (n=57) at Smith, and 4.0% (n=25) at Eagle.

Human exposure was included in the best model for differences in the proportion of alert seals (Table 7). The low-exposure sites (Gertrude and Smith) had greater percentage of alert behaviors in response to eagles than all other sites except for the medium-exposure site of Williamson Rocks. The sample size for bald eagle sightings at Williamson Rocks was extremely small (n=2) and the number of seals present for the two sightings was also minimal (n=1 and n=11, respectively).

***Eagle behavior.*** Bald eagle behaviors varied noticeably by site (Figure 4). The most common behavior I observed overall was eagle acoustics (130 total calls heard throughout the field season). Calls were heard at all six of my sites and were the most common eagle behavior at both Gertrude Island and Peapod Island. Powered flight was the second most commonly



**Figure 3.** Percentage of eagle interactions that resulted in an anti-predatory response (alert or flush behaviors) from harbor seals. Bar color indicates level of human exposure.



**Figure 4.** Total number and type of bald eagle behaviors observed at six different harbor seal haul-out sites in the Salish Sea from June-September 2012.

observed behavior overall and was the most common behavior for Smith Island, Williamson Rocks, and Eagle Island. I only once witnessed eagles engaged in powered flight at Spindle Rock; instead, eagles tended to be located at a much higher altitude at this site and were gliding/soaring on all other occasions. Eagles were observed landed on all haul-out sites except for Williamson Rocks and Spindle Rock.

Scavenging events were also observed at four of the sites, but occurred most commonly on Gertrude and Peapod. The only type of scavenging I saw at Peapod or Smith was eagles feeding on seal carcasses, likely pups. At both Eagle Island and Gertrude Island, I also observed eagles consuming placenta shortly after pupping events. I observed 4 total occasions of afterbirth consumption; in all cases, the eagle(s) reached the placenta in less than ten minutes of its coming into view of the observers. One such event occurred on Eagle Island and resulted in 22.6% of seals flushing from the island. The eagle landed within 5 m of the mother (with placenta still attached to body) and newborn pup. The mother eventually flushed, but the pup remained hauled-out near the eagle. The bald eagle appeared more interested in the placenta than the pup and flew away with the placenta after a total of 6 min. The other three afterbirth scavenging events took place at Gertrude Island and resulted in 90.3%, 16% and 32% of seals flushing in response to the eagles' presence, respectively.

There was also one extended interaction between an adult bald eagle and an adult harbor seal defending her stillborn pup at Gertrude Island. The adult female gave birth to the stillborn on July 17 at 14:20. At the same time as the birth, multiple bald eagle acoustics were heard around the haul-out site. By 14:21, an adult bald eagle had landed on the haul-out site within 2 adult seal body lengths of the stillborn. After initially flushing into the water, the mother of the stillborn returned to defend her pup. The eagle proceeded to linger by the mother-pup pair for 41

minutes, staying within 2-3 body lengths of the seals. On multiple occasions, the eagle decreased its distance to the seals causing the mother to vocalize and aggressively charge at the eagle while snapping at the air with her mouth. Throughout the duration of the event, a total of 82% of the harbor seals flushed. At 15:02, the mother managed to fully submerge her pup into the water at which point the eagle flew away.

### **Anthropogenic activities**

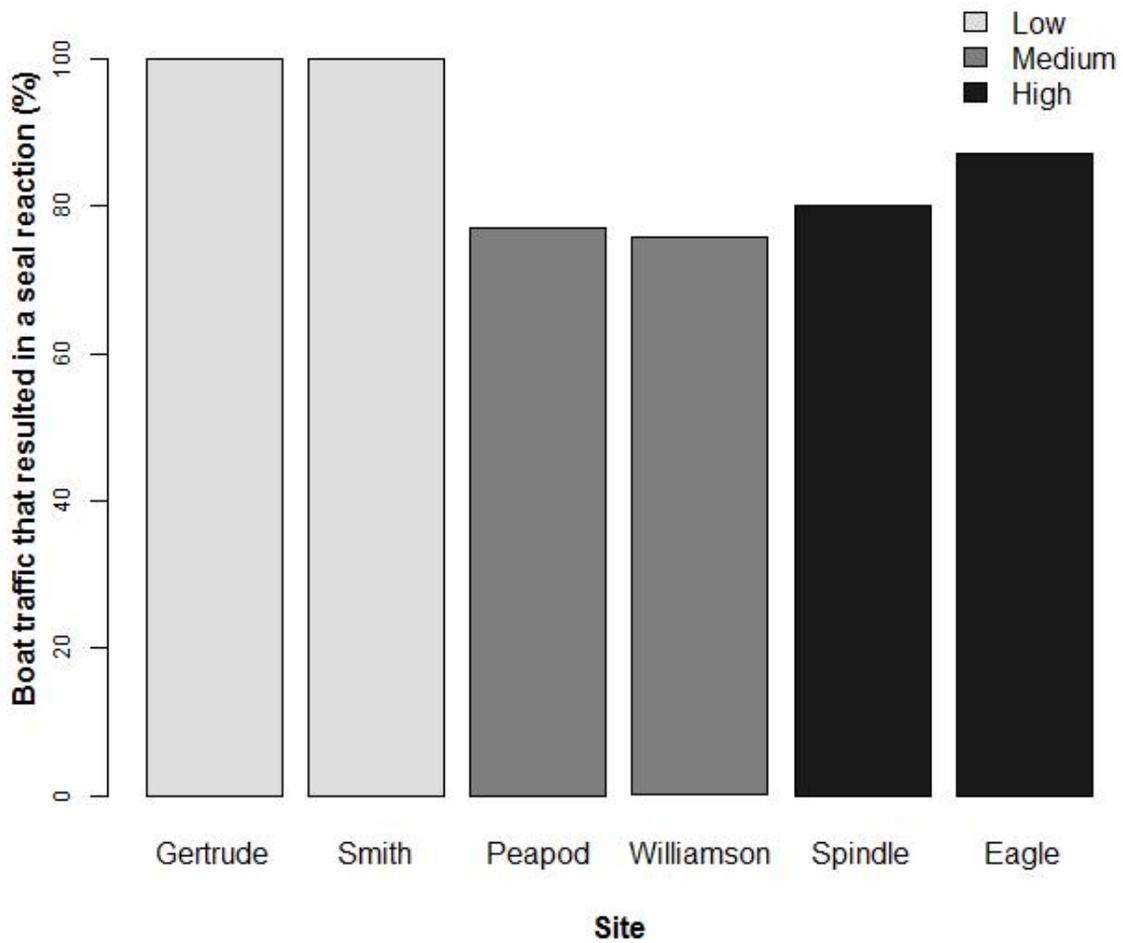
***Boat traffic.*** Harbor seal response to boat traffic varied according to the level of human exposure (Table 8). At the two low exposure sites, seals showed an anti-predatory response (alert or flush behavior) to 100% of passing boats (n=10; Figure 5), whereas seals reacted to only 83.2% of boats passing by the high exposure sites (n=208) and 77.8% of boat passing by the medium exposure sites (n=72).

Based on AIC values, the level of human exposure was not included in the model of best fit for differences in proportion of seals showing flush or alert behaviors (Table 8). The final models included only the random variables of site and seal numbers. The only site without a flushing event in response to boat traffic was Smith Island. During our observations, only 4 boats passed within 500 m of Smith Island, and none of them came closer than 250 m.

***Other human activities.*** Harbor seal response to aerial traffic did not vary according to different levels of exposure (Table 9). There were only two flushing events in response to aerial traffic, one at Smith Island and one at Williamson Rocks. Both flushing events involved a very small number of seals (n=5 and n=1, respectively). The aircraft that caused 5 seals to flush at Smith Island was an extremely loud and low-flying jet.

**Table 8.** Generalized Liner Mixed Model (GLMM) results for three different harbor seal responses to boat traffic: presence/absence of an anti-predatory response (alert or flush behaviors), proportion of seals showing flush behavior, and proportion of seals showing alert behavior. Responses are shown relative to the level of human exposure (Traffic) as well as seal numbers (Group), and haul-out site (Site) from June-September 2012. The model of best fit for each category is indicated by the lowest AIC value.

<b>Model</b>	<b>df</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
<b>Presence/Absence of Anti-Predatory Response</b>			
Response ~ Traffic + (1 Site)+(1 Group)	5	271.2	0
Response ~ (1 Site)+(1 Group)	3	272.1	0.9
<b>Proportion of Seals Flushing</b>			
Flush ~ (1 Site)+(1 Group)	3	1129.2	0
Flush ~ Traffic + (1 Site)+(1 Group)	5	1132	2.8
<b>Proportion of Seals Alert</b>			
Alert ~ (1 Site)+(1 Group)	3	723.4	0
Alert ~ Traffic + (1 Site)+(1 Group)	5	726.9	3.6



**Figure 5.** Percentage of all boat traffic that resulted in an anti-predatory response (alert or flush behaviors) from harbor seals. Bar color indicates level of human exposure.

**Table 9.** Generalized Linear Mixed Model (GLMM) results for proportion of seals that showed alert behaviors in response to air traffic relative to the level of human exposure (Traffic), seal numbers (Group), and haul-out site (Site) from June-September 2012.

<b>Model</b>	<b>Df</b>	<b>AIC</b>	<b><math>\Delta</math>AIC</b>
Alert ~ (1 Group) + (1 Site)	3	697.2	0
Alert ~ Traffic + (1 Site) + (1 Group)	5	699.4	2.2

I recorded a total of 477 potential anthropogenic disturbances, 36 of which (7.55%) resulted in an actual flushing event. Potential anthropogenic disturbances were comprised of boat traffic (60.8%), aerial traffic (38.8%), and human foot traffic (0.42%). There were 27 additional flushing events, the cause of which was something other than the pre-defined potential disturbances (e.g. large wake, loud sounds from shore). There were 17 flushing events for which I could not identify the source and they were thus classified as unknown. All but one of the unknown flushing events (94%) occurred at the two low exposure sites. Two data points were removed from analysis due to a simultaneous interaction of two or three potential causes (including eagle interactions) at the time of the flushing event.

Overall, anthropogenic disturbances caused the majority of flushing events at the medium and high exposure sites. On the other hand, natural disturbances were more common at Gertrude and Smith (Table 10). The primary cause of flushing events differed according to site (Table 10). Boat traffic accounted for 72.7% of all actual anthropogenic disturbances, 75% being from motorized boats and 25% being from non-motorized boats (e.g. sailboats or kayaks). Kayaks seemed to have an especially notable effect on the harbor seals with 86% of kayak approaches resulted in a flushing event. Additionally, both instances of human foot traffic on Eagle Island resulted in 100% of the seals flushing.

**Table 10.** Summary of total disturbances (i.e. flushing events) at six harbor seal haul-out sites in the Puget Sound and San Juan Islands. Causes of the flushing events are also shown and are organized according to type.

EXPOSURE LEVEL Site	LOW		MEDIUM		HIGH	
	Eagle	Spindle	Williamson	Peapod	Smith	Gertrude
Percent of days with flushing (n)	100% (4)	62.5% (8)	30% (10)	50% (12)	44.4% (9)	100% (8)
No. of flushing events	19	13	6	6	12	26
<b>ANTHROPOGENIC DISTURBANCES</b>	<b>94.7%</b>	<b>92.3%</b>	<b>83.3%</b>	<b>66.7%</b>	<b>8.3%</b>	<b>15.4%</b>
Boat Traffic	63.2%	84.6%	50.0%	66.7%	0	7.7%
<i>(motorized)</i>	47.4%	76.9%	33.3%	50.0%	0	7.7%
<i>(non-motorized)</i>	15.8%	7.7%	16.7%	16.7%	0	0
Air traffic	0.0%	0	16.7%	0	8.3%	0
Foot Traffic	10.5%	0	0	0	0	0
Other	21.1%	7.7%	16.7%	0	0	7.7%
<b>NATURAL DISTURBANCES</b>	<b>5.3%</b>	<b>0.0%</b>	<b>16.7%</b>	<b>33.3%</b>	<b>25.0%</b>	<b>53.8%</b>
Vulcher	0	0	0	33.3%	0	0
Merlin	0	0	16.7%	0	0	0
Eagle	5.3%	0	0	0	25.0%	53.8%
<b>UNKNOWN</b>	<b>0.0%</b>	<b>7.7%</b>	<b>0</b>	<b>0</b>	<b>66.7%</b>	<b>30.8%</b>

## DISCUSSION

Results indicate that the presence or absence of harbor seal anti-predatory response varied according to the level of exposure to humans. As predicted, seals reacted to eagles more often at sites with low levels of human activities than they did at sites with medium or high levels of human activities. Similarly, harbor seals reacted to boat traffic most often at the low-exposure sites. One possible explanation for this pattern in response behavior is that an increased tolerance to human activities, potentially as a result of habituation, has led to a decreased aversion to natural predators in harbor seals. The theory that habituation to humans could negatively impact wildlife populations by decreasing anti-predatory responses has been put forth by many scientists (Beale & Monaghan 2004; Bejder et al. 2009; Higham & Shelton 2011). However, to my knowledge this is the first study that provides empirical evidence to support this hypothesis in a non-urban environment.

The potential explanation for the results observed assumes that harbor seals are either unable to distinguish between different predators and respond to all predation threats equivalently or are able to distinguish between different predators but are facing weak selection for eagle predation. Evidence suggests that the first assumption is unlikely for this situation. Prey from many different taxa show predator-specific behavioral responses (Ghalambor & Martin 2000; Relyea 2001; Deecke et al. 2002). Even though harbor seals show consistent behavioral reactions to a variety of threats, such as humans, dogs, gun shots or aircrafts (Terhune 1985), they are capable of responding to visual, auditory, and spatial cues, all of which are important aspects of predator recognition (Schusterman 1982; Renouf & Gaboriko 1988). Also, harbor seals can distinguish between the calls of mammal-eating transient orcas and salmon-eating residents

and show stronger behavioral responses to the potentially threatening transients (Deecke et al. 2002). Furthermore, they may also possess a threat image of potential predators as evidenced by an experimental study where seal numbers declined at haul-outs in the presence of a black bear model but were unaffected by a control object of similar size and color (Nordstrom 2002). It is then likely that harbor seals have an analogous threat image of bald eagles and can differentiate between eagle and human threats.

Because harbor seals are most likely capable of predator-specific responses, one would not expect them to reduce their anti-predatory behaviors to a recognized high-risk threat. Thus, the decreased response to eagles at my high human exposure sites suggests that harbor seals are not faced with strong predation pressure from bald eagles, a reasonable assumption given the healthy status of harbor seals in the Salish Sea. This result is consistent with previous studies suggesting that the transfer of habituation is more likely to occur when the risk of predation is low (Mcleery 2009). However, it does not necessarily indicate a neutral outcome. For instance, it is possible that constant exposure to anthropogenic stimuli may impede the physiological ability to respond quickly to a threat by reducing overall levels of steroid hormones that are critical for stress response (Romero & Wikelski 2002). Thus, harbor seals at my high exposure sites may be more prone to ignore potential threats, regardless of predator recognition abilities, because they are constantly faced with anthropogenic stimuli that do not directly affect their survival.

Although populations of harbor seals in the Salish Sea are not currently at risk, my results should also be considered in the context of wildlife in general. The ability for prey species to react to predators is influenced by the evolutionary relationships between them, thus animals may be more likely to escape from predators with which they have co-evolved (Berger et al. 2007). Studies on Galapagos marine iguanas, for example, show that weak behavioral

adjustments to human-introduced predators (e.g. dogs) might not be enough for naïve island species to avoid extinction (Berger et al. 2007). Hence, animals that are habituated to humans might be especially vulnerable in these situations where prey species are unable to adapt quickly enough to an unfamiliar threat. This could be critical light of the constant rise of invasive and introduced species (Mack et al. 2000). It is also possible that this could be critical in situations with shifting preferences in prey-choice. For example, the previous endangerment of bald eagles in this area on a state and federal level (Watson et al. 2002) imply that the recent historical threat of bald eagles to harbor seal populations is negligible. However, changes in eagle abundance and food source availability may result in a rapid increase in the rate of attack on harbor seals. This shifting dynamic could represent a situation where an escalating threat of bald eagles is analogous to a novel predator. Even without increased human exposure, shifts in prey choice can have detrimental impacts on prey populations, as well as local food-webs and environments (Estes et al. 1998; Roemer et al. 2002; Rutz & Bijlsma 2006). My findings suggest that habituation to humans might add an additional level of vulnerability for prey species facing these already threatening novel predation situations.

It is important to note that an increased tolerance to human activities does not necessarily indicate that habituation has occurred (Bejder et al. 2009). Rather, increased tolerance to humans is one *result* of habituation. Habituation contains a spatio-temporal component and any assertions of habituation must also encompass factors such as specific types of responses from the focal animal, specific types of human behaviors, location, season, and duration of interactions (Higham & Shelton 2011). Thus, the increased tolerance of harbor seals to boat traffic at my medium and high exposure sites may possibly indicate habituation to humans, but further studies observing the same individuals over sequential field seasons are necessary to

confirm this possibility. Nevertheless, boat traffic at my study sites has occurred for many years, and evidence suggests that harbor seals exhibit high site fidelity (Suryan & Harvey 1998; Tollit et al. 1998; Hardee 2008; Thomas et al. 2011). The San Juan Islands have been replete with human activity since Europeans first settled in the mid-nineteenth century (Avery 2007). In addition, the protection and isolation provided to my low exposure sites has also been around for many years. The MacNeil Island Corrections Center was established before harbor seals were first spotted on Gertrude Island (Lambourn et al. 2010), and the establishment of the protected status of National Wildlife Refuge for the San Jan Islands began in the early 1900s (Don 2002). Thus, it is likely that the seals have been exposed to similar levels of boat traffic at my sites over an extended period of time.

My results also have implications in light of currently accepted perspectives concerning habituation. Within the scientific community, it is generally accepted that habituation is a negative result of increasing interactions with humans (Higham & Shelton 2011). Within wildlife recreation or ecotourism industries, however, habituation of animals to humans is often considered desirable and is even purposefully employed as a technique to improve education, study, and the efficiency of wildlife viewing tours (Nisbet 2000; Knight 2009). Wildlife viewing by means of habituation is thought to be a conservation-friendly alternative to activities such as hunting (Knight 2009). It is perceived as having little-to-no impact and has even been described as an activity in which the animal is “not permanently affected” by the interaction (Duffus & Dearden 1990; Bejder et al. 2009). Quite the contrary, my results suggest the potential impact that increased human exposure can have on the anti-predatory response of wildlife populations and dispute the idea of habituation as a low-impact activity.

The relationship between the magnitude of the anti-predatory response (i.e. the proportion of seals reacting) and the level of exposure to human activities was not as clear as that of the mere presence/absence of an anti-predatory response. The proportion of seals that flushed (in response to either eagles or human activities), did not vary with the level of human exposure. One likely explanation for the general lack of differences in flushing percentages could relate to the fact that when one seal is disturbed to the point of flushing, other individuals tend to follow with the same behavior (Terhune and Brilliant 1996). Although harbor seals do not form true social groups, evidence suggests that their orientation and spacing on the haul-outs serves an anti-predatory function and intentionally allows for easy escape into the water (Terhune & Brilliant 1996). It is then not surprising that the proportion of seals flushing into the water is unlikely to vary much across sites. Another non-mutually exclusive explanation is related to the higher costs associated with flushing when compared to scanning. Fleeing from a potential threat is likely more energetically costly than merely exhibiting increased vigilance and is more likely to reduce time devoted to critical behaviors such as thermoregulation and nursing. This idea is supported by studies where animals show increased physiological stress to threatening stimuli, yet resist any kind of escape behaviors (Nimon et al. 1995; Müllner et al. 2004; Bejder et al. 2009). A similar trade-off may have caused harbor seals to act more conservatively in regards to flushing behaviors in general.

Interestingly, results indicated that the proportion of seals that flushed in response to eagles was affected by exposure to the eagles themselves. In fact, 100% of flushing events in response to eagles occurred at the sites with high eagle exposure. A possible explanation for this result could relate to the harbor seals perceived risk of predation. It is possible that harbor seals at sites with high eagle exposure recognized bald eagles as a stronger threat than those at sites

with low eagle exposure and were thus more likely to flush in response. This explanation is supported by additional studies revealing that the intensity of behavioral responses increases with an increased perception of risk (Relyea 2001; Frid & Dill 2002). Perceived predation risk not only requires predator recognition, but also incorporates factors such as type of predatory behaviors, distribution of predators, and proximity to an alternative escape location (Frid & Dill 2002). Many of the flushing events that I witnessed were associated with rare and significant moments, such as afterbirth scavenging immediately following a pupping event. It is possible that the eagles were providing stronger threat stimuli during these particular events. As I did not observe any pupping events at four of my six sites, this could have greatly influenced my results. It is also likely that the proximity of the eagles to the seals influenced their response. Eighty-three percent of flushing events involved an eagle physically landing on the haul-out site. Anecdotally, it appeared that the harbor seals reacted more intensely when the eagles were closer, but my study lacks the appropriate data to support that claim. Additional studies with accurate distance estimates would undoubtedly contribute further insight into this relationship. Incorporating an experimental component may also provide a huge benefit by allowing for the control and manipulation of both the type and intensity of the predatory behaviors.

The proportion of seals that showed alert behaviors in response to boat or air traffic also did not vary with human exposure. However, the proportion of seals showing alert behaviors in response to eagles did vary according to the level of human exposure, with greater percentages of seals scanning in response to potential predators at the lower exposure sites. The high proportion of alert seals in response to eagles at my low human exposure sites matched my initial predictions and provides further support for the explanation of reduced anti-predatory response as a result of increased anthropogenic exposure. The fact that the magnitude of alert behaviors in

response to eagles varied with human exposure, unlike the magnitude of flushing, also compliments the idea of weak selection for eagle predation. That is, the patterns I expected showed up in the more nuanced behavioral responses rather than the more costly fleeing behaviors that would be more likely to occur in response to higher threat levels. Considering the effect of human exposure on the proportion of alert seals in response to eagles, it is surprising that I did not observe a similar pattern in response to human activities. Because passing boats and aircrafts are rarely linked to a true mortality event, the idea of perceived predation risk may help to rationalize this discrepancy.

Regardless of any anthropogenic factors, it is clear that there were some interesting interspecies dynamics occurring between bald eagles and harbor seals in the Salish Sea. My three sites with high levels of eagle exposure were also the three sites with the highest numbers of harbor seals. Similar observations have been shown at Protection Island, WA where the number of seals was positively correlated with the number of eagles (Hayward et al. 2010). Furthermore, the peak counts of eagles and seal pups occurred at similar times during my field season, and the presence of eagles at the haul-out sites was essentially eliminated after pupping season was over. Past observations at Gertrude Island also indicated that eagle sightings declined at the end of pupping season (Lambourn et al. 2010). Interactions between these two species are bound to increase along with rising eagle numbers, and my observations argue for the necessity of further investigations of the relationship between these two species.

## **Conclusions**

My results are consistent with the theory that increased interactions with humans may lead to a reduction in overall predator aversion. I observed fewer anti-predatory behavioral

responses from harbor seals to both humans and bald eagles at sites with high levels of anthropogenic activities than at sites with low levels of anthropogenic activities. Although harbor seal populations in the Salish Sea are at a healthy level and predation pressure by bald eagles is likely minimal, my findings have implications in situations involving introduced or invasive species and possibly in situations involving shifts in prey choice for generalist predators. They could also significantly alter perspectives of habituation as a beneficial response that are currently accepted within many wildlife viewing communities and highlight the importance of further longitudinal studies across additional taxa.

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