WATERBIRDS ALTER THEIR DISTRIBUTION AND BEHAVIOR IN THE PRESENCE OF BALD EAGLES (*HALIAEETUS LEUCOCEPHALUS*)

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ABSTRACT—We explored changes in seasonal distribution and behavior of waterbirds in the Strait of Georgia, Canada, in response to increased presence of a major avian predator, the Bald Eagle (*Haliaeetus leucocephalus*). Eagles were widespread and their increase through fall and winter coincided with migratory movements of waterbirds. Many species of waterbird used inshore waters in early fall when eagles were scarce. Diving birds moved away from inshore waters when eagles returned in late fall and winter, whereas dabbling ducks formed large flocks in inshore waters and spent proportionally more time being vigilant as winter progressed. Flock sizes and avoidance flight distances of scoters and dabblers, but not gulls, increased with proximity to eagles. Waterbirds did not alter vigilance with distance to eagles. We discuss our findings in context of management issues regarding apparent declines and importance of understanding indirect effects of predators on prey for wildlife monitoring.

Key words: Bald Eagle, dabblers, danger, direct predation, grebes, gulls, *Haliaeetus leucocephalus*, indirect effects, scoters, Strait of Georgia, wintering ecology

A growing body of evidence indicates that birds alter their distributions at local and regional scales in the presence of predators (Creswell 1994; Butler and others 2003; Lank and others 2003; Pomeroy and others 2008; Ydenberg and others 2010). The presence of predators is thought to instill fear in prey with subsequent ecologically important effects (Brown 1999; Ydenberg and others 2002; Butler and others 2003; Brown and Kotler 2004; Creswell 2008; Wirsing and others 2008).

Bald Eagles *(Haliaeetus leucocephalus*; hereafter "eagles") are well known predators of birds in the Pacific Northwest (Brooks 1922; Knight and others 1990; Watson and others 1991; Buehler 2000; Buchanan and Watson 2010). Eagles in the region kill and scavenge a variety of birds and fish (Elliot and others 2011; Anderson and others 2012). Eagle prey species include: (1) dabbling ducks: American Wigeon (*Anas americana*), Mallard (*Anas platyrhynchos*), Northern Pintail (*Anas acuta*), and Green-winged Teal (*Anas crecca*); (2) diving ducks: Scaup (*Aythya marila* and *A. affinis*), Long-tailed Duck (*Clangula hyemalis*), Hooded Merganser (*Lophodytes cucullatus*), Bufflehead (*Bucephala albeola*), Harlequin Duck (*Histrionicus histrionicus*), Surf Scoter (*Melanitta perspicillata*), White-winged Scoter (*M. fusca*), and Black Scoter (*M. nigra*); (3) divers: Red-throated Loon (*Gavia niger*) and Western Grebe (*Aechmophorus occidentalis*); and (4) gulls: Glaucous-winged Gull (*Larus glaucescens*), Bonaparte's Gull (*Chroicocephalus philadelphia*), California Gull (*L. californicus*), and Mew Gull (*Larus canus*) (Brooks 1922; Knight and others 1990; Buchanan and Watson 2010). Less well known are the indirect effects of the presence of eagles on their prey (Hipfner and others 2012).

Hundreds of thousands of waterbirds and thousands of eagles spend their non-breeding season in the Strait of Georgia, British Columbia (Butler and Campbell 1987; Baldwin and Lovvorn 1992; Lovvorn and Baldwin 1996; Eliott and others 2011). Eagle abundance is lowest in late summer when they depart to salmon spawning streams in Alaska and northern British Columbia, and highest during December to March when they return to hunt waterfowl

(Stinson and others 2001; Elliot and others 2011). Waterbird abundance is lowest in summer when many species depart for breeding grounds in western North America, and highest in early fall during migration. Waterbird abundance wanes slightly through winter, but remains high until spring when they migrate out of the region. An historical increase in the abundance of eagles in Puget Sound and the southern Strait of Georgia coincided with a decline of several waterbird species (Bower 2009; Elliot and others 2011; Anderson and others 2012).

Distributional and behavioral responses to predators may differ, depending on the degree of vulnerability of the prey. For example, diving birds, such as scoters and grebes, might be particularly vulnerable when they surface unaware of the proximity of eagles, unlike gulls and dabbling ducks that feed on the surface. The degree of vulnerability of each species should be reflected in its choice of where it resides and its behavior in the presence of eagles.

In this paper we examine temporal and spatial variation in distributions and behaviors of nonbreeding sea ducks, dabbling ducks, grebes, and gulls in relation to the Bald Eagle. We also discuss our findings in context of management issues regarding apparent declines and the importance of understanding indirect effects of predators on prey for wildlife monitoring.

Methods

Study Area

We studied waterbirds and eagles during their non-breeding season in Boundary Bay at the southeast end of the Strait of Georgia, British Columbia (49.0352° N, 122.9400° W), from September 2007 to February 2008. Boundary Bay is a shallow tidal bay approximately 12 km long in the Fraser River delta ecosystem of intertidal beaches, farmlands, and river estuary that supports large numbers of waterfowl, shorebirds, eagles, and seabirds (Butler and Campbell 1987).

Phenology of Bald Eagles and Their Prey

Data for phenologies and seasonal distributions of eagles and waterbirds in the Strait of Georgia, including Boundary Bay, were drawn from Bird Studies Canada, British Columbia Coastal Waterbird Survey database, 1999–2007 (http://www.birdscanada.org/ volunteer/ bccws). The protocol for this survey was a single monthly count within 2 h of the high tide made on 1 or 2 pre-selected days from September to April. Counts were made by birdwatchers who tallied or estimated all eagles and waterbirds along 177 1–2 km long polygons of beach on the Strait of Georgia (Fig. 1). Waterbirds and eagles were highly visible on the water and along the beaches. Waterbird and eagle density was calculated by dividing the number of individuals counted by polygon area. Areas of polygons were calculated using GIS. Indices of monthly regional density for Bald Eagles and each species of waterbirds were calculated by summing monthly densities for each polygon and averaging across all sites within the Strait.

To confirm that eagles depredated waterbirds in Boundary Bay, we examined prey remains at 4 channel markers used by eagles as hunting perches in Boundary Bay during our transect surveys. In August 2007, we collected all bones and body parts from prey that had accumulated on a channel marker for later identification. Falcons (*Falco* spp.) also hunted ducks mostly in early fall when eagles were largely absent and switched to smaller prey in response to the kleptoparastic behavior of eagles (Dekker and others 2012). Although falcons were present in our study, we only saw eagles with large prey on the channel markers. The collected remains were frozen for later processing in the Department of Archaeology at Simon Fraser University (Table 1). Bones were picked clean, boiled in a mixture of 4 L of water and 250 mL of bleach for 20 min, and cleaned with brushes and tweezers. Each sterna was identified to species using various keys (Woolfenden 1961; Woolfle 1967; Gilbert and others 1981; Oates and others 2003). We also identified all freshly killed prey at the channel markers to coincide with our transects between September 2007 and February 2008.

Predation Danger Hypothesis

We hypothesized that waterbirds returning to the Strait of Georgia following nesting would distribute across suitable habitat in equilibrium to expected rewards. In fall, when large numbers of eagles had returned to the Strait of Georgia, we proposed that waterbirds would alter their distribution and behavior to manage the danger from eagles. We predicted that diving birds and

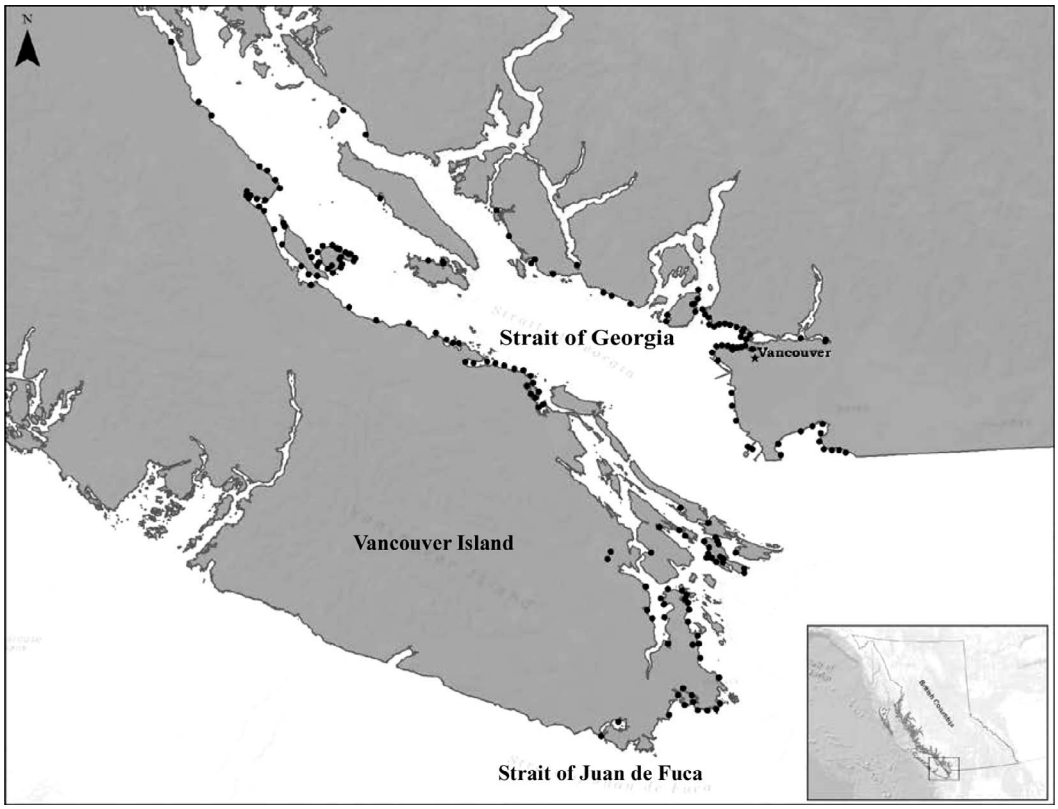

FIGURE 1. Locations of British Columbia Coastal Waterbird Survey stations in the Strait of Georgia, British Columbia.

gulls would move away from the shore where eagles congregated and dabbling ducks would form into larger flocks and heighten their vigilance.

We censused all waterbirds from a boat driven along 3 transects to explore whether waterbirds altered their distribution in the presence of eagles in Boundary Bay between September 2007 and February 2008. The 3 transects (nearshore, midshore, and offshore), ran for 6 km approximately parallel to the shoreline and about 6 km long. Each transect was visited every 2 wk near the high tide. Many eagles perched in trees along the shore of Boundary Bay, a few perched on channel markers midshore in the bay, and none were seen offshore beyond the markers. We selected 3 distances to align with the presence of eagles. The nearshore transect was approximately 2.3 km from shore and within the intertidal portion of Boundary Bay used by scores of eagles. The midshore route was at approximately 7.3 km from shore and near channel markers used by a few eagles. The offshore route was about 11 km from shore where we saw no eagles. Two observers counted all eagles and waterbirds within 100 m of either side of a 6-m-long skiff traveling at approximately 10 km/h. Birds were identified to species, when possible, or to 1 of 3 classes: (1) scoters (Surf Scoter, White-winged Scoter, and Black Scoter); (2) dabblers (American Wigeon, Mallard, Northern Pintail, and Green-winged Teal), and (3) gulls (Glaucous-winged Gull, Bonaparte's Gull, California Gull, and Mew Gull).

To assess the behavioral response of waterbirds to eagles, we conducted bi-weekly observations of nearshore waterbirds to the presence of eagles at 2 sites in Boundary Bay where eagles and flocks of waterbirds were numerous. Between September 2007 and March 2008, an observer estimated the number of birds in each single-species flock, and the distance (to the

TABLE 1. Number and percent of each bird species found in Bald Eagle prey remains collected from a channel marker in Boundary Bay, British Columbia, August 2007.

Species	Number	Percent
Surf Scoter (*Melanitta perspicillata*)	18	24.7
Long-tailed Duck (*Clangula hyemalis*)	14	19.2
White-winged Scoter (*Melanitta fusca*)	13	17.8
Greater Scaup (*Aythya marila*)	13	17.8
Black Scoter (*Melanitta nigra*)	8	10.1
Lesser Scaup (*Aythya affinis*)	2	2.7
Hooded Merganser (*Lophodytes cucullatus*)	2	2.7
Bufflehead (*Bucephala albeola*)	1	1.4
Harlequin Duck (*Histrionicus histrionicus*)	1	1.4
Mallard (*Anas platyrhynchos*)	1	1.4
Total	73	100.0

nearest 100 m) between the edge of the flock and the nearest eagle and the shore. Birds in flocks of approximately <500 birds were counted individually, and larger flocks were estimated by summing the number of multiples of an estimated 100 individuals. To quantify vigilance behavior, we scanned flocks to record the number of individuals that were feeding (not vigilant) and the number of birds that were vigilant with heads up so they presumably could see approaching danger. The procedure was repeated every 5 min until 10–20 samples were taken, and then the entire procedure was repeated with a new flock. If the flock flushed, we recorded the total flight distance from the location at flushing to when the flock resettled.

Statistical Analyses

As the transect survey data were zero-heavy and not normally distributed, non-parametric tests were applied to the transect dataset. Kruskal-Wallis tests were used to examine seasonal patterns of waterbird abundance at each of the 3 transect distances. Tests were run for each group examining relationships between the total number of birds found on each transect in each month and the transect distance from shore to determine whether spatial distributions

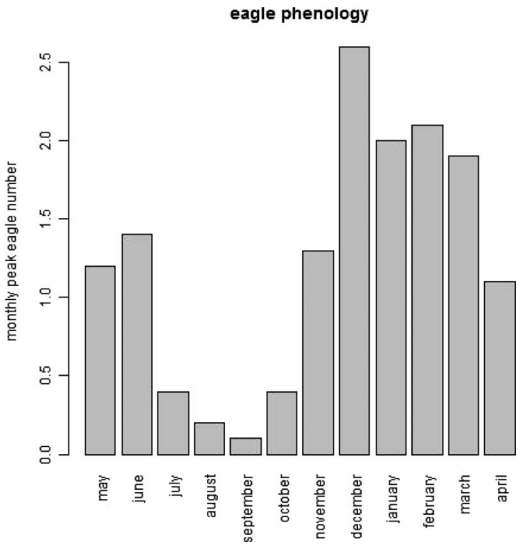

FIGURE 2. Monthly average density of Bald Eagles on 177 1-km-long stretches of beach from the British Columbia Coastal Waterbird Survey, 1999–2007.

shifted with time. Wilcoxon Signed Rank tests were used to test for differences in the total numbers of birds among transect distance categories for each species.

General linear models (GLM) were used to examine relationships between eagle proximity and behavioral responses of the 3 groups of waterbirds (scoters, dabblers, and gulls) at Boundary Bay. Three models were run for each waterbird group examining the relationship between the distance to the nearest eagle and: (1) proportion of the flock being vigilant; (2) flight distance; and (3) flock size. Date was included as a covariate to control for potential seasonal effects on behavior. Statistical analyses were performed using program R (R Development Core Team 2010).

Results

Regional and Seasonal Distribution

Eagles were least numerous in September and most numerous in December (Fig. 2). Eagles remained abundant from January to March, after which their numbers declined between April and June before plummeting through the summer. Eagle densities in the Strait of Georgia, which includes Boundary Bay, increased 3-fold from October to November (0.4 to 1.3 eagles/km^2), and nearly 6-fold by December (2.6

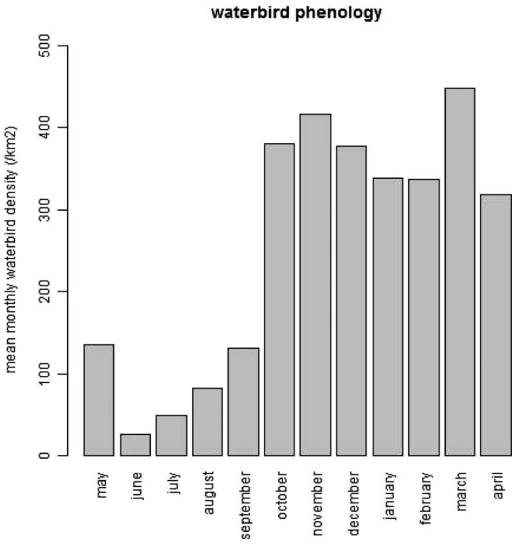

FIGURE 3. Monthly average density of waterbirds on 177 1-km-long stretches of beach from the British Columbia Coastal Waterbird Survey, 1999–2007.

eagles/km^2), after which density dropped (Fig. 2). The greatest number of waterbirds occurred in November, a month before peak abundance of eagles (Fig. 3). Overall, average density of waterbirds increased from September to November (130.8 to 415.2 birds/km^2) and slowly declined through February (Fig. 3). A 2nd peak occurred in March followed by a decline to a seasonal low in June.

Local Response of Prey to Eagle Presence

Eagles perched on channel markers where they ate freshly killed waterfowl in Boundary Bay. Although some of the eagle prey was likely scavenged, we frequently saw eagles launch attacks on live birds resting on the water and beaches. These attacks often resulted in pursuits that elicited other eagles to join the hunt. More than half the waterfowl remains identified on eagle feeding posts on channel markers in Boundary Bay belonged to scoters, and about a fifth each were from scaup and Long-tailed Ducks. The remaining proportion was from Hooded Merganser, Bufflehead, Harlequin Duck, and Mallard (Table 1). On other channel markers within 1 km of shore where eagles were often flushed, hung remains of Mallard, Glaucous-winged Gull, Surf Scoter, Red-throated Loon, Green-winged Teal, and American Wigeon. We found no remains from Western Grebes although we have seen eagles hunting them in the delta, and grebes are known to be eagle prey (Brooks 1922; Knight and others 1990).

All species of waterbirds used inshore waters of Boundary Bay in late summer and early autumn. Western Grebes were seen in inshore waters in early September and quickly moved offshore through September (Fig. 4). The distribution of grebes through this period were significantly different (Kruskal-Wallis, $\chi^2 = 12.1$, $P < 0.01$). Flocks of 400 or more were present in offshore waters through the winter, although few grebes were seen on the transects after early December.

Large numbers of scoters used inshore waters in early September and mostly midshore regions from October to February (Fig. 5). The distributions between the 3 transcects through this period were significantly different (Kruskal-Wallis, $\chi^2 = 13.6$, $P < 0.01$). The number of scoters on transects fell when eagles reached peak numbers in December and remained low through the winter (Fig. 2, Fig. 5). Scoters were by far the most numerous species found in prey remains on the channel markers (Table 1).

Dabbling ducks settled in inshore areas in late summer and fall and remained there through the winter. The dabbling ducks (mostly American Wigeon along with Mallard, Northern Pintail, and Green-winged Teal) clearly avoided midshore and offshore areas (Fig. 6; Kruskal-Wallis, $\chi^2 = 20.4$, $P < 0.01$). Thousands more dabbling ducks were present along the shore and off our transect. Gull observations were confounded by the presence of crab-fishing vessels in the midshore region in autumn, which possibly explains why abundance did not differ between transects across the winter (Kruskal-Wallis, $\chi^2 = 3.7$, $P = 0.16$).

Dabblers spent proportionally more time being vigilant as winter progressed (Table 2) after controlling for distance to eagles. This was not the case for gulls. Flight distances of dabblers and scoters, but not gulls, increased with proximity to eagles. Dabblers, scoters, and gulls did not alter the proportion of the flock that was feeding with distance to eagles. Dabbler flock size was not related to number of eagles present (GLM, $F = 0.5$, $P = 0.48$), but there was a date effect where flock sizes declined with study date (GLM, $F = 6.8$, $P = 0.01$).

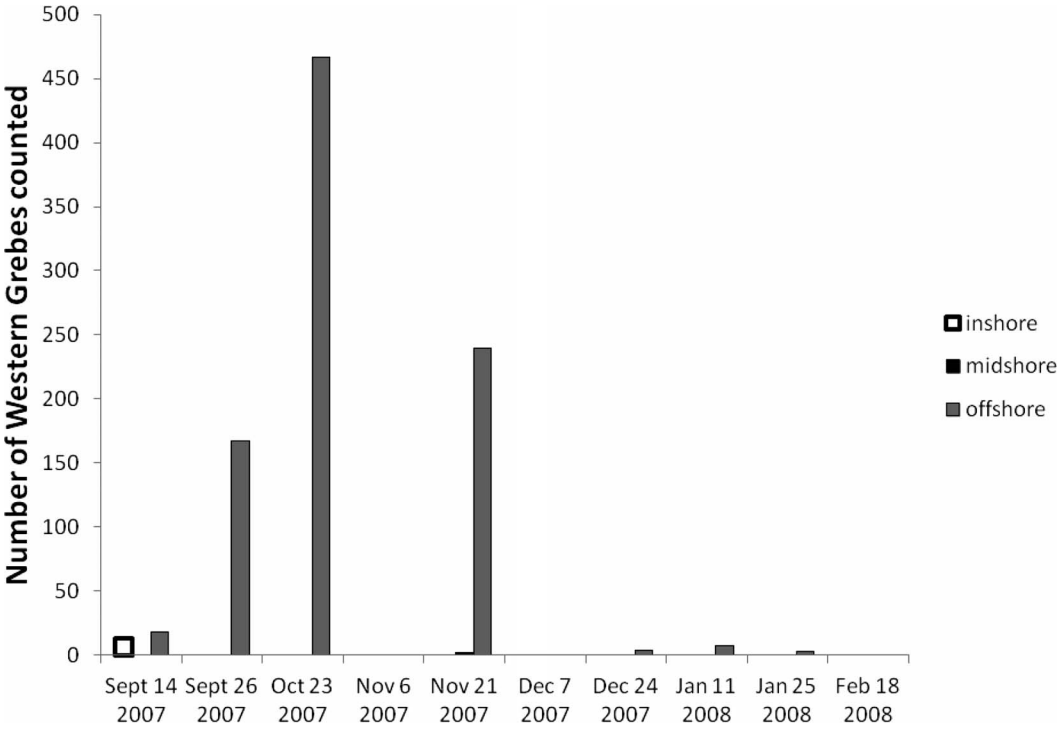

FIGURE 4. Number of Western Grebes counted on marine transect surveys at 3 distances from the shoreline of Boundary Bay, British Columbia, and Washington State, between September 2007 and February 2008.

Discussion

There is a growing body of evidence across many taxa that prey redistribute themselves spatially and temporally in response to changes in predator density (Holomuzki 1986; Ripple and Beschta 2004). We believe the seasonally-changing spatial and behavioral responses of waterbirds to changes in perceived danger are the same underlying processes seen in the variety of taxa cited above.

We present evidence that waterbirds altered their distribution and assert that the change in behavior was in response to eagles. The spatial and behavioral response of waterbirds occurred concurrently with the return of eagles in the fall. Our results join numerous studies indicating that prey species alter their behavior and use of habitats in response to the presence of predators (Kotler and others 1991, 1993; Mao and others 2005; Sansom and others 2009). Diving birds moved away from shore, and dabbling ducks and gulls formed large flocks where large numbers of eagles concentrated. Dabbling ducks became more vigilant through the winter, and when an eagle approached, diving ducks flew farther than dabbling ducks or gulls. Flock sizes increased with distance from eagles for dabblers and scoters (Table 2) suggesting they were avoiding the eagles.

Waterbirds likely gather in large numbers where prey are numerous and adjust where and how they forage in response to inherent danger of the site. We showed that the regional abundance of waterbirds peaked about a month in advance of the arrival of large numbers of eagles and declined as eagle numbers continued to increase. Waterbird and eagle numbers slowly declined through the winter. These changes in seasonal abundance might reflect migration and local movements of waterbirds searching for food that are subsequently followed by eagles. However, the danger from eagles might play a role in the number of waterbirds that forage on beaches. We propose that the beaches can support a large number of waterbirds in early autumn when relatively free from eagles and therefore safe, but diminishing food supplies and increasing danger from eagles later in

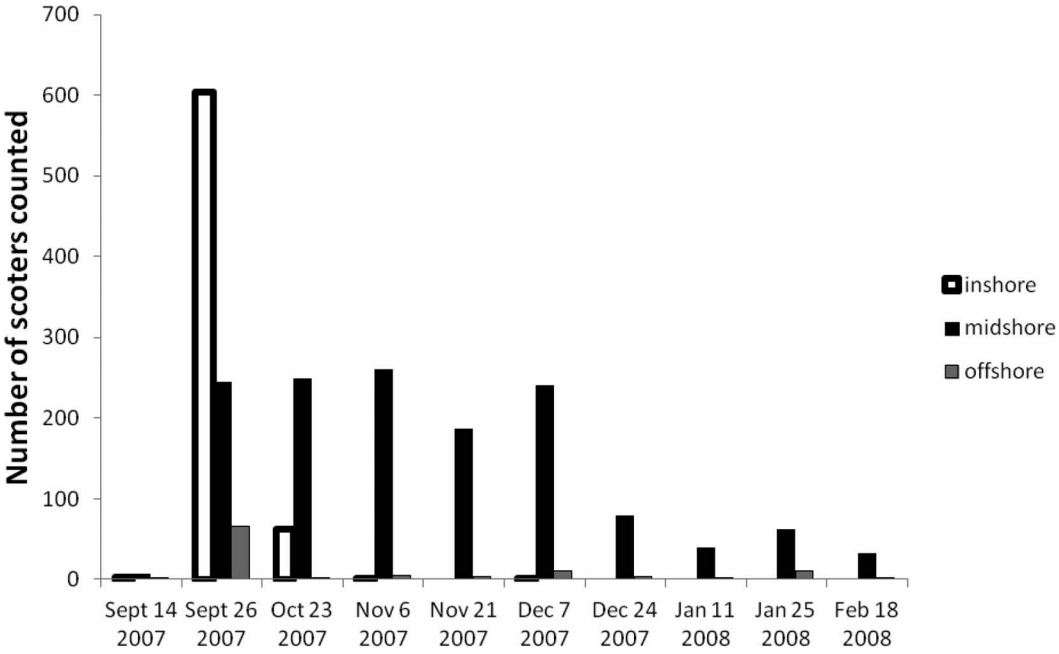

FIGURE 5. Number of scoters counted on marine transect surveys at 3 distances from the shoreline of Boundary Bay, British Columbia, and Washington State, between September 2007 and February 2008.

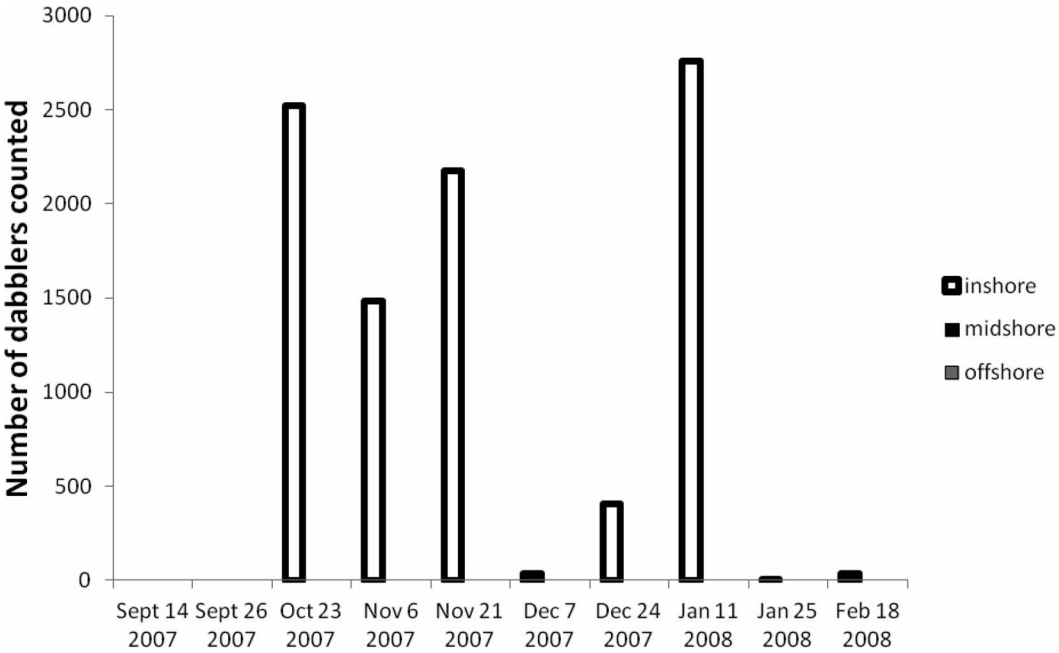

FIGURE 6. Number of dabblers counted on marine transect surveys at 3 distances from the shoreline of Boundary Bay, British Columbia, and Washington State, between September 2007 and February 2008.

TABLE 2. Results of the general linear model of seasonal behavioral responses of dabblers, scoters, and gulls to the presence of eagles. Significance values are in parentheses; level of significance is $P \leq 0.05$.

	Dabblers $n = 34$	Scoters $n = 20$	Gulls $n = 18$
Vigilance	$F_{(1,31)}$: 3.8 (0.06)	$F_{(1,17)}$: 0.4 (0.6)	$F_{(1,15)}$: 1.9 (0.2)
Flock size	$F_{(1,31)}$: 48.9 (<0.001)	$F_{(1,17)}$: 5.3 (0.03)	$F_{(1,15)}$: 2.2 (0.2)
Flight distance	$F_{(1,31)}$: 28.1 (<0.001)	$F_{(1,17)}$: 9.2 (<0.01)	$F_{(1,15)}$: 3.3 (0.09)
Date	$F_{(1,31)}$: 4.1 (0.05)	$F_{(1,17)}$: 2.9 (0.11)	$F_{(1,15)}$: 1.2 (0.3)

autumn requires some birds to depart until by mid-winter, the number of waterbirds and eagles stabilize when neither prey nor predator can improve its lot by relocating. We showed that large numbers of waterbirds were present in the Strait of Georgia in fall and we presented several examples of how waterbirds altered their distribution and behavior when eagles became more numerous. Diving ducks moved offshore as eagles became more numerous and dabblers, while remaining close to shore throughout winter, decreased the proportion of flock members that were feeding as the winter progressed. Ducks fled greater distances when flushed near eagles and formed larger flocks away from eagles than near them.

Scoters feed in shallow waters during the day and are hunted by eagles (Lewis and others 2008; Anderson and others 2012). Scoters spend 20% of their time foraging underwater and are probably most vulnerable to eagle predation when they surface, so their progressive avoidance of inshore areas was likely a response to danger from eagles. The majority of prey remains were of scoters on channel markers in midshore waters supporting the hypothesis that they are more vulnerable to predation by eagles. The ability of gulls to quickly respond to an approaching eagle possibly made them less sensitive to eagles, although eagles are known to kill them (Buchanan and Watson 2010).

The Western Grebe is a particularly interesting example of a species response to danger from eagles for the very reason that we did not detect any prey remains or see eagles eating grebes during our study. Clowater (1998) dismisses predation by eagles as a factor for nocturnal foraging by Western Grebes because few grebes were killed, but this is exactly what is expected if nocturnal foraging minimizes the risk of predation. Western Grebes do fall victim to eagles in the region (Knight and others 1990) and therefore should respond to the danger from eagles.

Western Grebes prey on schooling fish at night and rest offshore during the day (Clowater 1998). Offshore waters afford them safety where they can make long escape dives away from the danger of eagles. The grebes seen in the inshore waters in late summer in our study were diving during the day, presumably to forage on small fish. Western Grebes also used inshore waters in other parts of the Fraser River delta during August (R. Swanston, pers. comm.). Diving in shallow water during the day would be a dangerous proposition for Western Grebes in winter when eagles were abundant, but not so in late summer when eagles were largely absent from the coast. Fishing at night and resting far offshore during the day would reduce the threat from eagles and possibly explained why grebes were not among the list of eagle prey items. In contrast, scoters fed in flocks during the day by making shallow dives in search of benthic shellfish. Nocturnal foraging was very uncommon and most scoters spent the night in flocks away from shore (Lewis and others 2005).

An alternative hypothesis is that the redistribution of waterbirds was a response to shifting distributions of prey. Western Grebes forage at night and might rest close to their prey during the day. Moreover, most scoters are daytime foragers and they might remain near to their benthic prey (Lewis and others 2005). We acknowledge that food is an important factor in the distribution of birds, but posit that without considering danger, food alone would likely be only a partial explanation for the distribution of waterbirds.

Reasons for numerical declines on surveys of waterbirds in Puget Sound between 1966 and 2007 are not entirely clear (Anderson and others 2009). Our results suggest that redistribution in response to the presence of eagles is a plausible

factor to consider for some species. Many species identified by Anderson and others (2009) to have declined in Puget Sound were diving birds. Incidentally, Bower (2009) showed that Bald Eagles increased 187% over the same time period. Our study suggests that diving birds are particularly sensitive to eagle predation. An understanding of the interplay between predator and prey in distributions and behavior is an important tool for wildlife managers.

Acknowledgments

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Literature Cited

Anderson EM, Bower JL, Nyeswander DR, Evenson JR, Lovvorn JR. 2009. Changes in avifaunal abundance in a heavily used wintering and migration site in Puget Sound, Washington, during 1966–2007. Marine Ornithology 37:19–27.

Anderson EM, Esler D, Boyd WS, Evenson JR, Nyeswander DR, Ward DH, Dickson RD, Uher-Koch BC, Van Stratt CS, Hupp JW. 2012. Predation rate, timing, and predator composition or scoters (*Melanitta* spp.) in marine habitats. Canadian Journal of Zoology 90:42–50.

Baldwin JR, Lovvorn JR. 1992. Populations, diet, food availability and food requirements of dabbling ducks in Boundary Bay. In: Butler RW, editor. Abundance, distribution and conservation of birds in the vicinity of Boundary Bay, British Columbia. Technical Report Series No. 155. Delta, BC: Canadian Wildlife Service. p 42–69.

Bower JL. 2009. Changes in marine bird abundance the Salish Sea: 1975 to 2007. Marine Ornithology 37:9–17.

Brooks AC. 1922. Notes on the abundance and habits of the Bald Eagle in British Columbia. The Auk 39:556–559.

Brown JS. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. Evolutionary Ecology Research 1:49–71.

Brown JS, Kotler BP. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

Buchanan JB, Watson JW. 2010. Group hunting by immature Bald Eagles directed at gulls. Northwestern Naturalist 91:222–225.

Buehler DA. 2000. Bald Eagle (*Haliaetus leucocephalus*). In: Poole A, editor. The birds of North America. Ithaca, NY: Cornell Lab of Ornithology. No. 506.

Butler RW, Campbell RW. 1987. The birds of the Fraser River delta: Populations, ecology and international significance. Occasional Paper No. 65. Ottawa, ON: Canadian Wildlife Service.

Butler RW, Ydenberg RC, Lank DB. 2003. Wader migration on the changing predator landscape. Wader Study Group Bulletin 100:130–133.

Clowater JS. 1998. Distribution and foraging behaviour of wintering Western Grebes [thesis]. Burnaby, BC: Simon Fraser University. 76 p.

Creswell W. 1994. Age-dependant choice of Redshank (*Tringa totanus*) feeding location: Profitability or risk? Journal of Animal Ecology 63:589–600.

Creswell W. 2008. Non-lethal effects of predation in birds. Ibis 150:3–17.

Dekker D, Out M, Tabak M, Ydenberg RC. 2012. The effect of kleptoparasitic Bald Eagles and Gyrfalcons on the kill rate of Peregrine Falcons hunting Dunlins wintering in British Columbia. Condor 114:290–294.

Elliott KM, Elliott JE, Wilson LK, Jones I, Stenerson K. 2011. Density-dependence in the survival and reproduction of Bald Eagles: Linkages to Chum Salmon. Journal of Wildlife Management 75:1688–1699.

Gilbert BM, Martin LD, Savage HG. 1981. Avian osteology. Springfield, MO: Missouri Archaeological Society. 252 p.

Hipfner JM, Blight LK, Lowe RW, Wilhelm SI, Robertson GJ, Barrett RT, Anker-Nilssen T, Good TP. 2012. Unintended consequences: How the recovery of sea eagle *Haliaeetus* spp. populations in the Northern Hemisphere is affecting seabirds. Marine Ornithology 40:39–52.

Holomuzki JR. 1986. Predator avoidance and diel patterns of microhabitat use by larval Tiger Salamanders. Ecology 67:737–748.

Knight RL, Randolph PJ, Allen GT, Young LS, Wigen RT. 1990. Diets of nesting Bald Eagles, *Haliaeetus leucocephalus*, in western Washington. Canadian Field-Naturalist 104:545–551.

Kotler BP, Brown JS, Hasson O. 1991. Factors affecting Gerbil foraging behavior and rates of owl predation. Ecology 72:2249–2260.

Kotler BP, Brown JS, Mitchell WA. 1993. Environmental factors affecting patch use in two species of gerbilline rodents. Journal of Mammalogy 74:614–620.

Lank DB, Butler RW, Ireland J, Ydenberg RC. 2003. Effects of predation danger on migratory strategies of sandpipers. Oikos 103:303–319.

Lewis TL, Esler D, Boyd WS, Zydelis R. 2005. Nocturnal foraging behavior of wintering Surf Scoters and White-winged Scoters. Condor 107:637–647.

Lewis TL, Esler D, Boyd WS. 2008. Foraging behavior of Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*M. fusca*) in relation to clam density: Inferring food availability and habitat quality. The Auk 125:149–157.

Lovvorn JR, Baldwin JR. 1996. Intertidal and farmland habitats of ducks in the Puget Sound Region: A landscape perspective. Biological Conservation 77:97–114.

Mao JS, Boyce MS, Smith DW, Singer FJ, Vales DJ, Vore JM, Merrill EH. 2005. Habitat selection by Elk before and after Wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management 69:1691–1707.

Oates DW, Boyd ED, Ramaekers JS. 2003. Identification of waterfowl breastbones and avian osteology (sterna) of North American Anseriformes. Special Publication No. 10. Martinsville, VA: Virginia Museum of Natural History. 51 p.

Pomeroy AC, Seaman DAA, Butler RW, Elner RW, Williams TD, Ydenberg RC. 2008. Feeding-danger trade-offs underlie stopover site selection. Avian Conservation and Ecology 3:7.

R Development Core Team. 2010. R: A language and environment for statistical computing, v. 2.14.3. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org. Accessed 5 September 2010.

Ripple WJ, Beschta RL. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? BioScience 54:755–766.

Sansom A, Lind J, Creswell W. 2009. Individual behavior and survival: The roles of predator avoidance, foraging success and vigilance. Behavioral Ecology 20:1168–1174.

Stinson DW, Watson JW, McAllister KR. 2001. Washington State status report for the Bald Eagle. Olympia, WA: Washington Department of Fish and Wildlife. 102 p.

Watson JW, Garrett MG, Anthony RG. 1991. Foraging ecology of Bald Eagles in the Columbia River estuary. Journal of Wildlife Management 55:492–499.

Wirsing AJ, Heithaus MR, Frid A, Dill LM. 2008. Seascapes of fear: Evaluating sublethal predator effects experienced and generated by marine mammals. Marine Mammal Science 24:1–15.

Woolfle E. 1967. Vergleichend morphologische untersuchungen an einzelknochen des postcranialen skelettes in mitteleuropa vorkommender enten, halbganse und sager. Munchen: Institut fur Palaoanatomie, Domestikationsforschung und Geschichte der Tiermedizin der Universitat Munchen, Germany.

Woolfenden GE. 1961. Postcranial osteology of the waterfowl. Bulletin of the Florida State Museum 6:1–130.

Ydenberg RC, Butler RW, Lank DB, Guglielmo CG, Lemon M, Wolf N. 2002. Tradeoffs, condition dependence, and stopover site selection by migrating sandpipers. Journal of Avian Biology 33:47–55.

Ydenberg RC, Dekker D, Kaiser G, Sheperd PCF, Ogden LE, Rickards K, Lank DB. 2010. Winter body mass and over-ocean flocking as components of danger management by Pacific Dunlins. BioMed Central Ecology 10:1. doi: 10.1186/1472-6785-10-1.

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