

UNINTENDED CONSEQUENCES: HOW THE RECOVERY OF SEA EAGLE *HALIAEETUS* SPP. POPULATIONS IN THE NORTHERN HEMISPHERE IS AFFECTING SEABIRDS

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SUMMARY

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The recovery of sea eagle *Haliaeetus* spp. populations in the temperate northern hemisphere in the closing decades of the 20th century is one of the great conservation success stories of recent times, but the re-establishment of these apex predators in marine systems has had consequences for seabirds. Sea eagles affect seabirds both directly (by taking adults and offspring and by inducing potentially costly behaviors to minimize danger) and indirectly (by facilitating the nest predators of seabirds, mainly gulls and corvids). Repeated disturbance by hunting eagles has caused seabirds to abandon colonies and subcolonies in the tens to hundreds of thousands of pairs. In recent years, sea eagles have been widely implicated in local declines of surface-nesting seabirds in the northeast Pacific Ocean, the northwest Atlantic Ocean and northern Europe. The extent to which recent events simply reflect a return to a more “natural” ecological baseline as sea eagle populations recover from decades of persecution and chemical pollutants is discussed. We argue that there is need for a research effort to investigate the conservation implications of increasing sea eagles in the context of multiple threats to seabird populations.

Key words: direct and indirect effects, facilitation, *Haliaeetus*, predation, seabirds, top-down control

INTRODUCTION

Adult seabirds experience predation by many species. At sea, they are taken by predatory fish such as white sharks *Carcharodon carcharias* (Johnson *et al.* 2006), and by marine mammals including killer whales *Orca orcinus* (Dahleim & White 2010), true seals (Penny & Lowry 1967, Copley & Bell 1998), fur-seals and sea-lions (McHugh 1952, Long & Gilbert 1997, David *et al.* 2003, Lalas *et al.* 2007, Charbonnier *et al.* 2010), walrus *Odobenus rosmarus* (Mallory *et al.* 2004), and sea otters *Enhydra lutris* (Riedman & Estes 1988). On land, they are taken by native and non-native mammals including rodents (Sealy 1982, Blight *et al.* 2000, Angel *et al.* 2009) and carnivores ranging in size from short-tailed weasels *Mustela erminea* (Cairns 1985) to polar bears *Ursus maritimus* (Donaldson *et al.* 1995). In addition, many are taken on land by avian predators, including Giant Petrels *Macronectes* spp. (Emslie *et al.* 1995), hawks (Lewis 2003), falcons (Beebe 1960, Booms & Fuller 2003), eagles (Zaun 2009), owls (Morse 1971, Hayward *et al.* 1993, Velarde *et al.* 2007), rails (Brothers 1984), gulls (Spear 1993), skuas *Stercorarius* spp. (Müller-Schwarze &

Müller-Schwarze 1973), sheathbills *Chionis* spp. (Jouventin *et al.* 1996), and passerines (Verbeek 1982, Ryan & Moloney 1991, Gaston & Elliot 1996).

Despite the taxonomic and ecological breadth of their predators, the vast majority of the research on the demography and life-history evolution of seabirds has focused on bottom-up rather than top-down causes. This research effort has been successful in outlining mechanisms that link environmental, behavioral, physiological and demographic parameters to seabird population trends (Ashmole 1971, Aebischer *et al.* 1990, Kitaysky *et al.* 2007). By comparison, our understanding of the role of top-down control of seabird demography is limited, except for the effects of predators introduced to islands (Jones *et al.* 2008).

Native predators can strongly influence seabird population processes, at least under some circumstances (Murray *et al.* 1983, Gilchrist 1998, David *et al.* 2003, Ainley *et al.* 2005, Peery *et al.* 2007, Votier *et al.* 2008), and seabirds have evolved a variety of behavioral strategies to evade their predators. These strategies include using

subterranean burrows as nest sites and visiting the nest site under cover of darkness (Lack 1968, McNeil *et al.* 1993). In considering the effects of predators on prey populations generally, lethal (consumptive) rather than non-lethal (non-consumptive) effects have been the primary focus, at least until recently (Cresswell 2008, Peckarsky *et al.* 2008, Hammerschlag & Trussell 2011). Consequently, our understanding of the non-lethal effects of predators on seabirds is inadequate, although there are a few notable exceptions (e.g. Finney *et al.* 2003, Heithaus 2005, Ainley & Ballard 2012).

Following a long period during which populations were depressed by human persecution and latterly by pesticide poisoning, sea eagles *Haliaeetus* spp. in the temperate northern hemisphere have recovered strongly (Elliott & Harris 2002, Watts *et al.* 2007, Krüger *et al.* 2010, Elliot *et al.* 2011, Anderson *et al.* 2012), with substantial consequences for prey populations (e.g. Vennesland & Butler 2004), including seabirds (Parrish *et al.* 2001). Here, we review the variety of mechanisms by which sea eagles can affect seabird populations, including both direct and indirect effects, and discuss why it is important for wildlife managers and scientists to recognize and understand these effects.

SEA EAGLE POPULATION TRENDS

Populations of Bald Eagles *H. leucocephalus* in North America and White-tailed Eagles *H. albicilla* in northern Europe declined precipitously through the first half of the 20th century, as a result of direct persecution (e.g. bounty hunters in Alaska killed 128 000 Bald Eagles between 1917 and 1952; Zweifelhofer 2007), loss of habitat to agriculture (Willgohe 1961), and the effects of chemical pollutants, especially DDT and PCBs, on their reproduction (Wiemayer *et al.* 1993; Elliott & Harris 2002, Helander *et al.* 2008). The United States Fish and Wildlife Service listed the Bald Eagle as federally endangered in 1967 under the *Endangered Species Protection Act* of 1966, and later under the *Endangered Species Act* of 1973 (Watts *et al.* 2007). In Europe, the legal protection of White-tailed Eagles was a protracted affair initiated by Iceland in 1913 and finalized by Greece in 1973 (Love 1983). In what was probably the last safe stronghold in western Europe, Norway, they were protected beginning in 1968. Protection from direct persecution was granted by the 1950s (Zweifelhofer 2007), while the use of DDT was banned in the 1970s (Watts *et al.* 2007, Hailer *et al.* 2006).

Formal protection proved to be effective for the conservation of these apex predators. On Kodiak Island, Alaska, the number of active Bald Eagle eyries increased by a factor of 3.4 between 1963 and 2002 (Zweifelhofer 2007), while the number of adult eagles increased by a factor of 1.9 between 1967 and 1997 in southeast Alaska (Jacobson & Hodges 1999). In British Columbia, numbers of eagles on the Gulf Islands more than doubled between the early 1970s and late 1980s (Vermeer *et al.* 1989), while numbers in southern coastal areas of the mainland increased threefold between the late 1980s and early 2000s (Elliott *et al.* 2012). In western Washington State, United States, there was a 10% per annum rate of increase in Bald Eagle numbers, and very steep increases in the rates of nest occupancy and productivity between 1980 and 1998 (Watson *et al.* 2002), while counts of wintering eagles increased by a factor of 2.8 in the ~25 year period between 1978–1980 and 2003–2006 in Puget Sound (Bower 2009) and increased unevenly but strongly between 1973 and 1999 along the Skagit River (Dunwiddie & Kuntz 2001). The number of eagle eyries within a

25 km radius of the seabird colony at Tatoosh Island, on the outer Washington coast, increased from six to 27 between 1975 and 1999 (Parrish *et al.* 2001). In Oregon, Bald Eagle numbers increased from a near-historic low of 65 breeding pairs in 1978 to 496 pairs in 2007 (Isaacs & Anthony 2011); in coastal regions of Oregon, the number of breeding pairs increased from 15 to 100 during this period. Results from Breeding Bird Surveys and Christmas Bird Counts confirm these increasing trends (Environment Canada 2010, National Audubon Society 2010, Sauer *et al.* 2011; see Fig. 1 in Anderson *et al.* 2012).

Bald Eagles on the Atlantic coast of North America showed a similar pattern of recovery. In Chesapeake Bay, which supports a resident breeding group and is a site of convergence of post-breeding and subadult eagles from breeding aggregations in the southeastern and northeastern United States, numbers grew from 60 pairs in the early 1970s to 646 pairs in 2001, and reproductive rates returned to values recorded before the DDT era (Watts *et al.* 2007).

The rate of increase of Bald Eagles across much of the Pacific Northwest leveled off in the late 1990s, and the number of Bald Eagles has remained more or less stable since then (e.g. Crewe *et al.* 2011). However, Bald Eagle numbers in Oregon continue to grow, and Isaacs & Anthony (2011) estimate that the statewide population could increase two- or three-fold from the 496 pairs recorded in 2007 before carrying capacity is reached. Elliott *et al.* (2012) suggested that populations in western North America may now be approaching or at carrying capacity, limited by the overwinter survival of adult birds. Bald Eagle populations on the Atlantic coast of North America are also thought to be approaching carrying capacity (Watts *et al.* 2007).

The pattern of recovery of White-tailed Eagles across northern Europe was similar to that of Bald Eagles in North America. Norway remained the stronghold for White-tailed Eagles through the first half of the 20th century because the food supply was less contaminated there than in other parts of Europe (Helander *et al.* 1982). Yet, by the late 1950s, the eagles had been extirpated from former breeding sites along the coast from the Swedish border to Hordaland in western Norway, and by the late 1960s only 700–800 pairs remained (Folkestad 2003). This represented about 70% of the total population of central and northern Europe (Hailer *et al.* 2006). Mainly as a result of improved reproductive success (Helander *et al.* 2008), the number of eagles in Norway has since increased to ~3500 pairs, or up to one pair per 12–14 km of coastline (Folkestad 2003, www.birdlife.no). Currently, Norway supports ~50% of the White-tailed Eagles that reside in Europe, including northwestern Russia, and the species is thought to be at or approaching carrying capacity in Norway (Helander *et al.* 2003). Elsewhere in the Baltic Sea, White-tailed Eagle numbers increased from 40 to 250 pairs between 1974 and 2000 in southern and central Sweden, and from 10–15 to 116 pairs between 1965 and 2000 in Estonia (Helander *et al.* 2003).

Recolonizations and reintroductions into areas where White-tailed Eagles were extirpated have also been successful. Eagles naturally recolonized Schleswig-Holstein, in northern Germany, in 1947, and, from a single pair, numbers increased to nine pairs by the late 1950s, then remained stable until the 1980s. Mainly as a result of improved reproductive success, this group had grown to 57 territorial pairs by 2008, and emigrants recolonized Denmark in 1995 and the Netherlands in 2006 (Krüger *et al.* 2010). The reintroduction of White-tailed Eagle fledglings from Norway to western Scotland

in 1975–1985 and 1993–1998 created a breeding aggregation that increased by 9.7% per year between 1997 and 2007, to a total of 42 territorial pairs (Evans *et al.* 2009). All of these small groups are expected to continue to increase.

DIRECT AND INDIRECT EFFECTS OF SEA EAGLES ON SEABIRDS

There are three primary mechanisms by which sea eagles impact seabirds and seabird numbers. Two are direct effects, involving only eagles and a seabird species, with no intermediaries: (1) eagles reduce seabird numbers by killing adults, and/or reduce seabird breeding success by taking eggs and nestlings (Hayward *et al.* 1977, DeGange & Nelson 1982); and (2) eagles force individual seabirds to behave in a manner that reduces each seabird's risk of being killed, but such behavior imposes some cost, which may be subtle (Harfenist & Ydenberg 1995, Addison *et al.* 2007). The third is an indirect effect: (3) eagles reduce seabird productivity by forcing incubating and brooding birds to temporarily abandon their nest sites, facilitating the removal of seabird eggs and/or nestlings by other predators, usually gulls and/or corvids (Parrish *et al.* 1996, Galusha & Hayward 2002). Other activities of eagles that could affect seabirds, such as kleptoparasitism (Watson 2002) and interference competition (Ellis & Nelson 2010) are reported only very rarely and will not be considered here.

Direct effects: I. Predation on adults and offspring

Seabirds often figure prominently in sea eagle diets. These eagles take adults, juveniles, nestlings and even the eggs of seabirds (Thompson 1989, Utekhina *et al.* 2000, Barrett 2008, Hayward *et al.* 2010). They take adults on the surface of the ocean (Sherrod *et al.* 1976, Buchanan & Watson 2010), in the air (Sherrod *et al.* 1976, Vermeer *et al.* 1989) and on the ground—in the open (Hayward *et al.* 1977), under forest canopy (Kaiser 1989), and possibly from nesting burrows (DeGange & Nelson 1982). Eagles have been reported to group together to hunt seabirds (Sherrod *et al.* 1976, Buchanan & Watson 2010), and to kleptoparasitize other eagles (Campbell 1969, Hayward *et al.* 2010) and gulls, the latter more frequently in marine than freshwater habitats (Watson 2002). Both immature (or “subadult”) and adult eagles prey on seabirds, apparently with about equal success (Hayward *et al.* 2010). Bald Eagles (Todd *et al.* 1982, Knight *et al.* 1990, Stoeck 1990; but see Watson 2002) and Steller's Sea Eagles *H. pelagicus* (Utekhina *et al.* 2000) both tend to include more birds in their diets at coastal sites than at inland sites in the same region.

Sea eagles co-occur widely with colonial seabirds. Kaiser (1989) reported a statistically significant tendency for Bald Eagles to breed on islands that support seabird colonies in the Haida Gwaii archipelago, off the northern coast of British Columbia. Eagle eyries were present on 72% of 67 seabird colony islands (mean of 3.5 eyries per island), whereas only 18% of islands lacking a seabird colony had eagle eyries. Both breeding and nonbreeding eagles move daily into colonies of nocturnal seabirds in order to catch adults when they return to their nesting burrows at dusk (DeGange & Nelson 1982, Kaiser 1989) and into colonies of diurnal seabirds to take eggs, chicks and adults (Verbeek 1982, Vermeer & Devito 1989). In the Sea of Okhotsk, nonbreeding Steller's Sea Eagles fly to seabird colonies to hunt only until the sea ice clears and they are able to catch fish (Utekhina *et al.* 2000). Sea eagles take both seabirds and waterbirds in winter (Watson *et al.* 1992, Utekhina

2000). In the northeast Pacific, these prey become especially important to Bald Eagles late in the winter, after spawning runs of chum salmon *Oncorhynchus keta* are completed (Watson *et al.* 1991, Elliott *et al.* 2012).

Bald Eagle diets: western North America

Temporally and spatially comprehensive information on sea eagle diets is available only for Bald Eagles on the west coast of North America (Table 1). At least 39 seabird species have been reported as prey of Bald Eagles in western North America, including nine species of Procellariiformes, four Pelecaniformes, and 25 Charadriiformes (Table 1; see also Appendix 1, available on the Web site). All accounts in Table 1 are of seabirds taken dead or alive by Bald Eagles during the seabirds' breeding season, with the exception of southern hemisphere Procellariiformes, which are taken as migrants in the austral winter. Techniques used to derive the values in Table 1, especially studies based on remains of prey found in and around nests, tend to overestimate the contribution of birds and underestimate the contribution of fish (Mersmann *et al.* 1992), and they do not distinguish between scavenged and depredated items.

The proportion of Bald Eagle diets composed of seabirds, and the diversity of seabird prey species, is highest in the Aleutian Islands, Alaska (Table 1). There, the Northern Fulmar *Fulmarus glacialis* is the seabird most often included in eagle diets, whereas gulls *Larus* spp. and Common Murres *Uria aalge* become more important from the Gulf of Alaska south to California (where very few fulmars breed). Waterbirds such as loons, grebes and sea ducks are also taken (Knight *et al.* 1990), but while these species use marine habitats during their annual cycle they are not considered true seabirds.

Bald Eagle diets: eastern North America

In Newfoundland, Black-legged Kittiwakes *Rissa tridactyla*, Herring Gulls *L. argentatus* and Common Murres have been reported in Bald Eagle diets (Dominguez *et al.* 2003); in Nova Scotia and New Brunswick, Double-crested Cormorants *Phalacrocorax auritus*, Herring Gulls and Great Black-backed Gulls *L. marinus* have been reported (Cash *et al.* 1985, Stoeck 1990); and, in Maine, Great Cormorants *P. carbo*, Double-crested Cormorants, Ring-billed Gulls *L. delawarensis*, Herring Gulls, and Great Black-backed Gulls have been reported (Todd *et al.* 1982).

White-tailed Eagle diets

The diet of the White-tailed Eagle has not been as well studied. In Norway, remains found in and under eagle nests between 1956 and 1980 (Willgoos 1984) consisted of 2138 items, of which 56% were birds, 36% fish and 7% mammals. The bird remains included 355 Common Eiders *Somateria mollissima* (29%), 114 European Shags *P. aristotelis* (9%), 104 Common Murres (9%), 55 Atlantic Puffins *Fratercula arctica* (5%), 41 Black Guillemots *Cephus grylle* (3%), 38 Razorbills *Alca torda* or Common Murres (3%), and 30 Herring Gulls (2%). The bird component was probably overestimated, however (Mersmann *et al.* 1992). In Greenland, a study that used remote-controlled cameras positioned at six nests over four years (1976–1979) found seabirds in the diets of only the two White-tailed Eagle pairs that bred on large fjords; included among 137 items identified at these nests were 6 Black-legged

Kittiwakes (4%), 4 Glaucous Gulls *L. hyperboreus* (3%), 1 Black Guillemot (<1%), and 2 unidentified *Larus* gulls (1%). The camera study estimated that fish made up 87% of diet items at all six nests (Willie & Kampp 1983), much higher than the 34% estimated in a

previous study based on remains found at nests (Kampp & Willie 1979). Likewise, a video survey at two Norwegian nests over two years showed that fish up to 50 g in mass were the major prey (Staven 1994). Recently, White-tailed Eagles have been observed

TABLE 1

Seabirds as components of the diets of Bald Eagles in coastal regions of western North America (percentage of items identified)

State (US) or province (Canada)	Location(s)	Year(s)	Type(s) of assessment	% of items identified containing seabirds	Main seabird prey species (total number of species)	Reference
Alaska	Aleutian Is.	1936–37	Remains at nests and in pellets	>50%	Northern Fulmar (16)	Murie 1940
	Adak I. (Aleutians)	1993–94	Remains at nests	1–10%	Northern Fulmar (17)	Anthony <i>et al.</i> 1999
	Tanaga I. (Aleutians)	1993–94	Remains at nests	10–25%	Northern Fulmar (14)	Anthony <i>et al.</i> 1999
	Amchitka I. (Aleutians)	1993–94; 2000–02	Remains at nests	>50%	Glaucous-winged Gull, Northern Fulmar (14+)	Anthony <i>et al.</i> 1999; Anthony <i>et al.</i> 2008
	Amchitka I. (Aleutians)	1969–73	Remains at nests	25–50%	Northern Fulmar (15+)	Sherrod <i>et al.</i> 1975
	Kiska I. (Aleutians)	1993–94	Remains at nests	>50%	Northern Fulmar, Glaucous-winged Gull (14+)	Anthony <i>et al.</i> 1999
	Kodiak I.	1963, 1967, 1968	Remains at nests	25–50%	Glaucous-winged Gull (5)	Grubb & Hensel 1978
	Port Houghton	1971	Direct observation	<1%	Gull sp. (1+)	Ofelt 1975
British Columbia	Petrel I.	1977	Pellets at perches	>50%	Cassin's Auklet (6)	DeGange & Nelson 1982
	Barkley Sound	1988	Remains at nests	25–50%	Glaucous-winged Gull and cormorant sp. (2+)	Vermeer & Morgan 1989
	Crofton	1996	Direct observation	1–10%	Pigeon Guillemot (1)	Elliott <i>et al.</i> 2005
Washington	Gulf Is.	1988	Remains at nests	25–50%	Glaucous-winged Gull	Vermeer <i>et al.</i> 1989
	San Juan I.	1962–63	Direct observation and remains at nests	1–10%	Gull sp. and Common Murre (2)	Retfalvi 1970
	San Juan I.	1980–81	Remains at nests and perches	10–25%	Common Murre (9)	Knight <i>et al.</i> 1990
	Olympic Peninsula	1980–81	Remains at nests and perches	25–50%	Common Murre (10)	Knight <i>et al.</i> 1990
	Puget Sound	1980–81	Remains at nests and perches	10–25%	Common Murre (5)	Knight <i>et al.</i> 1990
	Puget Sound	1986–97	Remains at nest	10–25%	Gull sp. (4)	Watson 2002
Oregon	Protection I.	1996–02	Direct observation and remains at nest	>50%	Rhinoceros Auklet, Glaucous-winged Gull (5)	Hayward <i>et al.</i> 2010
	Columbia River Estuary	1984–86	Remains at nests	1–10%	Cormorant & gull spp. (3+)	Watson <i>et al.</i> 1991
California	Channel Is.	1991–98	Direct observation and remains at nests	1–10%	Western Gull (9)	Sharpe & Garcelon 1999
	Channel Is.	Pre-1950	Remains at historical nest	1–10%	Rhinoceros Auklet (25)	Erlandson <i>et al.</i> 2007

to prey on Northern Gannets *Morus bassanus*, Greylag Geese *Anser anser* (especially young and flightless, moulting adults) and Common Eiders in central and northern Norway (Barrett 2008, T. Anker-Nilssen pers. obs., A. Follestad pers. comm.).

Seabirds are important prey for White-tailed Eagles reintroduced into western Scotland as well (Watson *et al.* 1992). Of 854 items identified in pellets and remains at nests and roosts, 123 (14%) were seabirds: 45 Northern Fulmars (5%), 18 European Shags (2%), 1 Northern Gannet (<1%), 40 Common Gulls *L. canus* (5%), and 19 Common Murres (2%). Interestingly, eagle diets in winter and summer were quite similar.

Steller's Sea Eagle diets

Utekhina *et al.* (2000) quantified the diets of Steller's Sea Eagles on seabird colonies in the Sea of Okhotsk, based on remains found at nests and on direct observations. Seabirds formed the bulk of the diet (91% of 178 items) of adult and nestlings, with prey species including Pelagic Cormorants *P. pelagicus*, Black-legged Kittiwakes, Slaty-backed Gulls *L. schistasaugus*, Common and Thick-billed *U. lomvia* murres, Spectacled Guillemots *C. carbo*, Ancient Murrelets *Synthliboramphus antiquus*, Crested *Aethia cristatella* and Parakeet *A. psittacula* auklets, and Tufted *F. cirrhata* and Horned *F. corniculata* puffins. Anecdotal evidence suggested that the eagles preferred to feed on murres and kittiwakes over Slaty-backed Gulls.

Direct effects: II. Alteration of seabird behavior

The presence of sea eagles, or even the possibility that eagles *might* be present, can create the perception of danger for seabirds. The immediate behavioral responses of prey to real or perceived danger from predators can be either subtle or overt (Hammerschlag & Trussell 2011), and seabirds exhibit both types of responses. We first report on routine behaviors that breeding seabirds employ to reduce the day-to-day risk from sea eagles; we then consider evidence for broader effects of eagles on seabird behavior, especially their distributional patterns.

Time devoted to vigilance

The most obvious way in which prey respond to danger from predators is by becoming more vigilant. At Seabird Rocks, British Columbia, the number of Bald Eagles active on the Glaucous-winged Gull *L. glaucescens* colony reaches a peak when the gulls' eggs begin to hatch and developed embryos and nestlings become available as prey. White *et al.* (2006) showed that there was a 54% increase in the amount of time that gulls devoted to vigilance as the number of eagles increased, and gulls flushed from nests with increasing frequency, peaking at up to 6 times per hour. These behaviors left them less time to devote to other activities, such as foraging, and probably increased their energy expenditure.

Frequency and timing of colony visits

Many alcids, including both diurnal and nocturnal species, regularly engage in colony fly-by behavior, or "wheeling": individuals or small groups repeatedly approach the colony from the sea, but wheel away from the colony a number of times before eventually landing (Gaston & Jones 1998). The function of the behavior is not known. At Triangle Island, British Columbia, Addison *et al.* (2007) showed that

Tufted Puffins modified their fly-by behavior to minimize the risk posed by Bald Eagles. First, puffins synchronized their approaches towards the colony when eagles were present, and they synchronized their landings when eagles were absent. Second, puffins reduced their overall activity levels when eagles were present. And third, puffins switched to lower-risk activities, especially departing rather than approaching the colony, when eagles were present. In years when Bald Eagles regularly flew over and landed on the Tufted Puffin slope (Hipfner *et al.* 2011), the puffins spent much less time standing outside their burrows, almost always entered their burrows immediately after landing, and flew off to sea immediately after exiting their burrows (K. Morrison & J.M. Hipfner, pers. obs.).

Parents are sensitive to the risk of predation when they deliver food to offspring at the nest and balance the fitness benefits of continuing to provision their offspring against the risk that they themselves will be killed. At Pine Island, British Columbia, Harfenist & Ydenberg (1995) showed that Rhinoceros Auklets *Cerorhinca monocerata* breeding in areas of the colony where they were more susceptible to capture by Bald Eagles stopped provisioning their offspring several days earlier than individuals breeding in parts of the colony where they were less vulnerable to eagles. As a result, auklet nestlings in high-risk areas fledged several days earlier, despite similar hatching dates and growth rates between the two habitat types.

Foraging behavior

The risk of predation can also be a factor in the small-scale choice of foraging habitat. Marbled Murrelets *Brachyramphus marmoratus* routinely move farther from shore and out of sheltered inlets to feed at night (Whitworth *et al.* 2000, McFarlane-Tranquilla *et al.* 2005), and Haynes *et al.* (2010) suggested that they do this in order to reduce their exposure to nocturnally feeding Bald Eagles and Great-horned Owls *Bubo virginianus*. The same suggestion was made by Lewis *et al.* (2005) to explain nightly movements to offshore habitats in two species of scoters *Melanitta* spp. Similarly, Common Eiders moved out of areas of a Norwegian fjord where White-tailed Eagles were present on the shore, with eider numbers dropping by a factor of 30 (Hanssen *et al.* 2007).

Distribution at small, medium and large scales

Breeding is potentially dangerous for seabirds because it draws them onto land, where they are vulnerable to a broader suite of predators than they are while exclusively at sea. One behavioral mechanism that seabirds can employ to reduce the risk of predation is to choose a breeding site that affords safety from predators.

Barrett *et al.* (2006) showed that Common Murres that breed in protected sites in large cracks or stone scree are much more productive than those on exposed cliff ledges at colonies in Norway (Røst, Bleiksøya, Hjelmsøya) where White-tailed Eagle numbers are increasing. Likewise, Common Murres breeding on Tatoosh Island can seek refuge from Bald Eagles by nesting in crevices or under salmonberry, rather than in open cliff-top sites (Parrish & Paine 1996). And the murres in cliff-top sites respond more strongly to the appearance of eagles, and flush more frequently, than those in the better-protected sites (Parrish 1995). Common Murres breeding on Great Island, off eastern Newfoundland, abandoned subcolonies on flat areas at the top of cliffs between 2004 and 2010, a period during which Bald Eagles numbers increased dramatically (S.I. Wilhelm and G.J. Robertson, unpubl. data), and now breed only on

wide ledges in the middle of large cliffs where they are inaccessible to eagles. And Kildaw *et al.* (2005) noted that, during the period of rapid growth in the Bald Eagle population on Kodiak Island, Black-legged Kittiwakes actively shifted from tall cliffs to short cliffs for nesting, because Bald Eagles and other aerial predators hunted more effectively from taller cliffs where strong updrafts enabled them to attain higher speeds (Kildaw *et al.* 2008).

Unlike Common Murres, Glaucous-winged Gulls may prefer to nest in the open so they can see approaching predators such as Bald Eagles (Hayward *et al.* 1977) and river otters *Lontra canadensis* (Verbeek & Morgan 1978). At Protection Island, Washington, Bald Eagles took eggs more frequently from gull nests located in tall grass habitat than from those in sparse vegetation (Hayward *et al.* 2010). However, the consequences of the choice of habitat can vary from site to site. Among Western Gulls *L. occidentalis*, Glaucous-winged Gulls, and their hybrids, the productivity of nests located in areas of dense beachgrass or reeds was much greater than that of nests located in open sand areas in 1995 (0.14 vs. 0.01 fledglings) and 1996 (0.60 vs. 0.16) in Gray's Harbor, Washington, where Bald Eagles were active. On Tatoosh Island, where eagle disturbance was not a factor for these gulls, the productivity of gull nests was similar in dense beachgrass habitat and open rocky areas in both 1996 (0.92 vs. 1.42 fledglings) and 1997 (1.37 vs. 1.43) (Good *et al.* 2000, Good 2002).

Pelagic Cormorants can reduce their vulnerability to sea eagles by nesting in caves, as most do in Haida Gwaii (Harfenist *et al.* 2003), and under urban bridges, as increasing numbers have since 2000 in Vancouver, BC (Chatwin *et al.* 2002, L.K. Blight unpubl. data). Black-legged Kittiwakes breeding on Røst also benefit by nesting on man-made structures (Anker-Nilssen & Aarvak 2009, and unpubl. data). Over a 13-year period, kittiwakes averaged 0.79 fledglings per nest at colonies located on both cliffs and buildings. White-tailed Eagle numbers increased by a factor of five in the 11 years that followed, and during this latter period the kittiwakes that bred on buildings (eagle-free sites) fared almost twice as well (0.62 fledglings) as those that bred on cliffs (0.36) frequented daily by several tens of eagles during the chick period. There had been a strong correlation between breeding success and an index of local food supplies (0-group herring *Clupea harengus*); this correlation no longer held after the influx of eagles at the main colony, but was maintained throughout the entire study period at the colony on buildings.

Nesting in association with protective species is another common anti-predator strategy in birds (Quinn & Ueta 2008). At Triangle Island, large aggregations of Common Murres and Pelagic Cormorants were protected from Bald Eagles by the territorial behavior of a pair of Peregrine Falcons *Falco peregrinus* (Hipfner *et al.* 2011). After the falcons disappeared, the single large aggregation of murres decreased in size and several new subcolonies formed nearby, the largest in atypical habitat, a grass-covered slope, riddled with Tufted Puffin burrows, immediately above a second falcon eyrie. In some situations, seabirds can even gain protection from eagles by nesting with eagles. A Bald Eagle eyrie has been active on Gull Island, Newfoundland, since at least 1999. The resident eagles regularly flush seabirds, and researchers often find Common Murre carcasses under the eyrie (Robertson *et al.* 2004). However, transient eagles do not loaf at the top of murre breeding ledges on Gull Island, as they do on neighboring islands; it appears that in defending their territory from non-resident eagles the resident pair also provides protection to murres (Stalmaster 1987). Great Blue Herons *Ardea herodias* also benefit from this sort of nesting

association, in which resident eagles, although they do take herons, ultimately provide important protection by keeping the more numerous transient eagles away from the heronry (Kenyon *et al.* 2007). Eagles might also indirectly protect some seabirds by reducing or displacing large predatory gulls.

At medium scale, behavioral responses to sea eagles could cause seabirds to redistribute themselves among the islands within an archipelago. Common Murre numbers in the Scott Islands, British Columbia, declined by about 25% between 1989 and 2003, and the whole population aggregated to breed only on Puffin Rock, Triangle Island (Hipfner 2005), where, at some point during the intervening 14 years, a new Peregrine Falcon eyrie was established. It was around this eyrie that murres aggregated. In a similar fashion, the number of Common Murres and Pelagic Cormorants breeding at Tatoosh Island, Washington, increased through the 1980s in step with falcon numbers (Paine *et al.* 1990).

Finally, predation risk can be an important factor determining seabird community composition, i.e. distribution at large scales (e.g. Cairns *et al.* 2007). We speculate that British Columbia's very high density of nesting Bald Eagles (Kaiser 1989) could help to explain why its seabird fauna is heavily dominated in numbers and biomass by species that visit colonies at night and use fully enclosed nests (Rodway 1991), two adaptations that reduce predation risk (Lack 1968, McNeil *et al.* 1993). Gaston (2004) proposed that the high density of Bald Eagles could explain why the diurnal, surface-nesting murres are virtually absent as breeders along this coast. The province's small murre colonies of sizes up to several hundred pairs (such as that at the Kerouard Islands, in Haida Gwaii) tend to be ephemeral (Carter 2004, Carter *et al.* 2006), and suitable habitat occupied by Common Murres either for breeding or loafing while Bald Eagle numbers were low (e.g. cliff habitat at Sartine Island in the Scott Islands; flat, low-lying islands along the west coast of Vancouver Island) is currently unoccupied (Hipfner 2005). Even at Triangle Island, which supports British Columbia's largest murre colony of several thousand pairs, murres are extremely vulnerable to Bald Eagles (Hipfner *et al.* 2011). The effects of sea eagles on seabird community composition might be an interesting avenue of research to pursue.

Indirect effects: Facilitation of predation on seabird eggs and nestlings

When sea eagles hunt colonial seabirds, or merely fly over or past a seabird breeding colony, they often cause incubating and brooding birds to panic and flush *en masse* from nesting areas (Verbeek 1982, Galusha & Haywood 2002; White *et al.* 2006). Thousands of individuals can be flushed during a single event, and this can occur repeatedly. Seabirds that nest in the open are most likely to flush (Parrish & Paine 1995, Good *et al.* 2000), but even crevice-nesting species that would appear to be safe from eagles occasionally do as well (Hayward *et al.* 2010). The temporary abandonment of nests enables other avian predators to steal the seabirds' unattended eggs and nestlings (Verbeek 1982, Parrish 1995, Good 2002). In addition, in their panicked departures, birds may dislodge their own eggs, either breaking them or removing them from the nest so that incubation is terminated (Parrish 1995).

In western North America, at seabird colonies from central Oregon to Alaska, the list of seabird species reported to have been affected when Bald Eagles facilitate nest predators includes cormorants (Double-crested, Pelagic, and Brandt's *P. penicillatus*), Western and Glaucous-

winged gulls, Black-legged Kittiwakes, Caspian Terns *Sterna caspia*, Common Murres, and crevice-nesting Pigeon Guillemots *C. columba*. The nest predators that benefitted include Turkey Vultures *Cathartes aura*, Western and Glaucous-winged gulls, Common Raven *Corvus corax*, Northwestern Crow *C. caurinus*, American Crow *C. brachyrhynchos*, and Black-billed Magpie *Pica hudsonia* (Drent *et al.* 1964, Verbeek 1982, Rodway 1991, Parrish 1995, Good *et al.* 2000, Carter *et al.* 2001, Good 2002, Suryan *et al.* 2011, A. Robbins unpubl. data, Bird Research Northwest unpubl. data).

In Newfoundland, where Bald Eagle populations are increasing (G.J. Robertson & S.I. Wilhelm unpubl. data), the facilitation of nest predators has increased as Bald Eagle numbers have increased. At Cape St. Mary's Ecological Reserve, observers first witnessed Common Murres losing eggs to Common Ravens as a result of disturbance by eagles in 2006, and this has occurred in every year since (T. Power pers. comm., S.I. Wilhelm pers. obs.). And the number of murre eggshells found at the nests of Herring and Great Black-backed Gulls on Great Island has been rising in concert with Bald Eagle numbers (S.I. Wilhelm & G.J. Robertson unpubl. data).

In Norway, the list of seabirds affected when White-tailed Eagles facilitate nest predation by Herring and Great Black-backed gulls, Common Ravens and Hooded Crows *C. cornix* includes Great Cormorants, Northern Gannets, Common Eiders, Black-legged Kittiwakes and Common and Thick-billed Murres.

Although sea eagles' facilitation of nest predators of seabirds is widespread, the extent of the losses has rarely been quantified. At Mandarte Island, British Columbia, Verbeek (1982) estimated that 22% of cormorant eggs were taken by Northwestern Crows, mainly following Bald Eagle disturbances. Egg losses to gulls and crows caused the complete failure of Common Murres breeding in cliff-top habitat at Tatoosh Island in 1992, while murres nesting in protected crevices raised 0.73 to 1.0 chicks per pair per plot (Parrish & Paine 1996). At Triangle Island, Bald Eagle-facilitated losses of eggs to Glaucous-winged Gulls caused colony-wide breeding failure in the population of ~3000 pairs of Common Murres in two years, and hundreds of Pelagic Cormorants raised no offspring because they did not build nests (Hipfner *et al.* 2011); in earlier years, when Peregrine Falcons kept them safe from eagles, both murres (Hipfner & Greenwood 2008) and cormorants (Hipfner & Greenwood 2009) bred successfully. At Shoup Bay, Alaska, Bald Eagle disturbance preceded 84% of 159 episodes in which Northwestern Crows took eggs from Black-legged Kittiwakes (A. Robbins unpubl. data).

Population effects of sea eagles on seabirds

For many surface-nesting seabirds, we suspect that the loss of individuals to sea eagles is ultimately of less consequence to local populations than widespread breeding failure caused by the facilitation of nest predators. Indeed, in the most sophisticated assessment to date, Parrish *et al.* (2001) concluded that Bald Eagles had been a major factor causing a decline in Common Murres at Tatoosh Island, mainly due to facilitation. Even when egg losses due to eagle activities do not lead directly to reduced seabird breeding success because lost clutches are often replaced, success could still be reduced because the timing of breeding is delayed by the need for females to produce a replacement clutch (Parrish 1995). The cumulative effects of repeated disturbances by sea eagles could ultimately have the strongest impact, because they cause seabirds to abandon breeding sites. In the following, we assess on a region-

by-region basis some of most striking evidence that sea eagles are affecting local seabird populations as eagle numbers have increased.

Northeast Pacific

In western North America, Bald Eagles have been implicated (based on evidence of variable quality) in declines in local populations of Double-crested (Giesbrecht 2001, Harris *et al.* 2005) and Pelagic (Chatwin *et al.* 2002, Harris *et al.* 2005, Carter *et al.* 2009) cormorants, Glaucous-winged Gulls (Sullivan *et al.* 2002, Hayward *et al.* 2010), and Common Murres (Parrish *et al.* 2001, Hipfner *et al.* 2011), as well as at least one species of waterbird, the Great Blue Heron (Vennesland & Butler 2004). And Bald Eagles could have contributed to recent local declines of other marine birds, e.g. Western Grebes *Aechmophorus occidentalis* wintering in the Salish Sea (Anderson *et al.* 2009a, Bower 2009). This warrants further study, along with other factors such as forage fish declines (Anderson *et al.* 2009b, Blight 2011) and increases in human disturbance (Chatwin *et al.* 2002).

Bald Eagles have had particularly dramatic effects on seabirds in central and northern Oregon (R. Lowe, unpubl. data). Bald Eagle disturbance of seabirds was first noted on this coast in 1994 and is now so serious that few if any Common Murre offspring are produced in any year at colonies from Tillamook Head to Cape Foulweather, an ~131 km stretch of coastline that until recently supported >380 000 breeding pairs. Some colonies in this region now appear to be abandoned, while at others, murres attempt to breed but give up each year; Common Murre numbers appear to be in steep decline, and breeding by Brandt's and Pelagic cormorants is also being affected. Disturbance is rare and localized, but increasing, in southern Oregon and California (e.g. at the Channel Islands), where Bald Eagle numbers remain low (H. Carter, A. Little & P. Sharpe, pers. comm.).

Northwest Atlantic

Bald Eagles have had equally dramatic effects on Common Murres in the Witless Bay Ecological Reserve, Newfoundland, in recent years. As eagle disturbance increased (S.I. Wilhelm and G.J. Robertson unpubl. data), the breeding population of murres on Great Island fell 5.3% ± 1.8% per year between 2002 and 2009 (Canadian Wildlife Service, unpubl. data), while murre colonies on the entire west side of Green Island had been abandoned by 2010, reflecting the failed breeding of 25 000 to 40 000 pairs. Overall, an estimated ~25% of Common Murre pairs in the Ecological Reserve failed to breed in 2010, apparently because of Bald Eagle disturbance (S.I. Wilhelm and G.J. Robertson unpubl. data).

Numbers of Bald Eagles have increased dramatically in the northeastern United States in recent years (Watts *et al.* 2007). In Maine, Bald Eagle numbers increased from 30 pairs in the 1960s to over 500 pairs in 2009. By 2010, predation by Bald Eagles (as well as by American mink *Neovison vison* and river otters) on adults and nestlings had contributed to declines of 27% in Herring Gull numbers and of 33% in Great Black-backed Gull numbers from peaks in the mid-1990s; a decline of 67% in Double-Crested Cormorants from a peak of 28 000 pairs in the 1980s; and a decline in Great Cormorants from 260 pairs in 1992 to 80 pairs by 2008 (Maine Department of Inland Fisheries and Wildlife 2010). As Maine is the sole breeding location of Great Cormorants in the United States, Bald Eagle activities threaten to extirpate this species from the country.

Northern Europe

Disturbance by White-tailed Eagles is thought to be a major contributor to ongoing declines in Black-legged Kittiwake and Common Murre numbers along the Norwegian coast. After increasing by 1–2% per year through the 1960s and 1970s to ~500 000 pairs by 1980 (Barrett & Vader 1984), kittiwake numbers on the mainland started to decline in the 1980s, and the rate has accelerated to -6–8% per year at nearly all colonies (Barrett *et al.* 2006). In 2005, there were 336 000 pairs (Barrett *et al.* 2006), but numbers currently stand at half of the 2005 levels. Regional food shortages may be involved in the declines (Barrett *et al.* 2006), but there is convincing evidence that harassment by White-tailed Eagles at many colonies has caused repeated local breeding failures and declines in kittiwake numbers (Anker-Nilssen & Aarvak 2006, Anker-Nilsson 2010, Barrett *et al.* 2006). The kittiwake population on Røst, where the supply of 0-age herring is declining but effects of food supply on breeding success are reflected only for pairs using eagle-free sites on man-made structures and not those breeding on cliffs, declined from ~25 000 pairs in 1979 to only 7 500 in 2010 (Anker-Nilssen & Aarvak 2009, and unpubl. data).

Regarding Common Murres, numbers west of the North Cape were already in a steep decline in the 1960s (-5% per year between 1964 and 1974; Brun 1979), most likely due to hunting, fisheries bycatch, eggging, disturbance and food shortage. Although these threats are now all but absent, murre numbers continue to decline, and some colonies are close to extirpation (Barrett *et al.* 2006; Erikstad *et al.* 2007). Hjelmsøya, in West Finnmark, formerly supported the largest colony (110 000 pairs in 1964), but now numbers only a few thousand pairs, and most other colonies have dropped by more than 90% over the same time period. While the breakdown of the social structure of colonies (with single or small groups of birds on breeding ledges) is thought to have contributed to the declines, there is compelling evidence that White-tailed Eagles are exacerbating the situation, resulting in remnant populations (e.g. at Røst, Bleiksøya and Hjelmsøya) being forced to breed in protected sites under large cracks or stone scree, where they are much more productive than those on exposed cliff ledges (Barrett *et al.* 2006).

Northern Gannets are also being affected by sea eagles. They established two small colonies in the Lofoten-Vesterålen region in the 1960s and one in 1975. By 1991, ~1500 pairs bred on two of the colonies, while the third was no longer active after 1978 (Barrett & Folkestad 1996). In the early 1980s, harassment by White-tailed Eagles and predation of large gannet chicks was reported on one of the colonies, and in the 1990s there was also evidence of eagles preying on adult gannets (Barrett 2008). Numbers of gannets at the two remaining colonies declined, resulting in their extirpation by 2002 and 2005, while at the same time, six new colonies formed on small, low-lying islands in the region. These were, however, characteristically unstable and, by 2008, the total population had declined to ~400 pairs (Barrett 2008). Predation by eagles, combined with the facilitation of large gulls (Herring and Great Black-backed) and/or corvids (Common Raven or Hooded Crow), was probably the main cause of this decline.

CONSERVATION IMPLICATIONS

Changes in populations of certain apex predators are giving researchers novel insights into how predators structure ecosystems

through both direct and indirect effects (Estes *et al.* 2011). Increases in sea eagle populations provide an emerging opportunity to investigate the role of top-down forcing in seabird ecology. The recovery of sea eagle populations across the temperate northern hemisphere in the closing decades of the 20th century is one of the great conservation success stories of recent times (Watts *et al.* 2007, Hailer *et al.* 2006). Once severely depleted, sea eagles are now probably at or near carrying capacity in some parts of their historic range (Helander *et al.* 2003, Watts *et al.* 2007, Elliott *et al.* 2012). However, the recovery of sea eagles has had significant consequences for seabirds. This might reflect a return to a more “natural” ecological state, where direct and indirect top-down control by healthy populations of predators play a role, but whether that is the case should, nonetheless, be the subject of investigation and debate (Newsome *et al.* 2010). There will undoubtedly be important benefits for wildlife managers and wildlife scientists if we are successful in gaining a better understanding of the process as it veers towards a new equilibrium.

For example, Kenyon *et al.* (2007) used mathematical modeling to show how Great Blue Heron colonies redistributed themselves on the landscape in response to predation by Bald Eagles. The recent redistribution of Common Murres among the Scott Islands may have had a similar cause. If so, the apparent 25% decline in the local population (Hipfner 2005) need not have reflected a true reduction in the number of individual birds still alive. As noted by Parrish *et al.* (2001), a meaningful interpretation of population trends requires an explicit understanding of metapopulation dynamics, yet information of this sort is still lacking for many seabirds. Nonetheless, if eagles cause reductions in the number of individuals breeding each year, they could over time cause real population declines. Wildlife managers need to be aware of how behaviors employed by seabirds to reduce predation risk can muddy the interpretation of population trends, a point made previously in discussions of apparent declines in shorebird populations as Peregrine Falcon populations recovered (Ydenberg *et al.* 2004).

With conditions in marine ecosystems in flux, largely due to anthropogenic influences (Pauly *et al.* 2005, Halpern *et al.* 2008), seabird populations may in future be less resilient to predation than they were historically, and there is the strong possibility that sea eagles could increasingly affect seabirds as a result of trophic cascades. For example, reduced spawning runs of chum salmon, which form an important part of late-winter diets of Bald Eagles along the Pacific coast of North America (Knight & Knight 1983), may already be leading to increased rates of predation on secondary prey types such as seabirds and waterfowl (Watson *et al.* 1991, Elliott *et al.* 2012). Likewise, an inverse correlation between the availability of pink salmon *O. gorbuscha* to Bald Eagles and the number of Black-legged Kittiwake eggs taken concurrently by nest predators at Shoup Bay, Alaska, suggests the potential for future problems for breeding seabirds if pink salmon numbers decline (A. Robbins unpubl. data). In Alaska’s Aleutian Islands, Bald Eagles are taking seabirds with increasing frequency as sea otter populations decline and their pups become less available (Anthony *et al.* 2008).

Much of the information on which this review is based has been anecdotal and qualitative. To better inform management decisions, more rigorous investigations are needed. Several questions need to be addressed: (1) Are we witnessing a return to a prior situation

in which sea eagles strongly affect, and possibly limit, seabird populations through top-down forcing? (2) Are seabird populations now less resilient to sea eagle disturbance than they would have been historically as a result of anthropogenic stressors such as fisheries practices (i.e. removal of the eagles' primary prey and the prey required by seabirds to maximize reproductive success) and increasing human disturbance? (3) If the effects of sea eagles on seabird populations intensify, and perhaps affect seabird species at risk, would human intervention be warranted, would it be appropriate, and what would effective intervention look like? We hope that this review will serve as a basis for further discussion on this important conservation topic.

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