

AN ABSTRACT OF THE THESIS OF

Cheryl A. Horton for the degree of Master of Science in Wildlife Science presented on June 4, 2014.

Title: Top-down Influences of Bald Eagles on Common Murre Populations in Oregon.

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Populations of organisms are influenced by both top-down (predator driven) and bottom-up (environment or resource driven) effects. Seabird research has largely focused on bottom-up factors influencing reproduction, with little emphasis on top-down. Our goal was to better understand top-down impacts on colonial nesting seabirds over a range of spatio-temporal scales. We studied the coast-wide distribution and abundance of a Common Murre (*Uria aalge*) metapopulation during two decades (1988-2006) of Bald Eagle (*Haliaeetus leucocephalus*) recovery in Oregon. Bald Eagles prey on seabirds, but were functionally absent during much of the 20th century. After eagles were protected under the U.S. Endangered Species Act in 1978, populations increased rapidly especially along the coast where eagles cause disturbance at seabird colonies. We also studied the effects of predation and disturbance in 2012 at three Common Murre breeding sites located in regions of varying Bald Eagle density, and at a single site over a seven year period from 2007-2013.

We found regional changes in the distribution and abundance of Common Murres at breeding sites in Oregon associated with increases in coastal Bald Eagle nests over 20 years of study. Coast-wide Bald Eagle nest density was not uniform. The highest Bald Eagle nest density was found on the north coast, intermediate density on the central coast, and lowest density in on the south coast throughout the study. On the north coast, counts of murres declined by 50% between 1988 and 2006. In contrast, the number of murres counted and the number of breeding sites occupied increased substantially on the central coast, where Bald Eagle nest density was lower. Changes in the number and size of murre colonies on the north and central coast were associated with the regional density of Bald Eagle nests and initial number of murres present at each site, rather than immediate proximity of eagle nests to murre colonies.

Bald Eagles were the main predators causing disturbance at individual breeding sites studied. In 2012, we found differences in disturbance frequency, colony disruption, and predator activity among three sites in regions of high, medium and low Bald Eagle abundance. Eagles caused complete reproductive failure at the north coast site (high eagle density) in 2012. In addition to Bald Eagles, California Brown Pelicans (*Pelecanus occidentalis*) caused disturbance at the central and south coast sites, leading to low reproductive success and failure of remaining chicks at these sites in July 2012. We found no difference in reproductive loss between disturbances caused by adult and sub-adult eagles however, secondary nest predators (gulls, corvids and vultures) had a greater overall impact on reproductive loss than primary predators. From 2007-2013, we found a

negative association between mean reproductive success of murre and mean rate of eagle disturbance.

Our observations provide evidence for top-down regulation of breeding populations of Common Murres in Oregon, mediated by recently recovered native, avian predators. These findings challenge the effectiveness of site fidelity and natal philopatry for murre in the presence of avian predators. Scientists and managers on the U.S. West Coast should expect continued impacts from Bald Eagles as the population reoccupies its former range and increases to carrying capacity. Increased disturbance is likely at more Common Murre colonies in the future, particularly in years when alternative prey is limited for eagles or pelicans.

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Top-down Influences of Bald Eagles on Common Murre Populations in Oregon

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Cheryl A. Horton

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Cheryl A. Horton, Author

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TABLE OF CONTENTS

	<u>Page</u>
Chapter 1. GENERAL INTRODUCTION	1
INTRODUCTION	2
Background.....	2
Bald Eagles and Common Murres in the Pacific Northwest	3
Research approach	5
REFERENCES	8
Chapter 2. RETURN OF A NATIVE PREDATOR: COLONIAL SEABIRD RESPONSE TO AN EXPANDING BALD EAGLE POPULATION	11
ABSTRACT.....	12
INTRODUCTION	14
METHODS	18
Study area.....	18
Coast-wide data-sets	19
Interpolation and data summary.....	20
Statistical analysis.....	21
RESULTS	23
Regional changes in coastal Bald Eagle nest abundance and density	23
Local and regional redistribution of breeding murres.....	24
Temporal patterns in breeding site size and occupancy.....	25
Temporal patterns in index site size.....	26
DISCUSSION.....	27
Data limitations.....	31
CONCLUSION.....	33
REFERENCES	35
Chapter 3. SYNERGISTIC, TOP-DOWN PREDATION OF RECOVERING NATIVE AVIAN PREDATORS AT SEABIRD COLONIES IN OREGON	52
ABSTRACT.....	53

TABLE OF CONTENTS (Continued)

	<u>Page</u>
INTRODUCTION	55
METHODS	58
Study area.....	58
Video camera set-up and management	60
Video data description: metrics of disturbance.....	62
Observational data collection.....	63
Observational data description: predation processes and reproductive success	64
Data treatment and statistical analysis	66
RESULTS	69
Causes of disturbance	69
Metrics of disturbance.....	70
Primary and secondary predators.....	73
Predicting Common Murre reproductive loss.....	75
Common Murre demographics	77
DISCUSSION	78
Regional differences	78
Predators and age classes	81
Changes over time.....	84
Study limitations	86
CONCLUSION.....	87
REFERENCES	89
Chapter 4. GENERAL CONCLUSION	106
CONCLUSION.....	107
Research aims	107
Primary findings.....	107
Contributions and future directions	110
REFERENCES	113
BIBLIOGRAPHY.....	115

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
Figure 2.1. Map of Common Murre index sites (n=23) and census sites (n=88) along the Oregon coast	47
Figure 2.2. Map of all known, active Bald Eagle nest sites within 25km of shoreline in 1988 (n=20) and 2006 (n=58), with some sites occupied in both years	48
Figure 2.3. Regional density of Bald Eagle nests within 25km of shoreline in Oregon from 1988-2006	49
Figure 2.4. Annual Common Murre index site counts from 1988-2006 and census counts of all colonies in 1988 and 2006	50
Figure 2.5a and 2.5b. The number of Common Murres counted at index sites by region as a proportion of the total regional counts of murres during census years 1988 and 2006 (a) and as a proportion of the total coast-wide census counts in 1988 and 2006 (b)	51
Figure 3.1. Proportion of disturbances identified by observers in the field (Observer) and from video data (Video, in 2012 pooled among north, central, and south coast research sites)	99
Figure 3.2. Proportion of video disturbances caused by Bald Eagles in 2012, during which 1-25%, 26-50%, 51-75% and 76-100% of nesting adult common murres evacuated research sites on the north, central and south coast of Oregon	100
Figure 3.3. Proportion of video monitoring days when at least one disturbance or predator presence event (for all primary predator types) occurred at each study site	101
Figure 3.4. Proportion of video monitoring days when at least one disturbance or predator presence event occurred at the north and central coast research sites	102
Figure 3.5. Annual proportion of all disturbance events recorded by observers and categorized by month from 2007-2013 at Yaquina Head	103
Figure 3.6. Relationship between the single explanatory variable, “percent of colony evacuated” (x-axis) and the odds of actual and predicted reproductive loss occurring (y-axis)	104
Figure 3.7. Common murre mean reproductive success is negatively associated with the mean rate of eagle disturbance in each year at the central coast site	105

LIST OF TABLES

<u>Table</u>	<u>Page</u>
Table 2.1. Definitions and acronyms for covariates used to model Common Murre site occupancy and size during census years.....	40
Table 2.2. Regional eagle nest density (#/km of shoreline), number of active Bald Eagle nests, and percent increase in the number of eagle nests in 1988 vs. 2006	41
Table 2.3. Number of available Common Murre breeding sites in each region, number and percent of occupied murre breeding.....	42
Table 2.4. Total number of Common Murres counted at breeding sites during complete censuses of the population in 1988 and 2006 on the north, central and south coast	43
Table 2.5. Model selection results for logistic regression analyses predicting the odds that murres would occupy previously used breeding sites during	44
Table 2.6. Model selection results for logistic regression analyses investigating whether the number of Common Murres counted would increase in 2006 vs. 1988	45
Table 2.7. Model selection results for linear regression analyses relating linear trends in index site size over time (1988-2006).....	46
Table 3.1. Mean hourly rate of disturbance and mean length of disturbance in hours for all causes (excluding unknown causes and unknown end times) and Bald Eagle disturbances alone (excluding unknown end times) from video data.....	95
Table 3.2. Model selection results for the 7 single factor logistic regression models relating the response “odds of reproductive loss (1=loss occurs, 0=no loss occurs)”, to percent of the colony evacuated per disturbance (0-100%, PClear), median time of disturbance event (in h:m:s, Time), age of Bald Eagle (sub-adult or adult, BAEAage), an intercept only model (Null), Year, disturbance length (in minutes, DLength), and Julian Day of each disturbance caused by Bald Eagles at the central coast site	96
Table 3.3. Selection results for nine linear regression models relating the response “number of Common Murre eggs and chicks killed by secondary predators” to six single covariate models, one additive model, one interaction term model and a null model.....	97
Table 3.4. Summary metrics from observations of Common Murres at the north, central and south coast research sites in 2012. The number of field observation days and hours are provided, along with the number of reproductive plots monitored by site	98

Chapter 1

GENERAL INTRODUCTION

Cheryl A. Horton

INTRODUCTION

Background

Bald Eagles (*Haliaeetus leucocephalus*) were historically numerous throughout the continental United States, especially in areas with abundant aquatic habitat such as the Pacific Northwest (Buehler 2000). Although range-wide estimates of historical population size are not available, it is clear that eagles declined throughout the 19th century, and reached historic lows during the 20th century (Buehler 2000, Hipfner et al. 2012). Increased human populations, habitat loss, hunting and environmental contamination all contributed to the decline (Wiemeyer et al. 1993, Buehler 2000). Bald Eagles were protected as threatened or endangered in the lower 48 states in 1978, and remained listed under the Endangered Species Act until 2007 (Isaacs and Anthony 2011). The recovery and de-listing of Bald Eagles is considered a major success of this hallmark conservation legislation.

Bald Eagles are known to feed on a variety of fish, birds, mammals and reptiles (Todd et al. 1982, Warnke et al. 2002, Watson 2002). As apex predators in many systems, eagles have the ability to impact prey populations through top-down forcing, both directly and indirectly (Connell 1970, Lima 1998). During several decades when eagles were functionally absent from ecosystems, prey populations likely expanded, unchecked by predation (Baum and Worm 2009). This combined with rapid expansion of the human population and land use changes over the past century means eagles have recovered into vastly changed environments. Now that Bald Eagles are once again numerous on the landscape, ecological changes related to top-down forcing are

inevitable, but do not necessarily represent a “natural rebalancing” to a previously held state. Instead, Bald Eagles may act as novel predators in many ecosystems, with unknown impacts under current environmental conditions.

Bald Eagles and Common Murres in the Pacific Northwest

In the Pacific Northwest, Bald Eagles are native, avian predators of Common Murres (*Uria aalge*), the most abundant seabird on the Pacific coast of North America (Manuwal et al. 2001). Murres breed from April-August on offshore rock sand islands within 10km of shore, ranging in size from tens or hundreds, to dense aggregations with thousands of individuals (Naughton et al. 2007). The Bald Eagle breeding season peaks from March through June and chick provisioning for eagles overlaps with the return of murres to coastal breeding habitats (Isaacs et al. 1983, Elliott et al. 2011). Predation related disturbance at murre colonies has increased in recent decades, with some murre breeding sites abandoned or assumed reproductively unsuccessful (Manuwal et al. 2001, Hipfner et al. 2012). While the effects of native, avian predators on seabirds are not well studied, it is possible that predators such as Bald Eagles, may be exploiting these rich food patches, especially if other historically abundant food sources are limited (Hamilton 1971). For murres breeding in large, dense colonies in close proximity to nesting eagles, “predator swamping” may not always be an effective anti-predator defense (Oro 1996).

Adult murres lay a single egg, up to one replacement clutch if loss occurs early in the season, and both adults provide care until the chick fledges (Wanless et al. 1988, D.G. and Boekelheide 1990). For these long-lived birds, the cost of reproduction is high and

individuals must balance the needs of their offspring with their own survival. Common Murres exhibit high site fidelity and natal philopatry which are adaptive traits thought to enhance reproductive success (Swann and Ramsay 1983, Harris et al. 1996, Ainley et al. 2002, Zador et al. 2009). Despite the high likelihood murres will return to colonies where they were raised, or to previously occupied breeding sites, this does not always occur. Breeding failures may precipitate abandonment of nest sites or entire colonies, thus requiring birds to find alternative habitats within a season, or in subsequent seasons (Greenwood and Harvey 1982).

Bottom- up (environment or resource driven) and top-down (predation and disturbance driven) forces may influence reproductive success of seabirds (Suryan et al. 2006). Murres along the coast of Washington, Oregon and California exploit a wide- diversity of forage fish species, thereby buffering chicks and maintaining relatively high reproductive success, except in years with extremely poor oceanographic conditions that reduce food availability (D.G. and Boekelheide 1990, Gladics 2012, Schrimpf et al. 2012). Despite many years of seemingly adequate food availability, since the 1980's some murre colonies have been abandoned and new colonies have been established at previously unoccupied sites exhibiting growth rates unexplainable without immigration (Parrish 1995, Manuwal et al. 2001). This suggests movement of Common Murres among breeding sites, precipitated by some stimulus. It appears that chronic disturbance by predators is a top-down mechanism initiating murre colony abandonment and re-colonization over large spatial scales.

Research approach

Throughout the Northern Hemisphere, there is particular interest in the effects of recently recovered eagle populations on breeding seabirds (Hipfner et al. 2012). In the Pacific Northwest, a few studies have addressed Bald Eagle predation at individual seabird breeding colonies in Washington and British Columbia (Parrish et al. 2001, Hipfner et al. 2011). Although Oregon supports two-thirds of the Pacific coast population of Common Murres, prior to our research, there were no published studies addressing Bald Eagle predation at seabird colonies within the state (Naughton et al. 2007, Hipfner et al. 2012). Therefore, I developed two primary research objectives to understand the spatio-temporal impacts of Bald Eagle recovery on distribution and abundance of Common Murres at breeding colonies in Oregon, and identified the mechanisms of disturbance, while also quantifying regional effects of predators on reproduction at three murre breeding sites.

Common Murres were a suitable study species in Oregon because coast-wide aerial surveys of murre breeding sites were conducted by the U.S. Fish and Wildlife Service's Oregon Coast National Wildlife Refuge Complex annually from 1988 to 2006 and are ongoing (Naughton et al. 2007). Likewise, concurrent data were available for active Bald Eagle nest sites during the same time period from surveys conducted by the U.S. Geological Survey's Oregon Cooperative Fish and Wildlife Research Unit (Isaacs and Anthony 2011). Additionally, these highly visible and abundant seabirds form dense colonies, some of which are in close proximity to Bald Eagle nests and easily viewable from shore, thus facilitating observational data collection.

I used historic data in Chapter 2 to compare the regional and coast-wide distribution and abundance of Common Murres and Bald Eagles over a 20 year period (1988-2006). I modeled odds of murre breeding site occupancy and size in 2006, as a function of Bald Eagle density at various scales and initial murre colony size, using logistic regression. Additionally, I modeled change in murre abundance at index sites against covariates related to Bald Eagle density and initial murre colony size. For all models, Akaike's Information Criteria corrected for small sample sizes (AIC_c) and an information theoretic approach were used to evaluate single factor models including covariates selected *a priori* based on biological relevance to top-down hypotheses.

In Chapter 3 remote video cameras and human observers were used to study mechanisms of disturbance and reproductive loss at three Common Murre colonies in 2012 and at a single site over a 7-yr period, 2007-2013. Video and observer data were used to compare predator assemblages among sites, test for differences in frequency and length of disturbances as well as extent of breeding site evacuation at murre colonies in regions of high, intermediate and low Bald Eagle abundance. I also compared impacts of primary and secondary predators, including amount of murre adult, egg and chick mortality attributable to each predator type at a single site over multiple years. Finally, I tested for association between murre reproductive success and predation rate over time, and modeled relationships between reproductive loss and several *a priori* covariates related to disturbance.

The results of this study advance understanding of Common Murre breeding colony redistribution and metapopulation dynamics during the recovery of Bald Eagles in Oregon, and is one of the first studies to address broad scale movement of seabirds associated with top-down pressure in the Pacific Northwest. Additionally, this work increases our understanding of disturbance mechanisms acting on Common Murres at colonies and influencing reproductive success in areas of high, medium and low Bald Eagle abundance.

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Chapter 2

RETURN OF A NATIVE PREDATOR: COLONIAL SEABIRD RESPONSE TO AN
EXPANDING BALD EAGLE POPULATION

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ABSTRACT

Removal of apex predators from the environment is a relatively recent, widespread anthropogenic effect in global ecosystems. Bald Eagles (*Haliaeetus leucocephalus*), a native predator of Common Murres (*Uria aalge*) in the Pacific Northwest of North America, were functionally absent during the early- to mid-20th century because of habitat loss, human persecution and the effects of environmental contaminants. With protection under the U.S. Endangered Species Act, eagle populations rebounded and the species was delisted due to recovery in 2007. We studied the coast-wide distribution and abundance of a Common Murre metapopulation during two decades (1988-2006) of Bald Eagle recovery in Oregon. We found that changes in the distribution and abundance of Common Murres at breeding sites in Oregon were associated with increases in coastal Bald Eagle nests. Although number of Bald Eagle nests increased coast-wide over time, the highest density was found on the north coast, intermediate density on the central coast, and lowest density on the south coast throughout the study period. On the north coast, where Bald Eagle nest density is highest, counts of murres declined by 50%. In contrast, number of murres counted and number of breeding sites occupied increased substantially on the central coast, where eagle nest density was lower. Logistic regression models showed changes in the distribution and abundance of murres on the north and central coast were influenced by the regional density of Bald Eagle nests and the initial number of murres present at each site, rather than immediate proximity of eagle nests to murre colonies. These findings challenge the effectiveness of strong site fidelity and natal philopatry for Common Murres in the

presence of eagles, and question the effectiveness of very large colonies where avian predator densities are also high. Scientists and managers on the U.S. West Coast should expect continued impacts on surface nesting seabirds from Bald Eagles as the population reoccupies its former range and increases to carrying capacity.

INTRODUCTION

Trophic downgrading or the removal of apex predators from the environment is a relatively recent, widespread anthropogenic effect in global ecosystems (Estes et al. 2011). Absence of top-predators and top-down forces can cause cascading effects that resonate throughout multiple levels and impact entire ecosystems (Hebblewhite et al. 2005). Some of the most notable examples of trophic cascades include: removal of sea stars in rocky intertidal, sea otters in sub-tidal, wolves in Yellowstone National Park, and sharks and whales in ocean ecosystems (Menge 2000, Springer et al. 2003, Beyer et al. 2007, Myers et al. 2007). In addition to facilitating expansion of herbivore populations, removal of top-predators can also lead to “mesopredator release” where low- to mid-level predator populations expand, thereby increasing predation on small prey (Ritchie and Johnson 2009). Unchecked mesopredators have the potential to greatly reduce prey populations (Berger et al. 2008, Ritchie and Johnson 2009). Often, it is not clear that apex predators influence the environment until populations are reduced to the point of becoming functionally absent. Extirpation has allowed “natural experiments” to occur, which document before and after effects on the environment (Pace et al. 1999). In general, the associated trophic cascade effects have been documented at local scales for some mammals (Beyer et al. 2007), fishes (Knight et al. 2005) and invertebrates (Moran and Hurd 1997). Aside from avian predation on insects, birds remain largely understudied in this regard (Mäntylä et al. 2010). We document impacts from the recovery of a native, avian, apex predator, on a metapopulation of colonial nesting seabirds over a large geographic scale.

Bald eagles (*Haliaeetus leucocephalus*) are a native predator of Common Murres (*Uria aalge*) in the Pacific Northwest of North America (Parrish et al. 2001), but were functionally absent during the early- to mid-20th century because of artificially low population sizes (Isaacs and Anthony 2011). The combined effects of habitat loss, human persecution, and environmental contaminants nearly caused the extinction of Bald Eagles, which were protected within the contiguous United States under the Endangered Species Act (ESA) in 1978 (Isaacs and Anthony 2011). After protection under the ESA, eagle populations rebounded, and in Oregon the population increased 400% by 2007 (Isaacs and Anthony 2011). In the western part of the state, adult eagles filled available breeding territories along major rivers and the coast (Isaacs and Anthony 2011). In 2007, Bald Eagles were federally de-listed and later state de-listed in 2012 (USDOJ 2007, ODFW 2012). Eagles are generalist predators known to exploit seasonally abundant prey sources (Galusha and Hayward 2002, Marston et al. 2002). In the Pacific Northwest, the Bald Eagle breeding season peaks from March through June and chick provisioning for eagles overlaps with the return of murres to coastal breeding habitats (Isaacs et al. 1983, Elliott et al. 2011).

Given the murre population was allowed to expand for decades during a period of low population size for Bald Eagles, the recovery of eagles provides an opportunity to examine how a murre population might respond to the return of a potentially important predator. This brings into question the utility of strong site fidelity and colonial nesting as strategies for decreasing predation risk, in the presence of avian predators (Lack 1968, Kenward 1978). Breeding in dense aggregations may benefit seabirds by overwhelming

or “swamping” predators, thereby decreasing the chance any one individual will be taken from a colony (Anderson and Hodum 1993). Colonial nesting also benefits breeding birds in other ways, for example, by facilitating conspecific social attraction to aid in locating quality breeding habitat or aggregations of prey at sea (Oro 1996, Jovani et al. 2008). While upper limits to colony size are likely limited by available food (Erwin 1978, Ballance et al. 2009), it is also possible that predator number and type can influence colony size or distribution within a metapopulation. Dense aggregations of breeding seabirds may attract and increase susceptibility to some types of predation, if predators adapt, learn or are otherwise able to exploit breeding birds or their offspring at colonies (Hamilton 1971, Clode 1993).

In locations where predation at murre colonies is moderate to non-existent, benefits of colonial nesting may outweigh potential drawbacks. There may be thresholds of predation pressure and predator type determining whether large or small colonies benefit murre by decreasing predation risk. From studies of land-based, introduced predators at seabird breeding colonies in other regions, it is clear predation can have detrimental localized impacts on breeding seabirds and their young (Jones et al. 2008, Lavers et al. 2010). Presence of certain predators, number of breeding seabirds, nesting failures, and degree of synchrony at a particular colony may influence whether breeding sites are abandoned or rendered reproductively unsuccessful in a given season (Burger 1982, Velarde 1992, Oro 1996, Addison et al. 2007).

Chronic disturbance, often associated with aerial predators, is another mechanism that may initiate murre colony abandonment and re-colonization over a variety of spatial scales (Zador et al. 2009). We define colony disturbance as any event during which adult murrees evacuate or flush from breeding sites. Disturbance can result in both direct and indirect effects on reproduction (Paine et al. 1990, Thayer et al. 1999). When murrees flush from breeding sites, secondary nest predators, such as gulls, scavenge murre eggs and chicks from cleared areas (Schauer and Murphy 1996). It is possible these secondary predators are now bolstered by increased access to prey at murre colonies because of disturbance. If this is true, greater reproductive loss may occur during contemporary disturbance events with the combined effects of primary and secondary predators. Eagles are known to consume a wide variety of bird species, including gulls (White et al. 2006), but may not be pursuing these species, while Common Murres remain abundant and easy prey.

Although limited historical data exist, there is evidence new murre colonies were established at previously unoccupied sites along the Pacific coast of North America since the 1980's (Parrish 1995, Manuwal et al. 2001). As the Bald Eagle population recovered, disturbance to murre colonies increased, causing murre reproductive failure and presumably breeding site abandonment (Parrish et al. 2001, Hayward et al. 2010, Hipfner et al. 2012). There is growing evidence to suggest aerial predators may be attracted to seabird breeding colonies (Parrish et al. 2001, Igual et al. 2007). In the Northern Hemisphere there is particular interest in the impacts of recently recovered sea eagle

populations which have been associated with declines in nesting success at some seabird colonies (Hipfner et al. 2012).

In this study, we examined population dynamics of a colonial seabird, the Common Murre, and a recovering population of Bald Eagles (currently the main predator of murre during the nesting season) over two decades along the Oregon coast. We considered the network of Common Murre breeding sites to be a metapopulation, or a system of local populations, with distinct habitat patches linked by occasional dispersal (Groom et al. 2006). We assessed regional differences in growth of the Bald Eagle population and how this may have impacted the murre metapopulation over time. In regions with high Bald Eagle nest densities we anticipated murre might redistribute to fewer, larger breeding sites in an attempt to avoid or overwhelm (“swamp”) eagle predators. Regionally, we expected to find a redistribution of murre from breeding sites of highest to lower eagle nest densities. Finally, we modeled temporal patterns in murre colony occupancy using a variety of exploratory covariates including: initial murre colony size, regional density of breeding Bald Eagles, and abundance of eagle nests within 5, 10, 15 and 20km of individual murre colonies. We also compared the utility of murre census data to yearly index site counts for addressing our research questions over the entire study period.

METHODS

Study area

We partitioned the Oregon coast into three geographic regions: north, central, and south, closely matching designations of (Naughton et al. 2007, Fig. 2.1). Shoreline distance and available murre breeding habitat differed, with the majority of offshore rocks and islands occurring on the north and south coast, and fewer on the central coast. Our study area included all Common Murre breeding sites ($n=88$) along 515km of the Oregon coastline, and extended inland 25km from breeding sites along the entire length of coast. We chose the 25km distance to encompass all eagle nests that we reasonably expected to hunt murre colonies, based on the estimated range in eagle breeding territory size (Garrett et al. 1993, Watson 2002).

Coast-wide data-sets

Bald Eagle data were provided by the Oregon Cooperative Fish and Wildlife Research Unit at Oregon State University (Isaacs and Anthony 2011). We used data of eagle nest locations occupied annually from 1988-2006, which coincided with the available murre data (Fig. 2.2).

Data on Common Murres were obtained during the U.S. Fish and Wildlife Service's Oregon Coast National Wildlife Refuge Complex, aerial photographic surveys conducted once annually in early June 1988 through 2006. During these surveys, offshore rocks and islands spanning the entire Oregon coast were photographed, and later all (census) or a subset (index) of these breeding sites were counted. A census of murre counts at all occupied breeding sites was made in 1988 ($n=67$ sites) and 2006 ($n=71$

sites). Therefore, these two years represent complete censuses of the breeding population of murre in Oregon (Fig. 2.1).

A subset of index colonies ($n=23$ sites) were counted annually to provide a finer temporal resolution of trends in colony size. Index colonies included seven sites on the north coast, three on the central coast, and thirteen on the south coast (Fig. 2.1). The number and location of index sites were selected to reflect the available breeding habitat in each coastal region.

Interpolation and data summary

We created point shapefiles (North American Equidistant Conic projection ArcMap 10.0) of eagle nests and Common Murre colonies, and digitized a polyline connecting all murre colonies. We created a 25km buffer in all directions from this line to delineate our study area. The resultant polygon (16,849,757 km²) was used to clip the original state-wide Bald Eagle nest point shapefile to include only nests within 25km of murre colonies for our analysis. To further partition our spatial data, we created separate polygons representing the north, central and south coast regions (Fig. 2.1). Regional polygons were used to count the number of active coastal Bald Eagle nests within each region in each year. From these counts which are unadjusted for detection, we calculated trends in overall and regional Bald Eagle nest abundance over time (1988-2006). We used a polyline shape file (National Oceanic and Atmospheric Administration's Continually Updated Shoreline Product), to measure the shoreline distance (km) in each coastal region and calculated the regional density of active Bald Eagle nests per km of

shoreline in each year. Finally, we calculated distances (km) from index sites to the nearest Bald Eagle nest in each year of the study.

For census years ($n=2$), we calculated differences in the number of breeding sites used by murre regionally (north, central, south) and coast-wide. Additionally, we compared the number of murre counted at each site, within each region, and overall in 1988 and 2006. We also calculated the number of active Bald Eagle nests within 5, 10, 15, and 20km of each breeding site in 1988 and 2006.

We used index sites ($n=23$) monitored annually from 1988-2006 ($n=19$ years) to address regional abundance of murre over time, and compared the proportion of murre counted in each region to findings from the census years. We also calculated the trend in the number of murre at each index site over time.

Statistical analysis

We used contingency table analysis, Pearson's chi-square statistic and summary statistics to compare murre breeding site status and the number of Common Murre counted among regions in 1988 and 2006. Statistical analyses were conducted in R version 3.0.1.

We used logistic regression to model the odds a Common Murre breeding site would be occupied or abandoned in 2006 ($n=88$). We were unable to adjust for detection probability with these data, so constant detection was assumed. Covariates, selected *a priori* included: initial size of each Common Murre breeding site, change in regional Bald

Eagle nest density between census years, and change in the number of Bald Eagle nests within 5, 10, 15, and 20km of each murre breeding site (Table 2.1). We used a second logistic regression, with the same covariates, to model the odds that counts of murre at breeding sites increased between the two census years ($n=88$). We determined a minimum threshold to indicate a significant increase at all sites by analyzing trends in each of the 23 index sites over the entire study period. Index sites that showed statistically significant increasing trends in murre numbers across all 19 years based on R^2 , p-values and interpretation of betas were used to calculate the minimum percent change in counts made in 1988 and 2006 that corresponded to significant increasing trends. Based on this initial trend analysis, an increase of $\geq 60\%$ in the number of murre at a site between 1988 and 2006 corresponded with a significantly increasing trend at index colonies between census years, and was coded as 1 in our model. Any increase $<60\%$ was considered to show no change, and these sites were coded as 0.

We used package “stats” in R to develop *a priori* single-factor model sets to investigate the effect of our covariates of interest (Table 2.1) on Common Murre breeding site status and size between census years ($n=88$). For both of these analyses, we evaluated model sets using Akaike’s information criterion corrected for small sample sizes (AIC_c), with output from package “AICcmodave” in R. We used an information-theoretic approach including differences in model AIC_c compared to the model with the lowest AIC_c (ΔAIC_c), AIC_c weights, and model coefficients to determine strength of evidence for specific effects that we predicted would impact Common Murre site occupancy and size (Burnham and Anderson 2002). We considered models with the lowest AIC_c to be

best, but also used 95% confidence intervals for covariate coefficients to evaluate competing models ($\Delta AIC_c < 2$) (Arnold 2010). If initial model selection warranted it (i.e. >1 single-factor model was competitive), we developed two-factor models combining covariates. These were then added to the list of single-factor models and re-evaluated using AIC_c to determine if there was more support for models with multiple factors compared to single-factor models (Arnold 2010).

We used linear models to investigate trends in Common Murre index colony size over the entire study period ($n=23$). We used simple linear regression to determine the trend in murre counted at each of the 23 index sites over time, and then used the slope of the trendline as the response variable in our model. We included initial Common Murre colony size, mean distance to the nearest Bald Eagle nest, change in the number of Bald Eagle nests within 5, 10, 15 and 20km of each index site (1988 vs. 2006), and change in regional density of Bald Eagles (1988 vs. 2006) as covariates (Table 2.1). We selected best models and evaluated strength and direction of the effects using the information-theoretic model selection approach described above.

RESULTS

Regional changes in coastal Bald Eagle nest abundance and density

We found an increasing trend in the number of Bald Eagle nest sites coast-wide ($\beta = 2.5$, $SE = 3.5$, $R^2=0.94$, $p<0.001$, $n=19$, $df=1,17$) and within each coastal region: north ($\beta = 1.1$, $SE = 1.9$, $R^2=0.92$, $p<0.001$, $n=19$, $df=1,17$), central ($\beta = 0.59$, $SE = 0.9$, $R^2=0.93$, $p<0.001$, $n=19$, $df=1,17$), and south ($\beta = 0.74$, $SE = 1.6$, $R^2=0.86$, $p<0.001$,

$n=19$, $df=1,17$), from 1988 through 2006 (Table 2.2). The greatest percent increase in eagle nest density occurred on the central (225%) and north (211%) coasts, whereas growth was slowest on the south coast (143%) (Table 2.2). Overall, Bald Eagle nest density remained highest on the north coast (0.11 eagle nests km^{-1} of shoreline in 1988 and 0.35 in 2006), intermediate on the central coast and was lowest on the south coast (Fig. 2.3). Additionally, we found murre breeding sites on the north coast had on average, 3 (SE 0.13) active Bald Eagle nest sites within a 20km radius in 1988, and 9 (SE 0.29) in 2006. The mean number of Bald Eagle nests within a 20km radius of murre colonies was an order of magnitude less on the south coast in 1988 (0.17, SE 0.11) and 2006 (0.86, SE 0.18), and intermediate on the central coast in 1988 (1, SE 0.11) and 2006 (6, SE 0.65).

Local and regional redistribution of breeding murre

We found similar overall numbers of occupied Common Murre breeding sites within each region between census years (Pearson's chi-square = 4.6241 (2), $p=0.09$). In contrast, total regional counts of Common Murres differed between census years (Pearson's chi-square = 37143(2), $p<0.001$).

On the north coast, where Bald Eagle nest density was highest (0.35 nest/km) there was no significant change in the total number of occupied breeding sites between 1988 and 2006 (Pearson's chi-square=0.648(1), $p=0.42$; Table 2.3), even though, only half of the original sites occupied during the first census (1988) remained occupied during the second census (2006). Fifteen sites used in 1988 were abandoned by 2006, however, 11 sites used in 2006 were newly established since 1988, and 17 sites remained

occupied in both years on the north coast. Despite similar numbers of occupied breeding sites between census years, we found 50% fewer murre on the north coast in 2006, compared to 1988 (Table 2.4). Bald Eagle nest density was highest on the north coast throughout the study and peaked at $0.35 \text{ nest/km}^{-1}$ in 2006 (Fig. 2.3). Population trends were opposite on the central coast where Bald Eagle nest density was lower ($0.12/\text{km}^{-1}$ in 2006), the number of occupied Common Murre breeding sites increased by 350% and the total number counted increased by 104% between 1988 and 2006 (Tables 2.3 & 2.4). In contrast to the north and central coast, the south coast which had the lowest density of Bald Eagle nests ($0.03 /\text{km}^{-1}$ in 2006), showed no significant change in the number of occupied breeding sites or number of murre counted between 1988 and 2006 (Tables 2.3 & 2.4).

Temporal patterns in breeding site size and occupancy

For predicting the odds that Common Murres would occupy breeding sites in the second census year (2006), we found the single factor model that included change in regional density of Bald Eagles on the north, central and south coast, to be ranked highest, and no other models were competitive (Table 2.5). There was a significant relationship between the odds a site would be occupied in 2006 and the change in regional Bald Eagle nest density on the north coast, with a 9% decrease in the odds of a site being occupied for every 1% increase in the change in Bald Eagle nest density ($\beta = -0.10$, $SE = 0.79$ 95% CI: 0.02 – 0.43). We found little support for a relationship between the change in Bald Eagle nest density on central and south coasts, on the odds of Common Murre breeding sites being occupied in 2006 (Table 2.5).

Model selection results did support a strong association between the odds that Common Murre breeding sites increased in size between 1988 and 2006, and initial site size and regional change in Bald Eagle nest density (Table 2.6). This 2-factor model accounted for all the AIC_c weight, and suggested the odds that Common Murre breeding sites would increase in size in 2006 was related to initial site size in 1988, with a 1% decline in murre breeding site size for every 1% increase in initial site size ($\beta = 0.99$, SE = 0.00, 95% CI: 0.9991 – 0.9998). In addition, the odds that Common Murre breeding sites increased in size in 2006 increased in association with an increased change in regional Bald Eagle nest density on the central coast ($\beta = 428$, SE: 2.53, 95% CI: 10 – 215131).

Temporal patterns in index site size

We found that the rate of change in index colony size during our study was most strongly associated with the change in the number of Bald Eagles within 15km of each index site and the change in the number of Bald Eagle nests within 20km of each index site (Table 2.7). However, these single factor models were competitive with the intercept only model and 95% confidence limits on the coefficients associated with the change in the number of Bald Eagles within 15 or 20km of each study site overlapped zero ($\beta = 73$, 95% CI: -10 to 157; $\beta = 47$, 95% CI: -9 to 104, respectively). Thus, neither of these covariates had a very strong effect on the rate of change in index colony size.

DISCUSSION

Consistent with the statewide findings of Isaacs and Anthony 2011, we found an increasing trend in the number of Bald Eagle nests in coastal Oregon from 1988-2006, although this growth was not uniform along the coast. Instead, Bald Eagle density was highest on the north coast, intermediate on the central coast, and lowest on the south coast, supporting our initial impression that eagles have been filling available breeding territories from the Columbia River south. These differences in regional Bald Eagle nest density suggest differences in predation pressure on the north, central and south coast of Oregon. Indeed, we found corresponding regional differences in the number of Common Murres counted and breeding sites used over time, indicating that recovery of this native, avian predator is associated with changes in the distribution and abundance of murres breeding in Oregon.

We found some evidence for large colonies providing anti-predator defense for murres. In the literature, there is substantial argument for and against large colony sizes leading to decreased predation risk, without much agreement (Anderson and Hodum 1993, Varela et al. 2007). Lack (1968) was one of the first to assert coloniality as a method of nest defense, but Clode (1993) argues that colonial nesting in seabirds evolved to aid birds in locating a dispersed, unpredictable prey base, and therefore may lead to increased predation, instead of serving as a strategy to avoid predators. Regardless of origins, predators use seabird breeding colonies as food sources. Much of the predation literature focuses on mammalian predators or avian nest specialists, but few studies document the effects of raptors on breeding seabirds. A study of Audouin's gulls (*Larus audouinii*) in the Mediterranean found that birds nesting in dense sub-colonies within a

larger colony were less impacted by peregrines (*Falco peregrinus*), than conspecifics in loose aggregations highlighting the importance of nest density, independent of overall colony size (Oro 1996). The author suggested natural selection favoring small, dense nest aggregations were a more effective anti-predator strategy for aerial predators, such as peregrines, attracted to these gull breeding areas. The Oro (1996) study of raptor predation on gulls is interesting because it suggests there may be more complex mechanisms at work related to spacing within colonies, in addition to the dichotomy of anti-predator benefits associated with large and small breeding sites overall.

Available breeding habitat is determined by the number of existing offshore rocks and islands present in a region, and competition for nest sites within a colony may be another important determinant of reproductive success and survival of murre facing aerial predation. One recent study found ocean conditions better predicted murre subcolony colonization at Tatoosh Island, WA, than any other demographic parameter including predation by raptors (Zador et al. 2009). This finding suggests more murre attempt to breed at this location when environmental conditions are favorable regardless of the presence of aerial predators such as Bald Eagles and Peregrine Falcons (*Falco peregrinus*) (Zador et al. 2009). It would be interesting to compare the number of breeding murre and site specific reproductive success at Tatoosh Island in Washington with breeding sites in regions of high, medium and low Bald Eagle density in Oregon.

In Oregon, the abundance of seabirds at breeding colonies likely provides an important food source for coastal eagle pairs raising young, but additional research on

eagle diets would be required to confirm this. If true, it follows that effects of chronic disturbance at seabird colonies, resulting from eagle predation would be most pronounced in regions with the highest density of these avian predators. Indeed, we found the largest decline in regional counts and mean number of common murre per breeding site, as well as substantial movement among breeding sites on the north coast, where Bald Eagle densities were highest. In regions of intermediate or low density of eagles, predator swamping may be effective in allowing the majority of breeding murre to produce offspring, while absorbing limited predation pressure. This is consistent with our findings on the central coast, which supported an intermediate density of Bald Eagle nests, and experienced significant growth in the number and size of occupied murre breeding sites. The number and size of occupied murre breeding sites remained consistent on the south coast, which had the lowest density of eagle nests in our study. Additional years of complete census information, and the amount of Common Murre reproductive loss associated with coastal Bald Eagles densities would be needed to better understand how colony size might ameliorate predation pressure. Unfortunately, annual nest monitoring of Bald Eagles ended in 2007, when the species was removed from the federal Endangered Species List (Isaacs and Anthony 2011).

Our study provides the first evidence of an association between a recently recovered, native, avian predator, and changes in the distribution and abundance of Common Murres in Oregon. These findings challenge strong site fidelity and natal philopatry of murre in regions with high densities of nesting eagles (Swann and Ramsay 1983, Harris et al. 1996, Ainley et al. 2002). Instead of remaining at the same colonies

year after year, murre in our study showed substantial movement among breeding sites and from the north to central coast region. Odds of site occupancy declined with increases in density of Bald Eagles on the north coast, and increases in size of breeding sites were most strongly associated with the initial number of murre counted and the density of eagles on the central coast. Intermediate to high densities of eagles appeared to be associated with where murre nested and how many individuals were present at particular sites, suggesting that a native, aerial predator has impacted the murre metapopulation in Oregon.

Eagle populations are expected to increase at least 2-3 fold before carrying capacity is reached in Oregon (Isaacs and Anthony 2011). When the eagle population does reach carrying capacity, density dependent mortality may be imminent because of reduced territory sizes and food availability, related to increased competition with conspecifics (Elliot et al. 2011). Interspecific interactions between eagles and murre may change as eagles approach carrying capacity and this would be an interesting avenue of continued research. If the statewide murre metapopulation declines, carrying capacity for eagles may be lower than current projections, particularly if other prey sources for eagles are also limited. In the Pacific Northwest, reduced populations of spawning salmon, may cause eagles to rely more heavily on waterfowl or seabirds at different times of year (Elliot et al. 2011), but prey switching is normal for eagles which are generalist predators. Winter surveys of seabirds do not indicate population declines (Elliot et al. 2011), so localized colony abandonment may be counterbalanced by movement away from areas with high Bald Eagle densities, as our study suggested.

Data limitations

We addressed active Bald Eagle nests in proximity to Common Murre colonies in coastal Oregon. We did not address the abundance of non-breeding adults, sub-adult, or juvenile eagles present on the landscape. Immature eagles from California move north into Oregon during the seabird breeding season (Linthicum 2007), and may impact Common Murre colonies. Investigating the impacts of sub-adult, non-breeding, failed breeding, or transient adult eagles would be an interesting area for future.

Additionally, Peregrine Falcon breeding habitat overlaps with murre and eagles on the coast. At least one study has shown peregrines can create protective nesting assemblages by precluding eagles from hunting seabird colonies through aggressive, territorial behavior (Quinn and Ueta 2008, Hipfner et al. 2011). Intraguild predation among raptor species occurs; eagles, for example, will consume peregrine chicks (Sergio and Hiraldo 2008). There are Peregrine Falcon eyries located near murre colonies which are also in close proximity to eagle nests in Oregon. Examining relationships between raptor species and their combined impacts (additive vs. compensatory) on Common Murres at breeding sites would be another interesting direction for future work.

Throughout our study, we relied on the assumption that proximity to eagle nests meant disturbance to murre colonies occurred. We suggested that secondary nest predators, such as gulls, likely expanded in the absence of eagles (Ritchie and Johnson 2009). Understanding potential synergistic effects of predators causing disturbance and those benefiting from disturbance is another important area for future research, and was

not possible to address with historic data. Actual study of the mechanisms of disturbance is necessary to quantify effects of predators, and is the subject of Chapter 3.

Counts of Common Murre index sites did not adequately track the two population censuses in 1988 and 2006 (Fig. 2.4), particularly on the north coast (Fig. 2.5a and b). We believe the omission of the Three Arch Rocks colony complex from yearly index counts prevented the index from representing the north coast and overall coast-wide murre population. The Three Arch Rocks colony complex is the largest murre breeding site on the north coast and the largest Common Murre breeding colony in Oregon. It accounted for 49-56% of north coast population, as well as 16-29% of the coast-wide population during census years. Since Three Arch Rocks is not included as an index site, but declined by more than 50% between census years, it appears to be the main driver of discrepancies in population change between index and census counts.

Scope of inference related to the index sites was limited to site specific trends in the number of breeding murres counted over two decades, and was not representative of the coast-wide murre population. If we are interested in coast-wide or regional Common Murre population trends from index counts, it may be more appropriate to use a “rotating panel design” instead of the current protocol (Urquhart et al. 1998). Currently, the same 23 index sites are counted annually, with up to an additional 13 sites counted and selected ad hoc each year. In a rotating panel design, rotational groups would be selected in advance, and different sites would be counted each year, until all breeding sites were counted once within a specified period (Urquhart et al. 1998). If 20-24 sites were counted

annually, this would enable biologists to create a population estimate every 5 years without increasing the current level of counting effort, based on a total of 108 murre breeding sites photographed annually. If resources allowed, a complete population census could be conducted every 10 years to check the accuracy of trend estimates from the rotating panel design. Time and resources saved could be used to increase monitoring of coastal Bald Eagle nests, or non-surface nesting seabirds, which are more difficult to survey.

Finally, if all murre breeding sites continue to be photographed annually during the peak nesting period, it would be useful to document presence or absence of murres at each location. This would enable scientists and managers to understand where colonies are abandoned or established from year to year, in order to direct research efforts on the drivers of these changes. Additionally, this information would allow modeling of presence or absence of murres at all possible breeding habitat in Oregon over time in relation to covariates including top-down and bottom-up effects. While Common Murre and Bald Eagle data are limited by lack of accounting for detection probability, these datasets provide the best available information over two decades of change in Oregon.

CONCLUSION

Bald Eagles are recently recovered, native avian predators that are currently abundant in coastal Oregon. Over 20 years of study, these raptors increased in number, and were associated with redistribution of Common Murres from areas of high regional eagle nest density to areas of lower eagle density, although our results are equivocal

because they were only demonstrated for the two census years and not the annual surveys of index sites. Our study is the first to address potential impacts of recovered Bald Eagles on seabirds over large spatial and temporal scales. As the Bald Eagle population continues to expand, researchers and managers should expect additional movement of murre among breeding sites in response to eagle predation pressure. To determine if the murre population is stable, increasing or declining, there are several ways to modify data collection or processing of existing data to accurately answer these questions.

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Table 2.1. Definitions and acronyms for covariates used to model Common Murre site occupancy and size during census years (1988 and 2006), and slope of index site size over time (1988-2006) on the Oregon coast.

Acronym	Definition
IntColSize	Initial Common Murre breeding site size from census counts conducted in 1988
RBDchg	Regional change in Bald Eagle nest density between 1988 and 2006
BAEA20km	Change in number of Bald Eagle nests within 20km of each murre breeding site between 1988 and 2006
BAEA15km	Change in number of Bald Eagle nests within 15km of each murre breeding site between 1988 and 2006
BAEA10km	Change in number of Bald Eagle nests within 10km of each murre breeding site between 1988 and 2006
BAEA5km	Change in number of Bald Eagle nests within 5km of each murre breeding site between 1988 and 2006
AVEDIST	Mean distance to nearest Bald Eagle nest for each index site over 19 year period

Table 2.2. Regional eagle nest density (#/km of shoreline), number of active Bald Eagle nests, and percent increase in the number of eagle nests in 1988 vs. 2006.

Region	Bald Eagle nest density (# of nests)		% increase
	1988	2006	
North	0.11 (9)	0.35 (28)	211%
Central	0.04 (4)	0.12 (13)	225%
South	0.01 (7)	0.03 (17)	143%

Table 2.3. Number of available Common Murre breeding sites in each region, number and percent of occupied murre breeding sites in 1988 and 2006 (census years) by region, and percent change in number of occupied Common Murre breeding sites between years.

Region	# of available breeding sites ^a	# of occupied breeding sites (% of available sites)		% change in # of occupied sites
		1988	2006	
North	43	32 (74%)	28 (65%)	-13%
Central	9	2 (22%)	9 (100%)	350%
South	36	33 (92%)	34 (94%)	3%

^a total number of occupied breeding sites used by Common Mures during census years

Table 2.4. Total number of Common Murres counted at breeding sites during complete censuses of the population in 1988 and 2006 on the north, central and south coast of Oregon. Associated mean and median number of murres counted in each year are also included, along with the percent change in regional counts of murres between census years.

Region	1988			2006			% change 1988-2006
	# Common Murre counted	Mean (standard error)	Median	# Common Murre counted	Mean (standard error)	Median	
North	212744 (range: 5-72170)	6447 (± 2352 SE)	1473	106980 (range: 7-24910)	3962 (± 1206)	901	-50%
Central	27864 (range: 13730-14130)	13932 (± 202 SE)	13932	56723 (range: 32-41450)	7090 (± 5077 SE)	1166	104%
South	173672 (range: 2-24320)	5427 (± 1262 SE)	2039	172636 (range: 137-28420)	5078 (± 1187 SE)	1504	-1%

Table 2.5. Model selection results for logistic regression analyses predicting the odds that murrees would occupy previously used breeding sites during 2006 (1=occupied, 0=unoccupied; n=88) in relation to initial Common Murre breeding site size, regional change in Bald Eagle nest density, and change in number of Bald Eagle nests within 5km, 10km, 15km and 20km of each murre breeding site. We used Akaike's information criteria adjusted for small sample size (AIC_c), including the difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c), AIC_c weights (w), model deviance (-2LogL), and the number of parameters (K) to evaluate each model. Single factor models were developed *a priori* and the intercept-only model is included for comparison. Covariate acronyms are provided in Table 2.1.

Model	AIC_c	ΔAIC_c	w	-2LogL	K
RBDchange	83.63	0.00	0.68	-38.67	3
BAEA10km	87.15	3.52	0.12	-41.50	2
BAEA20km	88.36	4.73	0.06	-42.11	2
BAEA15km	88.89	5.36	0.05	-42.37	2
IntColSize	89.17	5.54	0.04	-42.51	2
BAEA5km	89.59	5.96	0.03	-42.72	2
Null ^a	91.22	7.58	0.02	-44.58	1

^a Intercept only model for comparison.

Table 2.6. Model selection results for logistic regression analyses investigating whether the number of Common Murres counted would increase in 2006 vs. 1988, on the Oregon coast (1=increase, 0=decrease or no change; n=88) in relation to initial Common Murre breeding site size, regional change in Bald Eagle nest density, and change in number of Bald Eagle nests within 5km, 10km, 15km and 20km of each murre breeding site. We used Akaike's information criteria adjusted for small sample size (AICc), including the difference in AICc between each candidate model and the model with the lowest AICc value ($\Delta AICc$), AICc weights (w), model deviance (-2LogL), and the number of parameters (K) to evaluate each model. Single factor models were developed *a priori* and the intercept only model is included for comparison. See Table 2.1 for covariate acronyms, and Table 2,4 for model set information and definition of column headings.

Model	AIC _c	$\Delta AICc$	w	-2LogL	K
IntColSize + RBDchange	87.87	0.00	1	-39.69	4
IntColSize	101.11	13.24	0	-48.48	2
RBDchange	103.41	15.53	0	-48.56	3
Null ^a	113.61	25.73	0	-55.78	1
BAEA10km	114.40	26.53	0	-55.13	2
BAEA20km	114.95	27.08	0	-55.41	2
BAEA15km	115.28	27.41	0	-55.57	2
BAEA5km	115.70	27.83	0	-55.78	2

^a Intercept only model for comparison.

Table 2.7. Model selection results for linear regression analyses relating linear trends in index site size over time (1988-2006) to initial Common Murre breeding site size, regional change in Bald Eagle nest density, change in number of Bald Eagles within 5km, 10km, 15km, and 20km of each murre breeding site, and mean distance to nearest Bald Eagle nest for each index site on the Oregon coast (n=23). We used Akaike's information criteria adjusted for small sample size (AICc), including the difference in AICc between each candidate model and the model with the lowest AICc value ($\Delta AICc$), AICc weights (w), model deviance (-2LogL), and the number of parameters (K) to evaluate each model. Single-factor models were developed a priori and the intercept-only model is included for comparison. See Table 2.1 for covariate acronyms, and Table 2.4 for model set information and definition of column headings.

Model	AIC _c	ΔAIC_c	w	-2LogL	K
BAEA15km	343.33	0.00	0.25	-168.03	3
BAEA20km	343.60	0.27	0.47	-168.17	3
Null ^a	344.01	0.68	0.65	-169.70	2
BAEA10km	344.58	1.25	0.78	-168.66	3
AVEDIST	345.60	2.27	0.86	-169.17	3
BAEA5km	345.85	2.52	0.93	-169.29	3
IntColSize	346.61	3.28	0.98	-169.67	3
RBDchg	348.22	4.89	1.00	-169.00	4

^a Intercept only model for comparison.

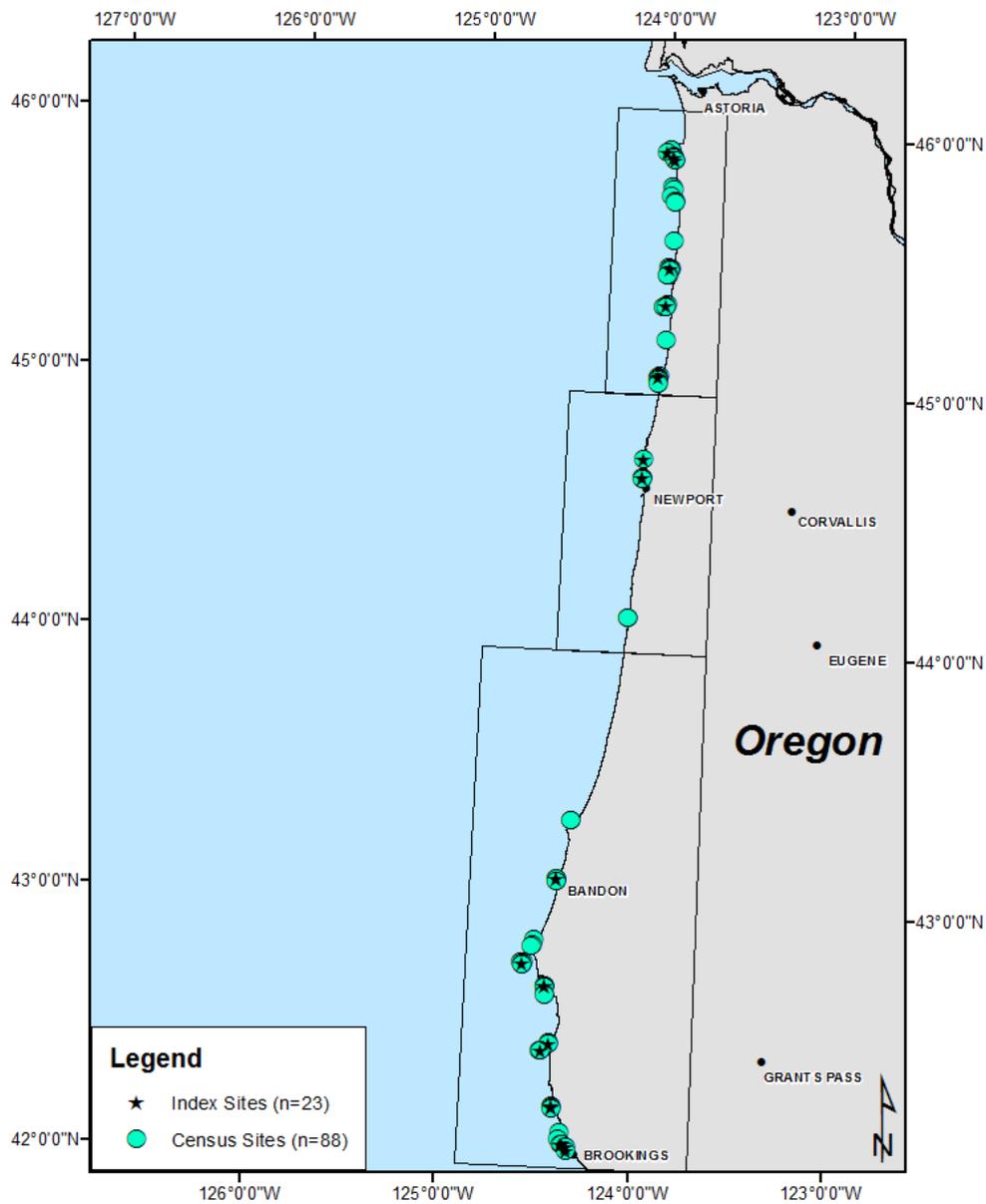


Figure 2.1. Map of Common Murre index sites (n=23) and census sites (n=88) along the Oregon coast with north, central and south coast regional designations. See methods section for description of census and index sites.

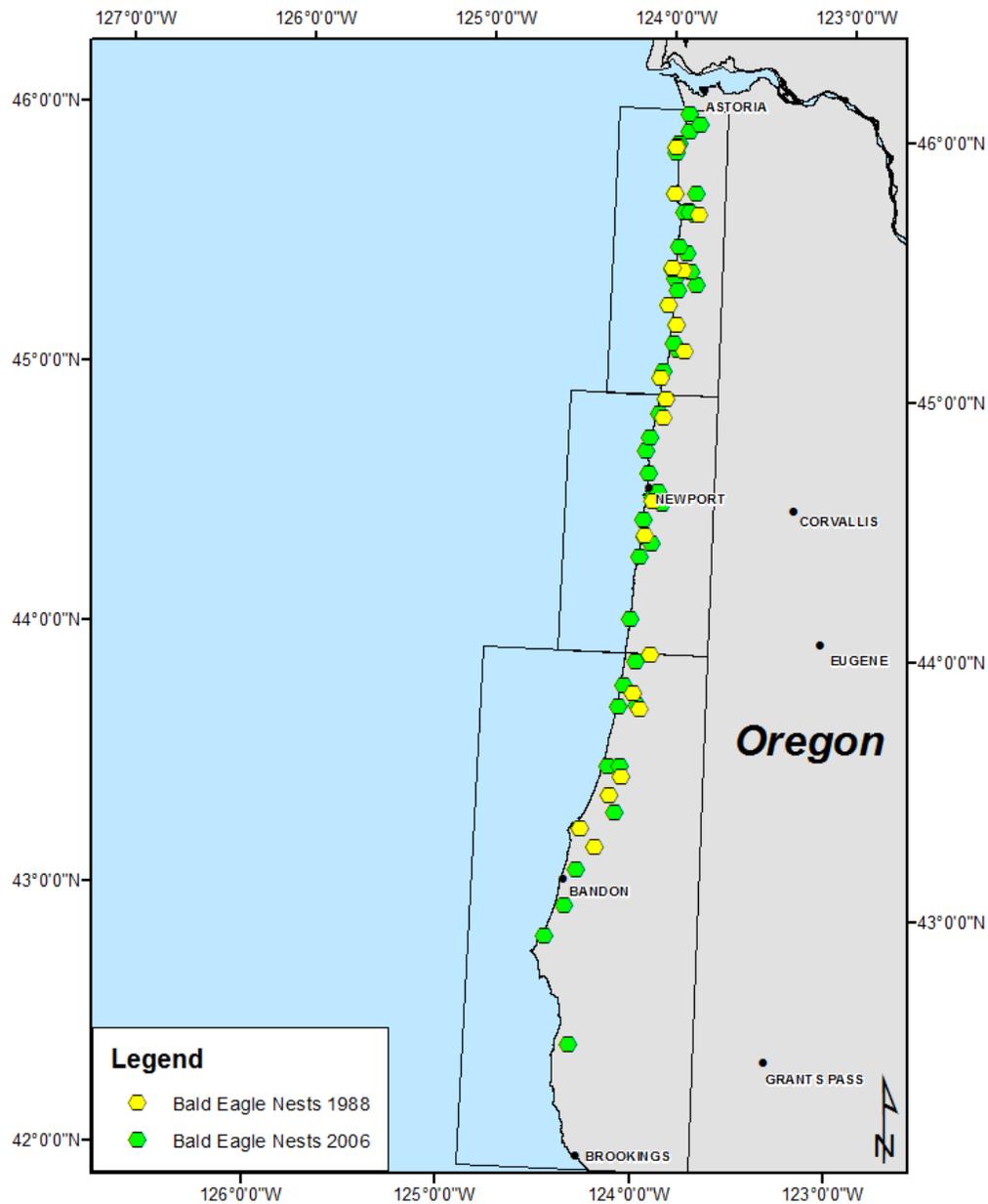


Figure 2.2. Map of all known, active Bald Eagle nest sites within 25km of shoreline in 1988 (n=20) and 2006 (n=58), with some sites occupied in both years.

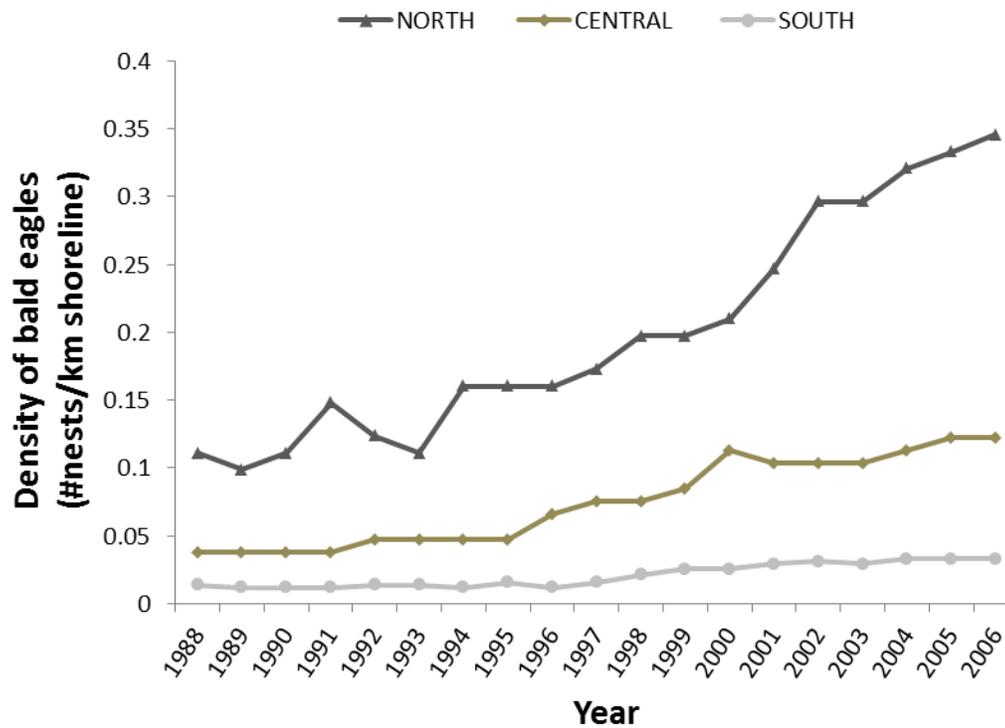


Figure 2.3. Regional density of Bald Eagle nests within 25km of shoreline in Oregon from 1988-2006.

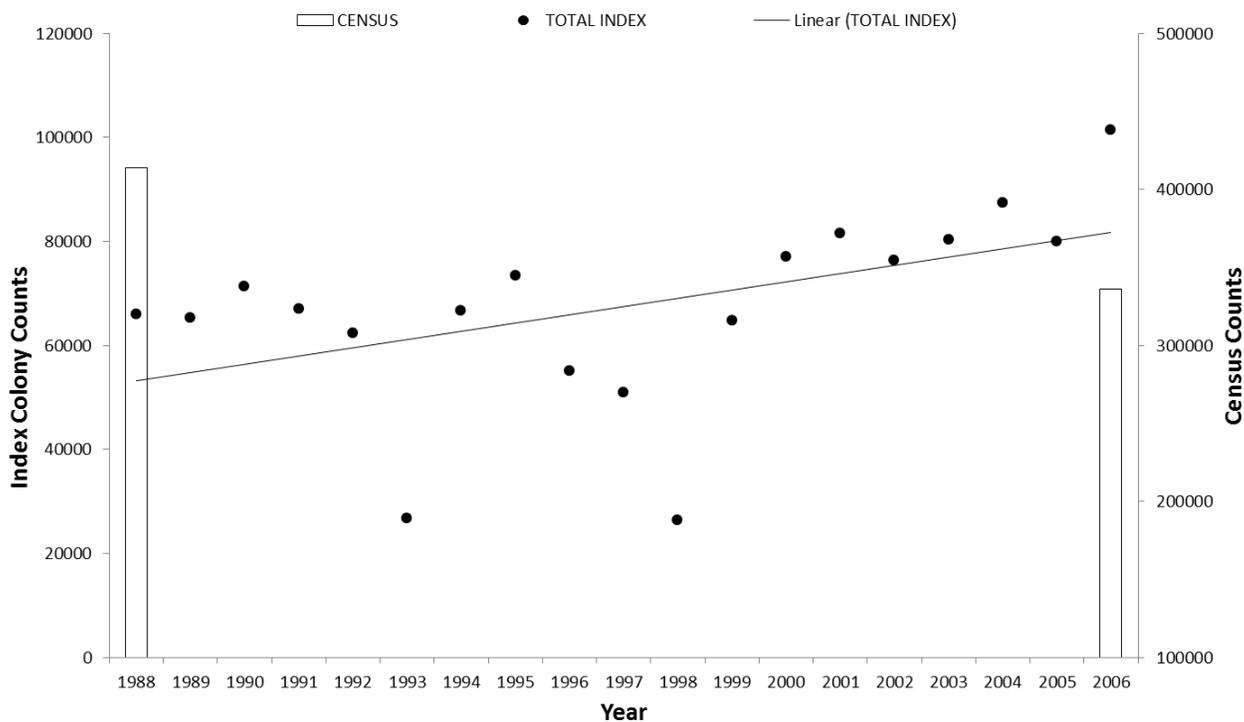


Figure 2.4. Annual Common Murre index site counts from 1988-2006 and census counts of all colonies in 1988 and 2006. Coast-wide, index sites show an increasing trend in the number of common murre counted over time ($R^2=0.19$, $p=0.04$, $n=19$, $df=1,17$), in contrast to the decline observed between census years at the beginning and end of this study (19%).

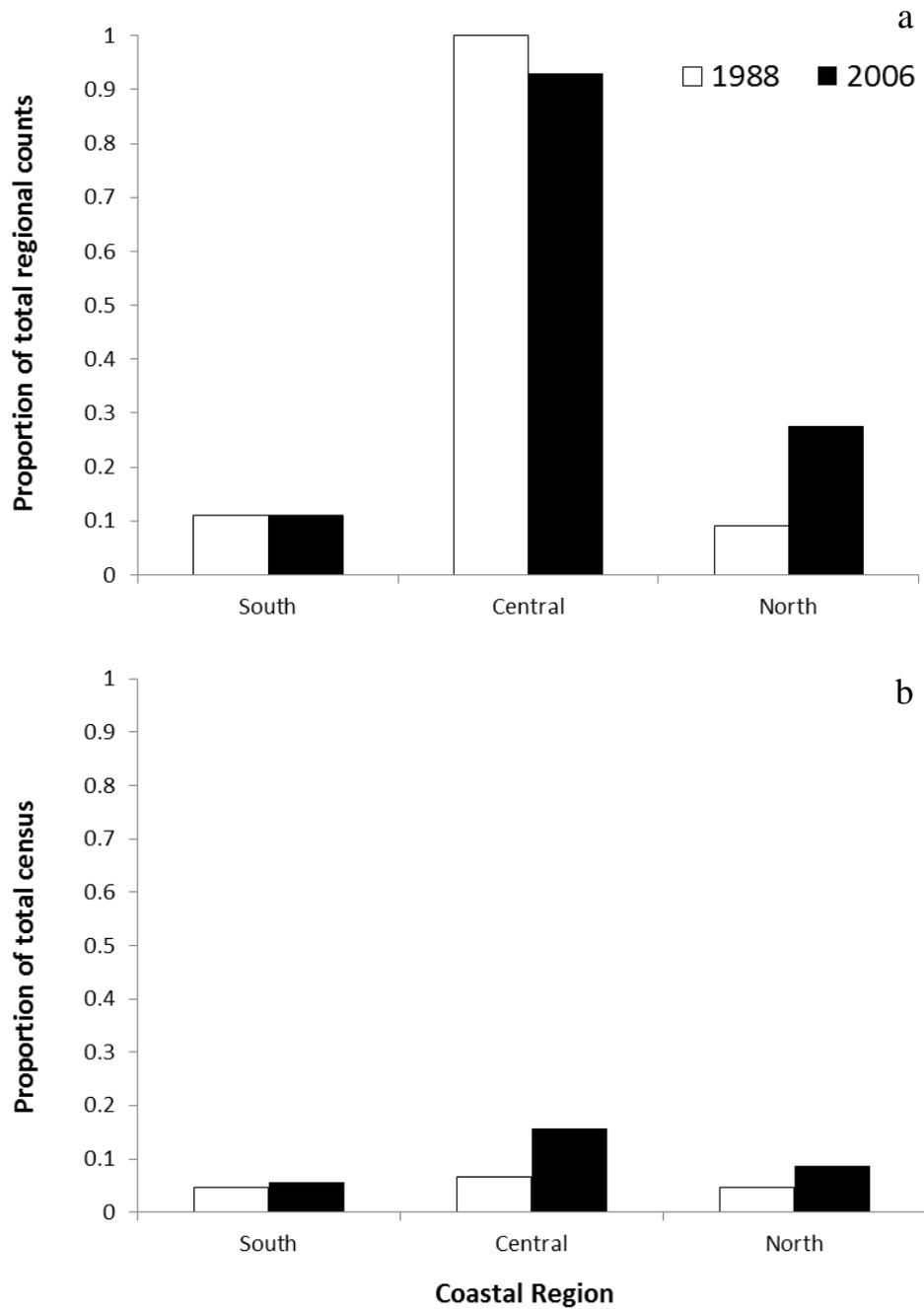


Figure 2.5a and 2.5b. The number of Common Murres counted at index sites by region as a proportion of the total regional counts of murres during census years 1988 and 2006 (a) and as a proportion of the total coast-wide census counts in 1988 and 2006 (b).

Chapter 3

SYNERGISTIC, TOP-DOWN PREDATION OF RECOVERING NATIVE AVIAN
PREDATORS AT SEABIRD COLONIES IN OREGON

Cheryl A. Horton, Robert M. Suryan, Katie M. Dugger, Amanda J. Gladics

ABSTRACT

Establishment of wildlife refuges, protection from hunting and egg collecting, and the decline in coastal Bald Eagles (*Haliaeetus leucocephalus*) during the early part of the 20th century, greatly reduced top-down pressure facilitating the expansion of Common Murre (*Uria aalge*) populations along the U.S. West Coast. Today, within the California Current ecosystem, Common Murres are the most abundance seabird species with an estimated population of 1.1 million breeding birds. The recovery of Bald Eagles in North America during the late 20th century is a conservation success story, but with widespread consequences for surface nesting seabirds. We investigated top-down impacts of recovered Bald Eagles on murre colonies, including mechanisms of disturbance and the extent of impacts from primary and secondary predators at three colonies along the Oregon coast in 2012 and one colony over seven years (2007-2013) on the central coast. In general, we found Bald Eagles were the main predators causing disturbance at breeding sites studied and there was no difference in reproductive loss between disturbances caused by adult and sub-adult eagles. Secondary nest predators (gulls, corvids, and vultures) caused greater reproductive loss compared to primary predators such as Bald Eagles. From 2007-2013, we found a negative correlation between mean reproductive success and mean rate of Bald Eagle disturbance. We found differences in disturbance frequency, colony disruption, and predator activity among three sites in regions of high, medium and low Bald Eagle abundance on the Oregon coast. Eagles were most abundant and caused complete reproductive failure at the north coast colony and were least abundant, causing minimal reproductive loss at the south coast colony.

During late chick-rearing in 2012, California Brown Pelicans (*Pelecanus occidentalis*) caused disturbances at the central and south coast sites, leading to low murre reproductive success. Our observations provide strong evidence for top-down regulation of local breeding populations of Common Murres in Oregon, mediated by recently recovered native, avian predators. As the Bald Eagle population continues to expand southward, scientists and managers on the U.S. West Coast should expect disturbance at more Common Murre colonies in the future, particularly in years when alternative prey is limited for eagles or pelicans.

INTRODUCTION

Within the field of community ecology, it is generally recognized that both bottom-up (environment or resource driven) and top-down (predator driven) effects can simultaneously or alternatively influence populations of organisms within biological communities (Hunt and McKinnell 2006). New questions focus on disentangling the relative importance of these factors at various life stages and scales, as well as understanding how these factors work together (Munch et al. 2005, Suryan et al. 2009). Most seabird research has focused on bottom-up factors, including those influencing prey availability or quality, and subsequent linkages to population level responses such as reproductive success at individual colonies (Ainley et al. 1995, Ainley et al. 2005, Wanless et al. 2005). While it is important to understand bottom-up drivers, we must also consider top-down effects resulting from human disturbance (Schauer and Murphy 1996, Wheeler et al. 2009), invasive predators (Wanless et al. 2007, Jones et al. 2008), native mammalian predators (Ainley et al. 2005), and more recently, recovery of native, avian predators (Watts et al. 2007, Kruger et al. 2010, Hipfner et al. 2012). Complex interactions at seabird breeding colonies require additional attention and in regions where bottom-up impacts are well understood, top-down effects should be studied in equal measure to allow a more complete understanding of the factors regulating populations in our changing world (Collar 2013).

The recovery of Bald Eagles (*Haliaeetus leucocephalus*) in North America during the late 20th century is a conservation success story, but with widespread consequences for surface nesting seabirds (Hipfner et al. 2011, Hipfner et al. 2012). As generalist

predators, eagles exploit seasonally abundant prey sources, and in coastal regions hunt seabirds at breeding colonies (Todd et al. 1982, Hayward et al. 2010, Elliott et al. 2011). While hunting the colonies for adult birds, eagles disrupt seabird breeding activities causing some or all adult seabirds to leave breeding sites to avoid predation (Parrish et al. 2001). During colony disturbance, seabirds may experience direct (consumptive or lethal) effects of primary predators and secondary nest predators, as well as indirect (non-consumptive or non-lethal) effects of predation (Paine et al. 1990, Parrish et al. 2001, Cresswell 2010).

Colony evacuation in response to a predator is one of the most obvious indirect effects during a disturbance. There are several costs when adult breeding birds flush from nest sites to avoid predators, including: increased stress levels and energy expenditure, reproductive loss through predation or scavenging, breakage of eggs, heating, cooling or displacement of eggs or chicks, and asynchrony in laying and hatch dates, which may reduce some of the benefits of predator swamping at large colonies (Murphy and Schauer 1996, White et al. 2006, Reed et al. 2009). Additionally, the combination of primary and secondary nest predators may have synergistic effects leading to more costly lethal consequences than either type of predation alone (Hixon and Carr 1997). Primary predators cause colony evacuation and facilitate access to secondary nest predators, thereby creating strong potential for synergistic effects (Schauer and Murphy 1996).

While some aspects of predation at seabird colonies are well studied, there remains a pressing need to address the impacts of native, avian predators, particularly in

regions where sea eagle populations have rebounded in recent years, such as the West Coast of North America (Isaacs and Anthony 2011, Hipfner et al. 2012). Within the California Current ecosystem, Common Murres (*Uria aalge*) are the most abundant seabird species with an estimated population of 1.1 million breeding birds (Manuwal et al. 2001). Two thirds of these birds nest off the coast of Oregon where breeding habitat is protected from human disturbance as part of Oregon Islands National Wildlife Refuge Complex (Naughton et al. 2007). Murres are long-lived, pursuit-diving, colonial nesting seabirds that lay a single egg each season (Moody et al. 2004, Regular et al. 2010). With the establishment of wildlife refuges, protection from hunting and egg collecting, and the decline in coastal Bald Eagles during the early part of the 20th century, murres experienced relatively little predation or disturbance at breeding colonies and it is likely their populations increased during this time period (Parrish 1995, Regular et al. 2010).

Bald Eagles were protected under the Endangered Species Act in 1978, after which the eagle population increased by ~7% annually in Oregon, with adults filling available breeding territories along major rivers and the coast (Isaacs and Anthony 2011). The Bald Eagle breeding season peaks from March through June and chick provisioning for eagles overlaps with the return of murres to coastal breeding habitats in Oregon (Isaacs et al. 1983, Elliott et al. 2011). In 1994, the first Bald Eagle disturbance to a murre colony was recorded within the state (Manuwal et al. 2001). Bald Eagles were removed from the U.S. Endangered Species List in 2007 and the State of Oregon Endangered Species List in 2012 (USDOJ 2007, ODFW 2012). Bald Eagles are once again numerous in Oregon where some projections estimate another 2-3 fold increase

before carrying capacity is achieved (Isaacs and Anthony 2011). With this in mind, it is reasonable to expect a concurrent increase in the impacts of these predators at murre colonies on the coast.

This situation in Oregon provides an excellent opportunity to study top-down impacts of Bald Eagles on murre colonies. We investigated the mechanisms of disturbance by eagles at murre colonies, and the extent of impacts from primary and secondary predators in regions of high, intermediate and low eagle abundance along the Oregon coast. We tested for differences in the frequency of disturbances, length of disturbance, and extent of colony evacuation among sites in a single year. We also compared the amount of murre adult, egg and chick loss attributable to primary and secondary predators, and the composition of predator assemblages among sites. Finally, we tested for differences among years, predator age classes, predator species assemblages, and correlations between murre reproductive success and predation rate over time.

METHODS

Study area

We studied Common Murre breeding colonies in three geographic regions all within 1km from the Oregon coastline including: 1) a site on the north coast at Cape Meares State Scenic Viewpoint (45° 29'22" N, 123° 58'47"W), 2) a site on the central coast at Yaquina Head Outstanding Natural Area in Newport, Oregon (40°40'30" N, 124°04'35" W), and 3) a site on the south coast at Coquille Point in Bandon, Oregon

(43°6'50"N, 124°26'7"W). Estimates of breeding population size for each study site were based on direct counts of aerial photographs taken during the breeding season (Naughton et al. 2007). Each of these colonies had one or more documented Bald Eagle nest site within 10km and experienced eagle predation during previous seasons. Regionally, however, Bald Eagle populations were larger on the north coast and smaller on the south coast (Isaacs and Anthony 2011). We used a combination of video monitoring and human observations to collect data at each site.

The north coast site adjacent to the headland at Cape Meares, known as Pillar Rock, (hereafter "Cape Meares" or "north coast") had ~13,000 nesting murrelets in 2006 (Naughton et al. 2007). Observation points on the headland's public viewing decks were ~350-500m from the colony. Additionally, a remote video camera was installed in a forested area on the headland, ~350m from Pillar Rock.

On the central coast at Yaquina Head, two sub-colonies, Flat Top and Colony Rock, were used for data collection. Breeding populations at Flat Top and Colony Rock (hereafter "Yaquina Head" or "central coast") totaled ~38,000 Common Murrelets in 2012 (Flat Top = 13,000; Colony Rock = 25,000) (Naughton et al. 2007). Observation points on public viewing decks at ground level and the lighthouse gallery deck (25m above ground) were ~100-150m from breeding murrelets. A remote camera at ground level on the edge of the headland collected video data of Colony Rock, at a distance of ~100m. At this site, we also utilized a seven year data series spanning 2007-2013 including reproductive success estimates for murrelets and predation events collected by observers. Reproductive

data were collected 3-5 days a week between 2007 and 2009, and 5 days a week from 2010-2013. We calculated hourly rates of disturbance for comparisons among years.

At the south coast site, North Coquille Point Rock, off Coquille Point, was used for data collection. This sub-colony, (hereafter “Coquille Point” or “south coast”) supported ~8,000 murrelets in 2006 (Naughton et al. 2007). Observation points along a public trail were ~400-500m from this sub-colony. We installed a remote camera 500m from the sub-colony in a stand of shore pines (*Pinus contorta*) on private land to collect digital video of nesting murrelets.

Video camera set-up and management

We installed remote operating IQeye 7.55 box-cameras with adjustable SL940M 10-40mm Zeiss lenses at all three research sites. Cameras were positioned to record the entire length of the shore-facing side and top of each sub-colony. Video was recorded at 1 frame per second from 0500-2200 hrs from April 26-August 8, 2012. Gaps in video coverage occurred due to poor visibility from temporary weather conditions, like fog and low clouds, heavy rain and afternoon glare, and also during maintenance activity. We did not record video for two weeks in May at the north coast site because of user error, and for two to four days at all sites in June during a mid-season performance check. Video images were stored on 32 GB Compact Flash (CF) cards in each camera.

Cameras were encapsulated in aluminum alloy security housings (Videotec VAHB 30-1 IP66 rated) with internal heater and fan to maintain optimal temperature. Silica gel packs were also used inside the housings to absorb excess moisture and were

changed periodically throughout the season. We mounted camera housings to 4 X 4 in pressure treated wooden posts and in one case, to the branch of a tree. Each camera was powered by a 12 volt marine deep cycle battery, connected through a power converter (model AIR802 PDCPOE1248DR) using 12 gauge wire and a Cat5e cable. Batteries and power converters were protected from the weather in plastic locking containers.

We performed camera maintenance and data download every 2-4 days. General maintenance included checking battery power and switching batteries if needed, changing CF cards, and checking the position and settings of the camera. In the lab, we exported the stored video from a proprietary format on the CF cards into a viewable .avi file format in 4 hr blocks (range 2-6 hrs per file) using IQMediaPlayer software. After exporting, each file was immediately checked for completeness in Quicktime Player to avoid saving corrupt files.

Trained technicians manually reviewed and cataloged all video files in the lab, using Quicktime Player or VLC Media Player software. When reviewing a typical 4 hr video file, technicians recorded the length in minutes (greater than 1 min), for every instance when the colony could not be seen. These poor visibility periods were totaled and subtracted from the total length of the video file. This allowed us to keep track of the total hours of video recorded, and the number of usable hours from that total. We summarized the total number of usable hours of video by day, month and season at each site and overall. In total, we recorded 3,500 hours of video during the 2012 season (April-August), of which 3,350 hours were usable for cataloging disturbance events (150 hours

were lost to poor visibility). This dataset was paired down further using additional criteria described in the “Data Treatment and Statistical Analysis” section below.

Video data description: metrics of disturbance

We used video images of one sub-colony at each site ($n=3$) to determine the number and cause of disturbances, disturbance rate (number of disturbances/hr), degree of colony evacuation per disturbance (0-100% cleared), and length of each disturbance (min). These metrics were summarized for all primary predators, and for disturbances caused by Bald Eagles alone. We also documented primary predator use, i.e. “predator presence”, of these areas when Common Murres were not on the breeding site. This metric served as a proxy for primary predator activity that prevented Common Murres from attending breeding sites. We originally expected “predator presence” would be important during the early season, before murres settled on colonies or laid eggs. If murres were not attending breeding sites, disturbances could not occur. Therefore, “disturbance” refers to predator presence events when Common Murre were on the breeding site and evacuated as a result of predator activity. There were no recorded instances of predator activity in the presence of murres, when murres did not evacuate the breeding site.

We calculated mean disturbance rate (or frequency) as the number of disturbances per usable hour of video, at each site over the entire season ($n=3$), and for May, June and July at each site ($n=3$ per month). We defined a disturbance as the period of time when 50 or more adult Common Murres evacuated together from the breeding site, until at least

80% of the vacated area of the colony was covered with returning birds. The use of 80% as the recovery criteria accounted for some individuals that would not immediately return to the colony following a disturbance, for example a roosting bird not engaged in incubation or chick-rearing duties that remained on the water or left on a foraging trip. For each disturbance, we also recorded the maximum percentage of the surface of the colony that cleared (“percent cleared,” 0-100%) and the type of primary predator that caused the disturbance.

We also documented predator presence (over-flight or roosting) at the colony when Common Murres were absent from breeding sites, and classified these as the number of “presence events” per day. A day was defined as 10 or more hours of usable video on a particular date. We also aggregated the number of disturbances per day, in order to compare the proportion of days when at least one predator presence or disturbance event occurred at each colony over the entire season and by month (May, June and July) in 2012. These daily summaries were calculated for all disturbances, regardless of primary predator type. All cataloged video data were recorded in standardized Microsoft Excel spreadsheets.

Observational data collection

In conjunction with cameras, trained observers collected detailed predation data at all three study sites (April 16-July 23, 2012). Observers viewed the same breeding sites as the cameras except on the central coast, where observers viewed all sub-colonies, in addition to the single sub-colony within view of the camera. Observers used high-

powered scopes (Nikon Prostaff and Vortex Viper 20-60X80 spotting scopes, Questar AP 89mm Focal Length telescope) and binoculars (Vortex Diamondback10X42), to view disturbance events at each site. We were able to capture some different information through observation than with video cameras, thus observer and video datasets were used to address separate objectives and hypotheses.

Observational data description: predation processes and reproductive success

Predation observation periods were generally five hours per day (range 2-7 hrs) occurring between sunrise and sunset, at least four days per week. Each week, the total observation period covered the equivalent of one full-daylight period (range: 13-17 hrs) based on sunrise and sunset times for each location. During observation periods, we documented disturbance events, along with primary and secondary predation at each site. Instances of predator presence were also recorded at each site in the same manner stated for video data collection above.

Species causing disturbances were classified as primary predators because these individuals initiated the event while hunting the murre colony. Secondary predators were those who arrived after primary predators and benefitted from the disturbance by consuming unattended murre eggs and chicks. Observers classified Bald Eagles causing disturbances as adult or sub-adult, based on plumage characteristics (McCollough 1989). During each disturbance, we watched primary predator(s) and counted number of murre eggs, chicks and adults consumed, carried off or otherwise killed. Observers also documented the suite of secondary nest predators and counted the number of each species

that landed on the cleared areas of the colony during each disturbance, recording a maximum count of each species per event. We also counted number of eggs and chicks consumed, killed or otherwise removed by secondary predators to document the amount of murre reproductive loss during each disturbance event. This detailed information about the number, age class and effect of primary and secondary predators was not possible to collect using video data.

In addition to observing disturbances, we also monitored reproductive success of murrelets at all three sites in 2012. At each colony we photographed and mapped 5-12 plots and used these to follow 10-25 pairs of murrelets per plot throughout the season (up to 211 total pairs per site). At least five mornings per week, we spent 2-8 hours observing reproductive plots. We recorded the first day an egg was observed for each pair, and followed the success of selected pairs through incubation and chick rearing. Murrelet chicks begin leaving natal sites at 15 days old therefore chicks reaching at least 15 days of age were considered old enough to successfully fledge (Ainley et al. 2002). Reproductive success at each site was calculated by averaging the proportion of pairs that raised chicks to fledging age among plots. We used median hatch date to measure breeding phenology across sites and at Yaquina Head, among years.

We also used reproductive success estimates and predation observations from a single site, Yaquina Head on the central coast from 2007-2013 in our analyses. From 2007-2010 and in 2013, predation data were collected only during reproductive plot monitoring. In 2011 dedicated predation watches were used for predation data collection,

as described for observer data collection in 2012. The same parameters were collected over the entire time period.

Data treatment and statistical analysis

All statistical analyses were conducted in R version 3.0.1. We tested the null hypothesis that the relative frequencies of disturbance causes were the same for both video and observational datasets using contingency table analysis and Pearson's chi-square statistic.

The video dataset was used to investigate regional differences in the effects of disturbances caused by all predators, and Bald Eagles alone, in 2012. We used video from May-July, the time period of complete overlap for the three sites, for a total of 3155 hours over 207 days, including: 937 hrs over 63 days on the north coast, 1055 hrs over 71 days on the central coast, and 1163 hrs over 73 days on the south coast. We used Kruskal-Wallis (when assumptions for parametric statistics were violated) and Analysis of Variance (ANOVA) with log-transformation, to test the hypotheses that the mean rank of disturbance frequency and the mean length of disturbance, respectively, would be greatest at the north coast where there were more eagles in 2012. We calculated mean disturbance frequency and mean disturbance length among sites ($n=3$) for disturbances caused by all predators ($n=279$ events) and Bald Eagles alone ($n=220$ events). Next, we grouped counts of disturbances into bins based on 25% increments (from 0-100%) in the percent of colony evacuation (PClear) among sites and used contingency table analysis and Pearson's chi-square statistic to test for differences. We also compared the proportion

of video days during which at least one predator presence event or disturbance event occurred, for all primary predators types, at each site over the entire season ($n=3$) and by month ($n=3$ per month).

Data collected by human observers were used to investigate specific processes associated with Bald Eagle predation at the central coast site (Yaquina Head) during June and July of 2011, 2012 and 2013. We included observational data from the central coast site only, because this colony was the closest and most easily viewable. It therefore allowed reliable data collection of reproductive loss attributable to both primary and secondary predators in multiple years. We tested the hypothesis that mean reproductive loss (Common Murre eggs and chicks killed) attributable to secondary nest predators would be greater than mean loss (Common Murre adults, eggs and chicks killed) attributable to Bald Eagles per disturbance in each year using ANOVA. The dataset included 138 eagle induced disturbances, including: 80 events in 2011, 27 events in 2012, and 31 events in 2013. Only disturbances from June and July, when murre eggs and chicks were present on breeding sites were included because this is the only time period when reproductive loss from secondary nest predators may occur.

Using the same observational data from the central coast, we were interested in potential causal factors leading to reproductive loss (number of Common Murre eggs and chicks killed by secondary predators), during disturbance events initiated by Bald Eagles. Based on observations and literature, we assumed sub-adult eagles would make multiple approaches to the murre colony during hunting attempts, thereby causing longer duration

disturbances and greater colony clearance when compared to adult eagles (Buchanan and Watson 2010). We hypothesized that eagle age and other variables would impact reproductive loss during disturbance events. To test these hypotheses, we developed two approaches.

In the first approach, we grouped all eagle disturbances regardless of whether or not reproductive loss occurred and used package “stats” in R to create seven, single factor binomial logistic regression models. These *a priori* models were designed to test the strength of association between single predictor variables, and the response “odds reproductive loss occurred (1) vs. did not occur (0).” Each single factor model included one of the following covariates: Bald Eagle age (adult or sub-adult; BAEAage), length of each disturbance (min; DLength), percent of colony cleared per disturbance (0-100%; PClear), year (2011, 2012, 2013), Julian day, and median time of each disturbance event. An intercept only model was also included for comparison.

In the second approach, we modeled the number of eggs and chicks killed by secondary predators as a continuous response variable for Bald Eagle disturbance events when reproductive loss was known to occur. We again used package “stats” in R to create seven, single factor models, this time using simple linear regression. These single factor models included the same covariates listed above. We log-transformed the response variable, “number of eggs and chicks killed by secondary predators,” to meet the assumptions of linear regression. For both of these analyses, we ranked models according to Akaike’s information criterion adjusted for small sample size (AIC_c) using package

“AICcmodavg” in R (Burnham and Anderson 2002). We used an information-theoretic approach including differences in model AIC_c compared to models with lowest AIC_c (ΔAIC_c), AIC_c weights (w), and model coefficients (betas: β) to determine strength of evidence for specific effects predicted to impact Common Murre reproductive loss (Burnham and Anderson 2002). We evaluated competing models ($\Delta AIC_c < 2$) using 95% confidence intervals, and if 95% confidence limits on >1 covariate did not overlap zero suggesting a strong effect; we created two-factor models for additional consideration via model selection results.

Using observational data from 2007-2010 collected at Yaquina Head, we compared the proportion of Bald Eagle disturbances that occurred in May, June and July over time. We also used simple linear regression to test for associations between mean disturbance rate and reproductive success in each year over this time period ($n=7$). Finally, we compared mean reproductive success estimates for each site studied in 2012 ($n=3$).

RESULTS

Causes of disturbance

We classified the cause of each disturbance detected in video and observational data into six categories: 1) Bald Eagle, 2) California Brown Pelican (*Pelecanus occidentalis*), 3) Turkey Vulture (*Cathartes aura*), 4) Peregrine Falcon (*Falco peregrinus*), 5) other, and 6) unknown (Fig. 3.1). These causes of disturbance were similar at research sites on the north, central and south coast of Oregon in 2012. Out of

all individual disturbance events recorded, both observer and video data indicated the greatest number of disturbances were caused by Bald Eagles (video 0.55, $n=453$, observer 0.54, $n=226$; Fig. 3.1). We found differences in the relative proportion of all six disturbance sources detected from video and observer data (Pearson chi-square = 55.19 (5), $P < 0.001$). For example, disturbances with unknown causes were four times more numerous in video data, compared to observer data. Conversely, we found double the number of disturbances in the “other” category for observer vs. video data. We therefore removed disturbances with unknown causes from both datasets and further analyses. We used observer and video datasets containing only data where disturbance cause was known to address separate questions and hypotheses.

We used video data to compare disturbance metrics including: disturbance rate (number of disturbance events/hr), daily predator activity (number of days when at least one predator presence or disturbance event occurred), percent of colony cleared (0-100%), and length of disturbance (minutes/disturbance event) among sites during the 2012 breeding season. Data from observers were used to investigate differences in the effects of primary and secondary predators, and the effects of eagles by age class at the central coast site from 2011-2013. We also used observer data to compare differences in mean reproductive success among sites in 2012, and among years at the central coast site from 2007-2013.

Metrics of disturbance

The mean video disturbance rate (disturbance/hr) from all primary predators and Bald Eagles alone were an order of magnitude greater on the north (0.12/hr all primary predators; 0.10/hr Bald Eagles only) and central (0.15/hr all primary predators; 0.11/hr Bald Eagles only) coast sites, compared to the south coast site (0.01/hr all primary predators; 0.002/hr Bald Eagles only), in 2012 ($H=64.4942$, 2 df, $P < 0.001$ and $H=64.5118$, 2 df, $P < 0.001$ for primary predators and Bald Eagles, respectively; Table 3.1).

Length of Bald Eagle disturbances from video data ranged from ~1 minute to 900 minutes (15 hrs) per disturbance event at our study sites. We found the overall mean length of a Bald Eagle disturbance event was 114.6 minutes (1.91 hrs, SE 0.18), and mean disturbance length by site was: 112.8 minutes (1.88 hrs, SE 0.27) on the north coast, 118.2 minutes (1.97 hrs, SE 0.25) on the central coast, and 22.2 minutes (0.37 hr, SE 0.09) on the south coast (Table 3.1). An ANOVA on log-transformed DLength, did not find a significant difference among means at these three sites in 2012 ($F_{2, 280}=0.8$, $P = 0.45$ all primary predators, $F_{2, 216}=2.06$, $P = 0.13$ Bald Eagles).

Colony evacuation was most pronounced in video data from the north coast, where Bald Eagle disturbances cleared 76-100% of the colony during 89 out of 91 events (Pearson chi-square = 215.4079 (6), $P < 0.001$; Fig. 3.2). On the central coast, only 1 out of 125 events cleared 76-100% of the colony. At this site, 64.8% of eagle disturbances cleared only small percentages of the colony (1-25%), in direct contrast to our

observations on the north coast. On the south coast very little of the colony was cleared and disturbances were much lower than on the north or central coast.

Overall, the north coast site experienced the greatest amount of predator activity, regardless of whether or not murrees were attending this colony (Fig. 3.3). At the north coast site, predator presence when murrees were not attending the breeding colony and disturbances occurred on 38% and 56% of video collection days ($n=63$ days) respectively. Presence and disturbance days were not mutually exclusive. For example, murrees may have been absent from the breeding colony from dawn through noon, and during this period eagles may have flown over or landed on the breeding site. Later during the same day, murrees may have landed on the breeding site, after which eagles caused disturbance clearing all or a portion of the site. In this case, the same day would count as one disturbance day and one predator presence day. On average, the north coast had 1.73 (SE 0.27) disturbances per video day, and 1.63 (SE 0.38) predator presence events per video day from May –July 2012. In total, at least one instance of predator disturbance or presence occurred on 80% of video days at the north coast site.

When looking at these differences by month, the north coast site experienced more days during which predators were active in the absence of murrees, than days when murrees were on colony and predators caused disturbances in May and June (Fig. 3.4). In July, this finding reversed, with more disturbance days and fewer predator presence days (Fig. 3.4). At the central coast site, we observed only one instance of predator presence, before murrees had settled on the colony in May. We documented disturbances on 75% of

video days at this site, with an average of 2.27 (SE 0.22) disturbances per video day from May-July 2012. Results for the north and central coast contrasted sharply with the south coast, which experienced disturbance on only 9% of video days for an average of 0.12 (SE 0.04) disturbances per video day, and zero instances of predator presence while murre were absent

Primary and secondary predators

We defined primary predators as species that caused disturbance while hunting Common Murres at breeding colonies. Using observer data collected at the central coast site from 2011-2013, we classified primary predators into five categories: 1) Bald Eagle, 2) California Brown Pelican, 3) Turkey Vulture, 4) Peregrine Falcon, and 5) other. Bald Eagles and Peregrine Falcons were the only primary predator species that actively hunted and consumed adult Common Murres. Some eagles also consumed murre eggs and chicks. All other primary predators consumed Common Murre eggs and chicks, after causing disturbance during arrival on the colony.

We defined secondary predators as species that arrived at and landed on the Common Murre breeding colony after primary predators initiated a disturbance and created some cleared areas of the colony. Secondary predators benefitted from disturbances by gaining access to unprotected murre eggs and chicks, and were classified into three categories: 1) gulls, mainly Western Gulls (*Larus occidentalis*), 2) corvids including Common Ravens (*Corvus corax*) and American Crows (*Corvus brachyrhynchos*), and 3) Turkey Vultures. We observed secondary predators consuming

Common Murre eggs and chicks, as well as fish remains on the colony. Turkey Vultures scavenged carcasses of murre adults and chicks, and consumed eggs and fish remains.

Certain species or taxonomic groups were classified as both primary and secondary predators, depending on their behavior during a disturbance event. For example, we classified a Turkey Vulture flying over a colony as a primary predator if it initiated a disturbance. Additional Turkey Vultures, gulls and corvids that arrived after adult murrees evacuated from the colony were classified as secondary predators.

Since Bald Eagles caused the majority of disturbance events, we compared the average number of Common Murre adults, eggs and chicks taken by eagles, to the average number of murre eggs and chicks consumed by secondary predators per disturbance event at the central coast site in each year: 2011 (primary predator mean # killed: 0.74, SE 0.1; secondary predator mean # killed: 6, SE 1.6), 2012 (primary predator mean # killed: 0.85, SE 0.26; secondary predator mean # killed: 5.7, SE 2.6), and 2013 (primary predator mean # killed: 0.32, SE 0.09; secondary predator mean # killed: 3.8, SE 1.8). We found no differences between loss attributable to primary predators ($F_{1,136}=0.577$, $P = 0.08$) among years and no difference in loss attributable to secondary predators ($F_{1,136}=0.577$, $P = 0.45$) among years. Therefore, we pooled data for all years (2011-2013) and found that on average, secondary predators were responsible for five times more Common Murre egg and chick mortality (5.5, SE 1.1) than Bald Eagles (0.67, SE 0.83) at the central coast site ($F_{1,274}=18.47$, $P < 0.001$).

From 2007-2013, the suite of primary predators causing disturbance at the central coast site increased to include Turkey Vultures and juvenile California Brown Pelicans. Percent of disturbances initiated by Bald Eagles declined, from 83% ($n=61$) during 2007-2009, to 65% ($n=506$) during 2010-2013, although the total number of disturbances increased dramatically between these time periods, (from 61 observed disturbances during 2007-2009 to 506 observed disturbances during 2010-2013). During the later period, turkey vultures initiated 11% and juvenile California Brown Pelicans initiated 14% of all disturbances ($n=506$). The suite of secondary predators also expanded to include Turkey Vultures over this seven year time period.

We observed secondary predators taking only eggs during 2007-2009, but both eggs and chicks during 2010-2013. This corresponded with a shift in the proportion of disturbances we observed during each month over time. From 2007-2009, the greatest proportion of disturbances occurred in June each year (Fig. 3.5). In contrast, from 2010-2013, the majority of disturbances occurred in June and July when chicks were present on the colony (Fig. 3.5).

Predicting Common Murre reproductive loss

We used AIC_c model selection to determine the covariate with the strongest support suggesting an association with the odds that reproductive loss would occur during Bald Eagle induced disturbance events at the central coast site from 2011-2013 (Table 3.2). We found that the model including the “percent of colony cleared” (PClear) received the most support and no other models were competitive (Table 3.2). There was a

positive relationship between PClear and the odds of reproductive loss occurring, with a 3% increase in the odds of reproductive loss occurring for every 1% increase in colony clearance ($\beta = 1.03$, 95% CI: 1.01-1.04; Fig. 3.6). Contrary to our original hypothesis, the mean percentage of colony clearance during disturbances caused by adult eagles was 28.9% (SE 2.85; 95% CI: 23.3-34.5) vs. 21.5% (SE 2.62; 16.4-26.6) for sub-adult eagles, supporting model selection results indicating no difference in the percent of colony clearance between eagle age classes.

We also investigated factors related to the number of Common Murre eggs and chicks killed by secondary predators, when reproductive loss was known to occur during eagle disturbances on the central coast from 2011-2013 (Table 3.3). The best model for predicting Common Murre reproductive loss was the additive model including Julian day and percent of colony cleared. This model predicted a one day increase would be associated with a 3% decline in median reproductive loss ($\beta = 0.97$, 95% CI: 0.955-0.993). Conversely, the model predicted a one percent increase in colony clearance would be associated with a 1% increase in median reproductive loss ($\beta = 1.01$, 95% CI: 1.001-1.025). A second model including the interaction of Julian day and percent of colony cleared was found to be competitive using AIC_c, but confidence intervals for all of the betas overlapped one, indicating none of the variables in this model were significant predictors (Julian day: $\beta = 0.98$, 95% CI: 0.95 – 1.00; PClear: $\beta = 1.06$, 95% CI: 0.92 – 1.21; Julian day * PClear: $\beta = 0.99$, 95% CI: 0.99 – 1.00). Contrary to our original hypothesis, we found no difference in the mean number of Common Murre eggs and

chicks killed by secondary predators, between disturbance events caused by adult (1.58, SE 0.18) and sub-adult (1.6, SE 0.22) Bald Eagles.

Common Murre demographics

In 2012, no young were produced by Common Murres at the north coast site (Table 3.4). Observers documented predator presence in the absence of murres 249 times (1.5 times per hour), and predation events 54 times (0.34 times per hour) over 161 hours of observation on 41 days, between May and July 2012 at the north coast site. We documented the first Common Murre eggs at the north coast site on June 6, 2012. During Bald Eagle induced disturbances with 100% of the breeding site evacuated by adult Common Murres, we documented loss of all visible murre eggs to secondary predators on June 6, 18, 19 and 22, and July 4, 2012. We observed a mean of 30 (SE 9.4) murre eggs being consumed by secondary predators per disturbance. On July 11, 2012 we suspended daily field observations, but continued monitoring the site for predator activity using the remote video camera. When conducting camera maintenance, we checked this site for eggs or chicks, and noted whether or not adult Common Murres were present on the breeding site. No additional eggs and zero chicks were observed at this site after July 11, 2012, although adult murres continued to attend the colony sporadically until mid-August. Therefore, we considered this site to have zero reproductive output in 2012.

At the central and south coast sites in 2012, reproductive success was 27% and 32% respectively (Table 3.4). We suspended field observations on July 18, 2012 on the central coast and July 23, 2012 on the south coast, after ongoing disturbances from

juvenile California Brown Pelicans impacted these colonies for five days or more. Pelican disturbance events kept 80-100% of these colonies cleared of adult murre for several days, which prevented adult murre from attending young. The lack of parental care, heavy rain, premature fledging, and predation by juvenile pelicans, eagles, gulls, corvids, and vultures during these prolonged disturbances combined to cause reproductive failure of remaining chicks at these two sites. Concomitantly, several hundred dead Common Murre chicks were found along beaches adjacent to the central and south coast breeding sites (Horton and Suryan 2012). Remote video cameras were left in place and continued to monitor these sites for predator activity. Though no chicks remained on either site, adult murre continued to attend these breeding colonies sporadically through mid-August, after pelicans left these areas.

From 2007-2013 on the central coast, median hatch dates ranged from Julian date 174 to 189, and reproductive success varied from a low of 21% in 2011 to a high of 77% in 2008 and 2009. Reproductive success was negatively correlated with the mean hourly rate of Bald Eagle disturbance over this 7 year time period ($R^2=0.6981$, $p=0.01$; Fig. 3.7), suggesting that increased frequency of Bald Eagle disturbance was related to decreased reproductive success of this murre colony.

DISCUSSION

Regional differences

Our results identify mechanisms by which predator-prey interactions are occurring and influencing reproductive success at individual Common Murre colonies

studied. We found regional and temporal differences in the rate of primary predator disturbance of Common Murre colonies, particularly for events caused by Bald Eagles. This was consistent with our expectations based on what is known about breeding Bald Eagle abundance in proximity to murre colonies regionally in coastal Oregon (Isaacs and Anthony 2011).

We observed the highest percentages of breeding site clearance per disturbance at the north coast site where there are ~13,000 nesting murre. This differed from the central coast, where disturbance events occurred more frequently, involved similar numbers of Bald Eagles on average per disturbance, but cleared smaller portions of the colony on average. It is possible the larger size of the central coast colony (38,000 murre) may have enabled production of murre chicks on less disturbed areas of the breeding site. One major assumption of the predator swamping hypothesis postulates the maximum number predators in an area must be fixed and take a consistent number of prey throughout the breeding season for this predator avoidance strategy to be successful (Burger 1982). It is possible we observed this phenomenon at the larger central coast murre breeding site where similar numbers of eagles impacted the site, but not on the smaller north coast site where more Bald Eagles, and variable numbers of eagles impacted the site. In a study of Least Terns (*Sterna antillarum*) Brunton (1999) found evidence for thresholds of optimal colony size with regard to different types of predators, and suggested intermediate colony size might be best for this species. They found large aerial predators, such as Black-crowned Night-Herons (*Nycticorax nycticorax*), were more successful at large tern colonies and tended to target the center of these colonies, whereas small mammals, gulls

and corvids were more successful hunting at small colonies. Although terns nest on sandy beach habitats in much less dense aggregations than murre, this concept of optimal colony size in the presence of different types of predators may apply, and warrens continued study in other species.

Both the north and central coast sites contrasted sharply with the south coast (8,000 murre), where disturbances were infrequent, cleared only small areas of the colony, and included only one eagle at a time. The north and south coast sites were similar in size and in close proximity to other large Common Murre breeding sites, but differed greatly in the intensity of disturbance. Since more eagles were present in the area surrounding the north coast colony, it is possible that murre were constantly stressed by predator presence. Since eagles pose a real lethal threat to adult survival, murre may be hypervigilant and prone to evacuating colonies in regions where predators are plentiful. This is in contrast to studies where birds become less reactive to benign or repeated disturbances (Blumstein 2006).

Interestingly, we found that predator activity in close proximity to murre colonies may preclude murre from remaining at nest sites during the breeding season. This is not without precedence since studies of Tufted Puffins (*Fratercula cirrhata*) indicate these seabirds switch to low risk activities and may avoid breeding sites when predation danger is imminent from Bald Eagles or Peregrine Falcons (Addison et al. 2007). We believe the combined effects of Bald Eagle presence, which is a direct threat to adult survival, and accompanying disturbance associated with murre fleeing when Bald Eagles are present,

impacted reproductive success of the north coast colony in 2012. Avoidance of the colony, compounded with disturbances that cleared most of this site, and the additive effects of both primary and secondary predators, led to reproductive failure of murre on the north coast colony during egg laying.

Since murre are long-lived species, tradeoffs associated with breeding vs. survival may favor murre forgoing reproduction when predation risk is high (Cresswell 2008). On the south coast, murre may be less reactive because disturbances are rare and the direct threat to murre survival is lower since Bald Eagles are less numerous. At the south and central coast sites, many chicks were produced, despite Bald Eagle disturbances in May and June. Late season disturbances caused by juvenile California Brown Pelicans, led to failure of remaining murre chicks at the central and south coast sites in July (Horton and Suryan 2012). We strongly suggest monitoring primary predator use of areas surrounding colonies, even when murre are absent, in addition to documenting disturbances, because threats to adult mortality that result in avoidance of predators and disturbance to nesting birds can both impact reproductive output through decreased breeding propensity (proportion of birds that attempt to breed on a site) and direct nest or chick loss. The combined effects of primary predators such as Bald Eagles and pelicans, frequency of disturbance, associated colony disruption, and the subsequent facilitation of secondary nest predators made colony disturbance a powerful mechanism of top-down control at all three sites studied in 2012.

Predators and age classes

Our study found differences in the amount of loss attributable to primary vs. secondary predators from 2011-2013 at the central coast site. Over this time period, Bald Eagles took on average, less than one individual murre adult, egg or chick per event, while secondary nest predators took more than five times that number of murre eggs or chicks per event. Secondary nest predation would not be possible on this scale, without the indirect effect of colony disruption caused by primary predators. Our models supported this claim, finding percent of colony clearance to be the best predictor of both the odds reproductive loss would occur and the number of murre eggs and chicks killed by secondary predators during eagle disturbance events. This is important because the synergy of consumptive effects from primary and secondary predators combine to equal larger lethal effects than either type of predation alone. If disturbance and predation leads to loss of adults and complete failure of large colonies over many consecutive years, this could lead to population level effects for murre (Hixon and Carr 1997, Brunton 1999, Hixon and Johnson 2009). This idea warrants continued study at murre or other seabird colonies experiencing avian predation from recently recovered Bald Eagles.

While there is some evidence reaching back to the Pleistocene showing seabirds were important prey items in the diets of eagles in the Pacific Northwest, reconstructions of eagle diets over the past 200 hundred years show much more variation tied to other locally and seasonally abundant prey sources (Newsome et al. 2010). It is possible that on the U.S. West Coast, eagles may have fewer prey options today and thus rely more heavily on seabirds in their diets (Marston et al. 2002, Anthony et al. 2008, Fondell et al. 2008, Elliott et al. 2011). As a result, eagle predation may be continuing later in the

season as the population increases and more individuals are in need of food, especially while rearing eaglets. It is possible after local juvenile eagles fledge they remain in the nest area and are taught to hunt at murre colonies by their parents, thus suggesting this learned habit could produce a sub-population of seabird specialists. Alternatively, studies have shown that juvenile eagles from California travel north during May-June, which coincides with the arrival of young eagles to the Oregon coast in recent years (Linthicum et al. 2007). Older sub-adults raised in this region may return with potential mates to prospect for breeding territories, since pre-breeding eagles travel great distances during this exploratory life stage (McGrady et al. 2003). With regard to adults, failed or non-breeders may arrive on the Oregon coast in June or July to take advantage of the seasonally abundant prey provided by large seabird breeding colonies.

We expected sub-adult eagles to be less efficient hunters, thereby facilitating greater access to secondary nest predators, but the data did not support this hypothesis. Instead, we found both adults and sub-adults exhibited a range of behaviors we assumed were related to inexperience such as making multiple unsuccessful attempts hunting murrens and landing on the colony. It is possible these behaviors may be the result of individual variation, meaning that some individuals may inherently outperform others when hunting murrens at colonies irrespective of age or other factors (Lescroël et al. 2009). Lack of distinction in behavior between some adult and sub-adult eagles could also be due to breeding status. For example, it is possible that adult eagles with active nests hunt efficiently, in order to bring prey items back to the nest, resulting in relatively small, though frequent colony disruptions resulting in little reproductive loss from

secondary predators, but increased risk of mortality for breeding adult murre. Non-breeding adults and sub-adult eagles may be more likely to spend time at and around the murre colony, or landing on site to consume individual murre since they do not have young to provision. Without marked birds, it would be impossible to distinguish among breeding and non-breeding adults, but this could be an interesting avenue for future research. Furthermore, adult and sub-adult eagles have been shown to be equally successful at capturing gull chicks, and have been observed hunting in groups, so it may not be appropriate to expect differences in hunting ability based on age-class alone (Buchanan and Watson 2010, Hayward et al. 2010).

Changes over time

At the central coast site, where we have multiple years of predation data, we found several changes in primary predator occurrence over time. While Bald Eagles were the dominant cause of disturbance over the entire time period, the primary predator assemblage expanded to include juvenile California Brown Pelicans and Turkey Vultures in the later period. Prior to 2010, we found that disturbances were most frequent during egg laying and incubation in May and early June, then decreased during chick-rearing in June – July, thereby reducing reproductive loss to the colony. After 2010, however, disturbances continued through chick-rearing in June and July, greatly impacting reproductive output. A corresponding addition of murre chicks to the diet of nest predators occurred during the latter period, which follows the extension of predation pressure into the chick rearing month of July.

There are many possible reasons for the addition of new predator species at murre colonies, and the expansion of predation pressure into late June and July. One explanation has to do with breeding phenology. Historically, murre egg laying occurred in early to mid-May in Oregon (Manuwal et al. 2001), but this shifted to late-May and early June in more recent years. There is little support that this shift was due to changes in climatic factors (Gladics 2012); instead we believe it is largely a result of increased predation pressure from Bald Eagles in spring when murre colonies are attempting to settle on colonies to begin egg laying. The return of murre colonies to breeding sites in April-May overlaps with peak provisioning time for eaglets (Elliott et al. 2005). As the number of active, coastal Bald Eagle nests increase, it follows that eagle predation pressure at murre colonies should also increase.

Regardless of the cause, if disruption of murre colonies during the early season leads to delayed settlement, this will then delay murre egg laying and incubation, chick rearing and fledging as well. When this occurs, murre colonies and their chicks are still tied to colonies in July, when northward post-breeding California Brown Pelicans are also moving through these areas (Horton and Suryan 2012). Pelicans move north from their breeding colonies in Baja California, Mexico and the Channel Islands in southern California, from July through October to find food (Everett and Anderson 1991, Gress 1995). They use offshore rocks and islands, which are the sites of other seabird breeding colonies, as roost sites in Oregon (Wright et al. 2007). When the murre breeding season was initiated earlier, it is unlikely that overlap occurred between these species. However, the shift in murre breeding chronology, likely initiated by Bald Eagle disturbance in April

and May, along with the resultant overlap of habitat needs for murre and pelicans in July, have combined to create a novel situation.

Additionally, there is some evidence to suggest that pelicans' main prey, anchovy (*Engaulis mordax*) and sardine (*Sardinops sagax*) have been limited within California Current waters in recent years (Bjorkstedt et al. 2012). Lack of available prey and inexperience may have led pelicans to switch from eating fish to murre, thereby supplementing their diets with what amounts to a new seasonally abundant prey source – murre chicks and their regurgitants – in 2010, 2011 and 2012. Pelican populations, like Bald Eagle populations, have recently rebounded and pelicans were removed from the federal Endangered Species List in 2009 (U.S. Fish and Wildlife Service 2009, USDO I 2009). As the populations of eagles and pelicans continue to increase, it is likely we will see early and late season top-down effects on nesting murre. In years with poor alternative food availability for eagles or pelicans, it is reasonable to expect intensified activity by these predators at Common Murre or other seabird colonies in Oregon.

In general, the increasing frequency of large scale disturbance, means it is more likely that direct and indirect effects of primary and secondary predators will combine to reduce reproductive output for Common Murre at individually affected sites. If these top-down effects are wide-spread, population level effects may be observed over time.

Study limitations

We used a case study approach, in which we selected Common Murre breeding sites to monitor based on several criteria, including our ability to view these sites from

the mainland in order to collect data on disturbance and reproduction. Comparison among sites occurred within a single year, 2012, while comparisons over time occurred at a single site. The scope of inference for this study is limited to the years and locations we monitored. Specific findings at these sites are not representative of a larger population, in space or time. As with any observational study, our results show associations, but do not prove causation. We acknowledge there may be factors contributing to our results that we did not measure or include in the analyses presented here. With this type of field based, observational study, it is impossible to control for all external factors. Despite these limitations, we found striking results consistent with the findings of Chapter 2 that add important insights to the body of knowledge on avian predators at seabird colonies.

CONCLUSION

Our observations provide strong evidence for top-down regulation of local breeding populations of Common Murres in Oregon, mediated by disturbances caused by recently recovered native, avian predators, such as Bald Eagles and California Brown Pelicans. We found both direct (consumptive) and indirect (non-consumptive) effects of primary and secondary nest predators to be important determinants of reproductive output of murres at colonies studied. As the Bald Eagle population continues to expand along the U.S. West Coast, scientists and managers should expect to see the mechanisms and effects of disturbance described here, at more Common Murre colony locations.

Additionally, if murre breeding phenology continues to be pushed later into May and June, by eagle disturbance or other factors, predation by post-breeding, north migrating

California Brown Pelicans during murre chick rearing should also be expected, particularly in years of poor anchovy or sardine recruitment.

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Table 3.1. Mean hourly rate of disturbance and mean length of disturbance in hours for all causes (excluding unknown causes and unknown end times) and Bald Eagle disturbances alone (excluding unknown end times) from video data collected between May-July 2012 at the north, central and south coast research sites, Oregon, USA.

Location	Cause of Event	Disturbance Rate (mean # events per hour, range, standard error)	Mean Disturbance Length (mean hrs per disturbance, range, standard error)
North	All Causes	0.12 (range: 0-0.63, \pm 0.02 SE)	1.64 (range: 0.01-10.27, \pm 0.23 SE)
	Bald Eagle	0.10 (range: 0-0.40, \pm 0.22 SE)	1.88 (range: 0.25-10.26, \pm 0.27 SE)
Central	All Causes	0.15 (range: 0-0.44, \pm 0.01 SE)	2.25 (range: 0.02-15.50, \pm 0.24 SE)
	Bald Eagle	0.11 (range: 0-0.41, \pm 0.20 SE)	1.97 (range: 0.02-14.65, \pm 0.25 SE)
South	All Causes	0.01 (range: 0-0.33, \pm 0.005 SE)	0.78 (range: 0.17-2.82, \pm 0.29 SE)
	Bald Eagle	0.002 (range: 0-0.12, \pm 0.03 SE)	0.37 (range: 0.21, 0.52, \pm 0.09 SE)

Table 3.2. Model selection results for the 7 single factor logistic regression models relating the response “odds of reproductive loss (1=loss occurs, 0=no loss occurs)”, to percent of the colony evacuated per disturbance (0-100%, PClear), median time of disturbance event (in h:m:s, Time), age of Bald Eagle (sub-adult or adult, BAEAage), an intercept only model (Null), Year, disturbance length (in minutes, DLength), and Julian Day of each disturbance caused by Bald Eagles at the central coast site, Yaquina Head, Oregon, USA (2011-2013).

Model	ΔAIC_c	K	w	Deviance
PClear	0.00	2	0.96	183.37
Time	9.18	2	0.01	192.55
BAEAage	9.51	2	0.01	192.88
Null	9.71	1	0.01	193.08
Year	10.03	3	0.01	193.39
DLength	10.08	2	0.01	193.45
Julian Day	11.70	2	0.00	195.07

Notes: Models were ranked according to Akaike’s information criterion adjusted for small sample size (AIC_c). The model deviance, number of parameter (K), ΔAIC_c , and AIC_c weights (w) are given for all models.

Table 3.3. Selection results for nine linear regression models relating the response “number of Common Murre eggs and chicks killed by secondary predators” to six single covariate models, one additive model, one interaction term model and a null model. Model covariates included: an intercept only model for comparison (Null), percent of the colony evacuated per disturbance (0-100%, PClear), disturbance length (in minutes, DLength), median time of disturbance event (in h:m:s, Time), age of Bald Eagle (sub-adult or adult, BAEAage), Year (2011, 2012, 2013), Julian Day of each disturbance caused by Bald Eagles, Julian day + PClear, and Julian day*PClear at the central coast site, Yaquina Head, Oregon, USA (2011-2013).

Model	ΔAIC_c	K	w	Deviance
Julian day + PClear	0.00	4	0.51	227.69
Julian day*PClear	1.97	5	0.19	229.66
Julian day	2.80	3	0.13	230.49
PClear	4.42	3	0.06	232.11
DLength	5.17	3	0.04	232.86
Null	5.25	2	0.04	232.94
Time	7.01	3	0.02	234.70
BAEAage	7.41	3	0.01	235.10
Year	8.93	4	0.01	236.62

Notes: Models were ranked according to Akaike’s information criterion adjusted for small sample size (AIC_c). The model deviance, number of parameter (K), ΔAIC_c , and AIC_c weights (w) are given for all models.

Table 3.4. Summary metrics from observations of Common Murres at the north, central and south coast research sites in 2012. The number of field observation days and hours are provided, along with the number of reproductive plots monitored by site. Also included are the first (1st) and median (Med) hatch dates, estimates of hatching success and overall reproductive success. Additionally, the number of disturbances, as well as the hourly rate of primary and secondary predation on Common Murre adults, eggs and chicks are provided.

Site	Observation		# plots	Hatch Date		Hatching success ^a	Reproductive success ^b	# disturbances	Primary Predation Rate # per hour ^c (total #)			Secondary Predation Rate # per hour ^c (total #)	
	Hours	Days		1 st	Med				Egg	Chick	Adult	Egg	Chick
North	161	41	0 ^d	NA ^d	NA ^d	0 ^d	0 ^d	53	0.00 (0)	0.00 (0)	0.01 (4)	0.68 (109)	0.00 (0)
Central	273	56	12	5/21	5/30	0.46 (± 0.09 SE)	0.27 (± 0.06 SE)	140	0.07 (19)	0.32 (87)	0.17 (47)	2.76 (754)	0.81 (220)
South	283	53	5	5/29	6/3	0.70 (± 0.08 SE)	0.32 (± 0.07 SE)	21	0.00 (0)	0.007 (2)	0.01 (3)	0.00 (0)	0.02 (7)

^aChicks hatched per eggs laid (mean among plots)

^bChicks fledged (≥15 days old) per eggs laid (mean among plots)

^cTotal # observed taken/total # observation hours

^dPredator activity prevented murres from staying on the breeding site to incubate eggs. All eggs laid were consumed by predators.

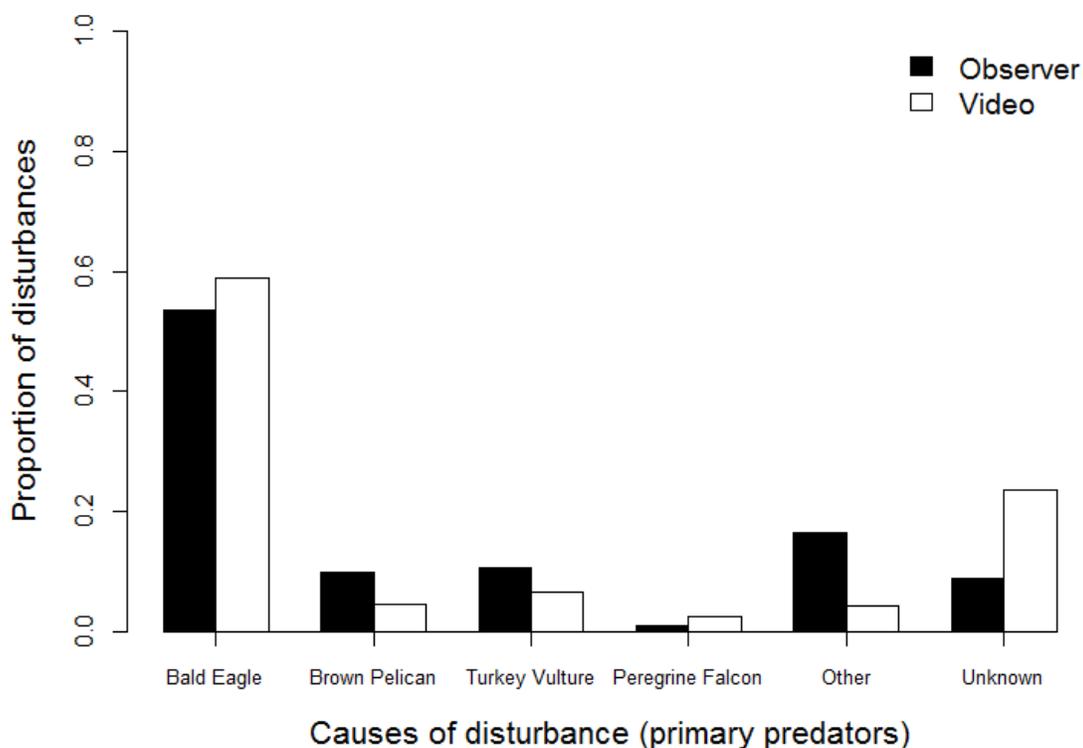


Figure 3.1. Proportion of disturbances identified by observers in the field (Observer) and from video data (Video, in 2012 pooled among north, central, and south coast research sites), Oregon, USA. Causes of disturbance include six categories: 1) Bald Eagle (*Haliaeetus leucocephalus*) [observer=121, video=249], 2) California Brown Pelican (*Pelecanus occidentalis*) [observer=22, video=19], 3) Turkey Vulture (*Cathartes aura*) [observer=24, video=27], 4) Peregrine Falcon (*Falco peregrinus*) [observer=2, video=10], 5) Other [observer=37, video=18], and; 6) Unknown [observer=20, video=130]. The “Other” category includes: corvids, gulls, cormorants, multiple species, large wave, and weather.

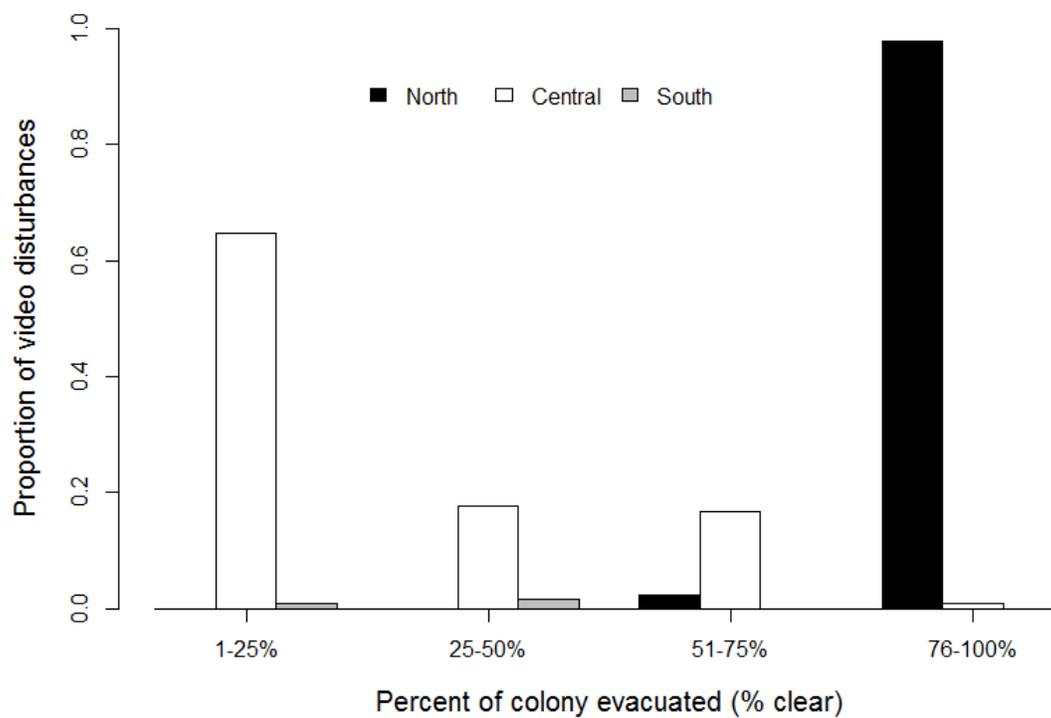


Figure 3.2. Proportion of video disturbances caused by Bald Eagles in 2012, during which 1-25%, 26-50%, 51-75% and 76-100% of nesting adult common murrens evacuated research sites on the north, central and south coast of Oregon, USA.

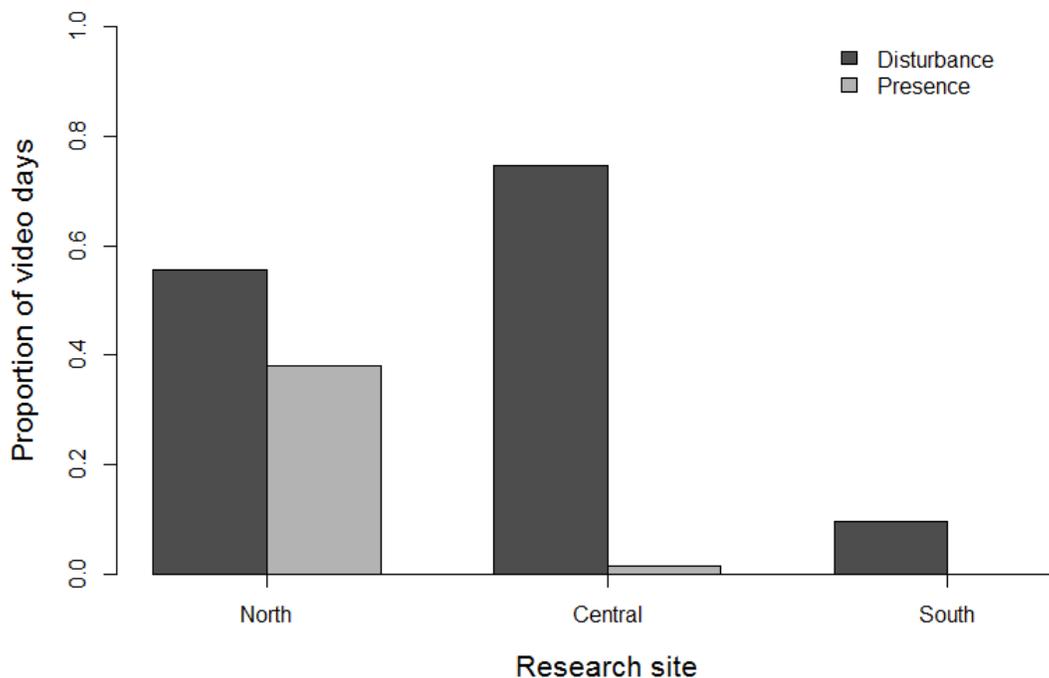


Figure 3.3. Proportion of video monitoring days when at least one disturbance or predator presence event (for all primary predator types) occurred at each study site during May, June and July of 2012, Oregon, USA. A “video day” consisted of ≥ 10 hours of usable video coverage. Disturbance and presence days were not mutually exclusive. We recorded disturbances on 35 days and presence events on 24 days, out of 63 total video days at the north coast site. Of these, 9 days included both disturbance and predator presence events within the same day. Predator presence or disturbance affected the north coast colony on 80% of all video days. On the central coast, we recorded Bald Eagle disturbance on 53 days and presence events on 1 day, out of 71 total video days. One video day included both disturbance and predator presence events, for a total of 75% of video days affected by either disturbance or predator presence. The south coast had zero instances of Bald Eagle presence with murrelets absent. We recorded disturbances on 7 out of 73, or 9% of video days on the south coast.

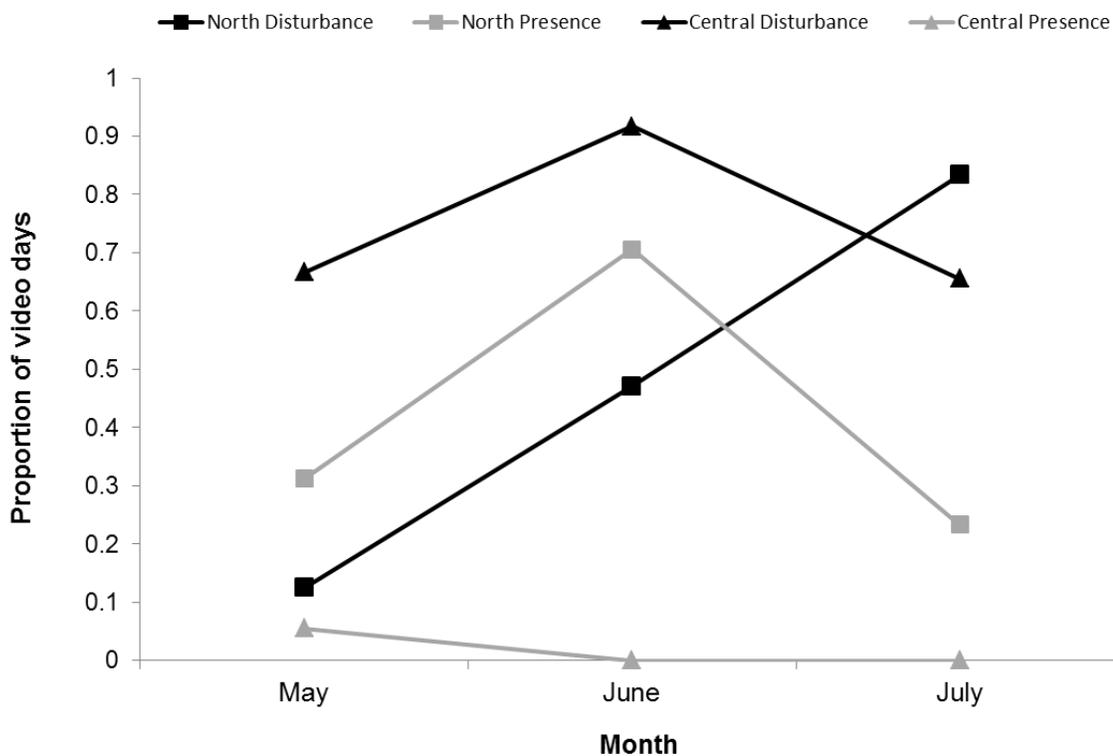


Figure 3.4. Proportion of video monitoring days when at least one disturbance or predator presence event occurred at the north and central coast research sites, out of the total number of video days in May (north=16 days, central=18 days), June (north=17 days, central=24 days), and July (north=30 days, central=29 days) of 2012, Oregon, USA. No predator presence events occurred on the south coast, so this site is not included. In May and June, more predator presence versus disturbance events occurred on the north coast. Murres should be laying and incubating eggs in May, and rearing chicks in June and July. This figure indicates that murres were absent from the breeding colony for all or part of the day, on 80% of video days on the north coast. Murres were disturbed by predators on 75% of all video days on the central coast.

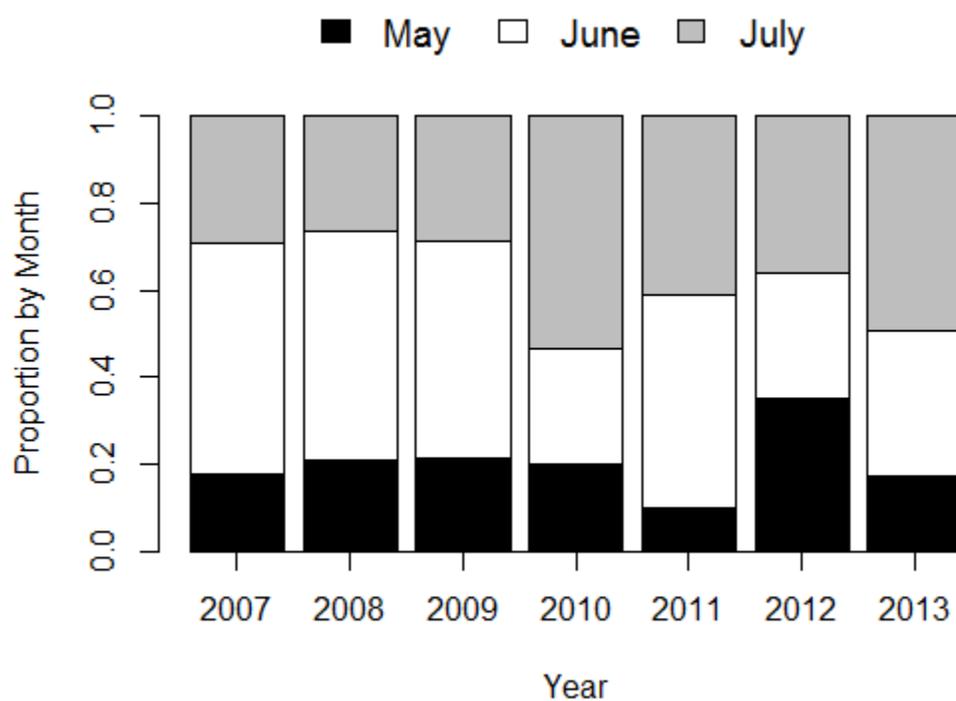


Figure 3.5. Annual proportion of all disturbance events recorded by observers and categorized by month from 2007-2013 at Yaquina Head on the central coast, Oregon, USA. The proportion of disturbances occurring in July increased and remained higher from 2010-2013, when compared to 2007-2009.

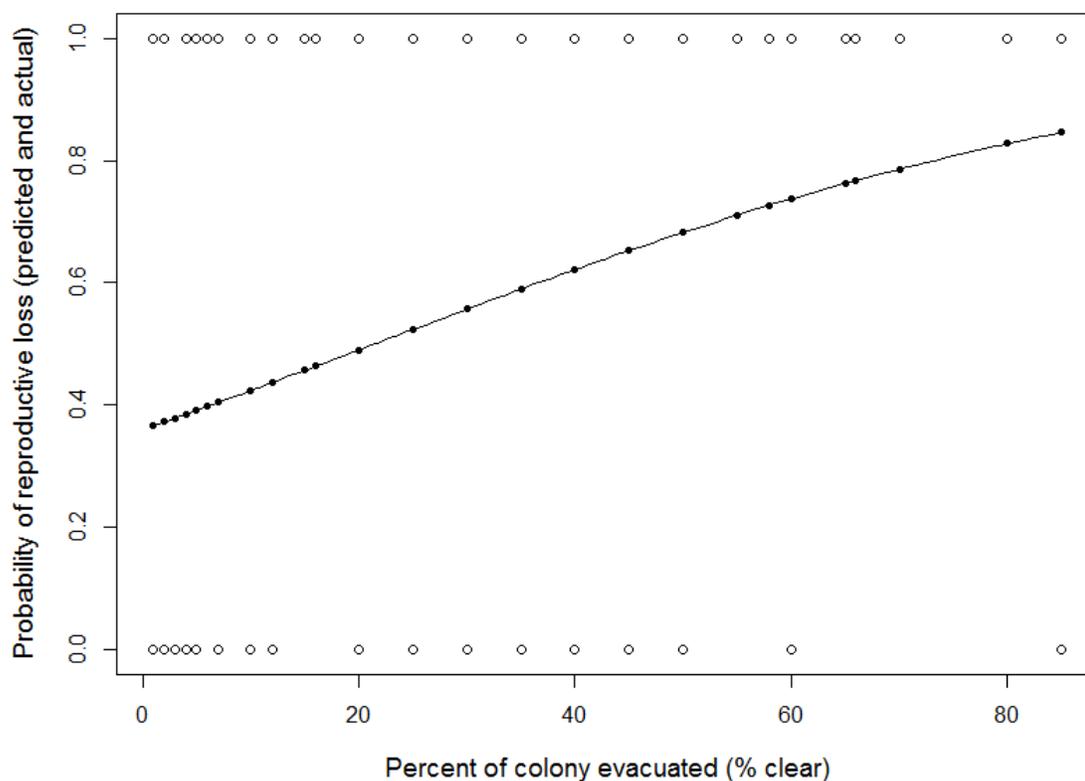


Figure 3.6. Relationship between the single explanatory variable, “percent of colony evacuated” (x-axis) and the odds of actual and predicted reproductive loss occurring (y-axis) based on observer data collected at Yaquina Head, Oregon, USA (2011-2013). Predicted values are represented by the solid black dots and line. Actual values are represented by open circles. This single factor binomial logistic regression model was selected from a pool of seven *a priori* candidate models using Akaike’s information criterion adjusted for small sample size (AICc). Based on the model, we expect a 3% increase in the odds of reproductive loss occurring, for every one percent increase in colony evacuation ($\beta = 0.03$, 95% CI: 1.01 – 1.04).

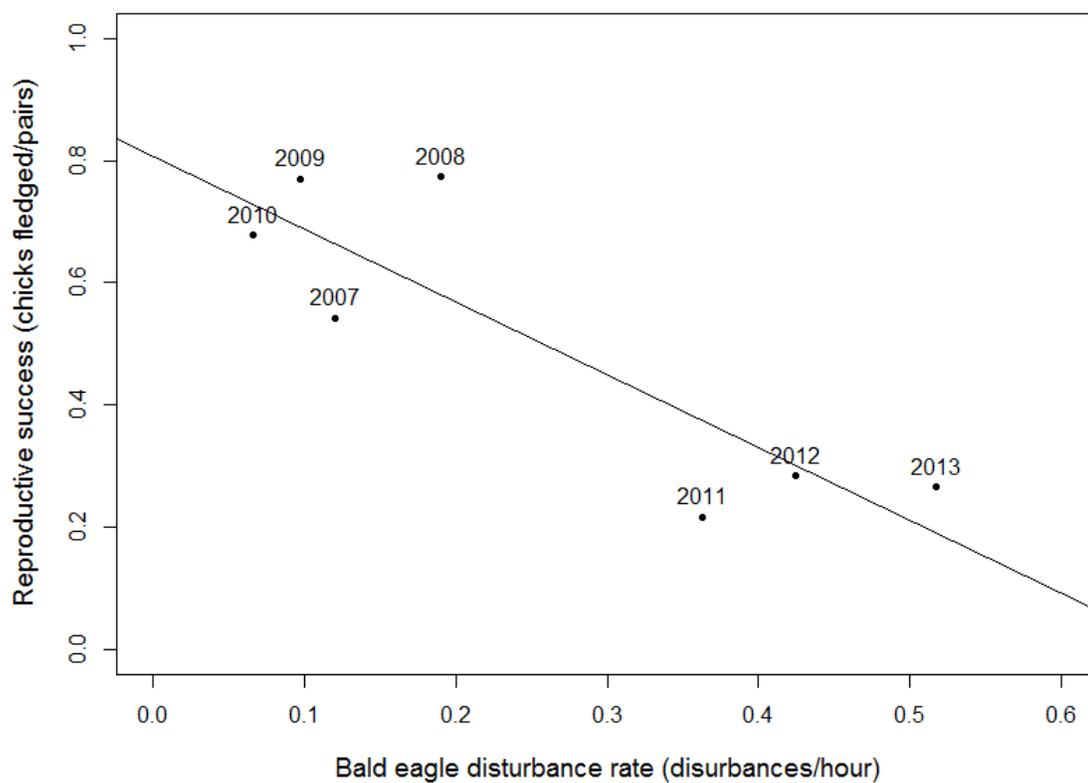


Figure 3.7. Common murre mean reproductive success is negatively associated with the mean rate of eagle disturbance in each year at the central coast site ($R^2=0.6981$, $p=0.01$).

Chapter 4

GENERAL CONCLUSION

Cheryl A. Horton

CONCLUSION

Research aims

In this study, I set out to understand changes in the distribution and abundance of Common Murres over a period of Bald Eagle recovery and delisting in Oregon. Additionally, I aimed to quantify impacts of disturbance and predation at individual Common Murre breeding sites within the state. The approach included spatio-temporal analysis of murre breeding sites and coastal Bald Eagle nest territories over time ($n=19$ years), and examined the mechanisms of disturbance at three Common Murre breeding sites ($n=1$ year), and at a single site ($n=7$ years), all known to experience Bald Eagle predation. Determining the distribution of occupied breeding sites and number of Common Murres present at those sites over two decades allowed me to test whether Bald Eagle nesting density and abundance at various scales, was associated with changes observed in the murre population (Chapter 2). My work to quantify causes and mechanisms of disturbance at individual murre breeding sites (Chapter 3) provided needed insight into top-down regulation, including both direct (consumptive) and indirect (non-consumptive) effects of recently recovered, native avian predators.

Primary findings

Analyses of occupied breeding sites and number of murres counted in the second census year supported an association between distribution and abundance of Common Murres with density of Bald Eagle nest territories regionally in coastal Oregon (Chapter 2), but not the abundance of eagle nests in close proximity to murre colonies. The north coast consistently supported the highest density of Bald Eagle nests, while the central

coast supported an intermediate density, and the south coast supported the lowest density over time.

Studies have shown strong negative effects of density dependence on eagle nest success when territories were less than 1.6km apart (Anthony et al. 1994), and eagles nesting along shorelines in Oregon are thought to be at or near carrying capacity when breeding territories are 1.6-3.2 km apart (Isaacs and Anthony 2011). Territoriality may limit the number of eagle nests occurring within certain spatial scales around seabird colonies. If eagle nest density is high in regions where seabirds also nest, there may be more non-breeding eagles present on the landscape impacting seabird colonies.

Researchers estimate 60% of Bald Eagles in Oregon exhibit natal philopatry and are non-migratory, year round residents with overlapping winter and breeding habitat (Isaacs and Anthony 2011). Hatch year eagles tend to fledge by June, but remain near nest sites through August, and have been documented in natal territories through October (Isaacs et al. 1983). This provides further support for increased abundance of non-breeding eagles in regions of high eagle nest density. These findings suggest high densities of Bald Eagles can influence where murrens choose to nest in a given year. I found that the Common Murre population redistributed from regions of high to lower Bald Eagle density from 1988-2006. Additionally, the density of eagles in proximity to murre breeding sites may also influence colony size if large, medium or small colonies provide differing amounts of protection from avian predators.

Predators (both primary and secondary) had negative top-down effects on Common Murre reproduction, through direct consumption and indirectly through colony clearance associated with disturbance (Chapter 3), which is consistent with other studies of murre and eagles in the Pacific Northwest (Hipfner et al. 2012, Parrish et al. 2001). The majority of disturbance events were initiated by Bald Eagles in 2012. Overall, suites of predators, and therefore, causes of disturbance were similar among sites studied. Predators were most active at the north coast colony studied. This site experienced the highest rate of disturbance and the greatest amount of colony evacuation per disturbance event, which is consistent with predictions based on findings from coast-wide population analyses (Chapter 2).

Unexpectedly, the central and south coast sites, experienced late-season disturbance from juvenile California Brown Pelicans which caused failure of remaining chicks and greatly reduced reproductive output of these two sites in 2012. Early season disruption by Bald Eagles has likely changed murre breeding chronology so that pre-fledgling murre chicks remain on colony later in the season and overlap with the arrival of pelicans. It is possible food limitation for eagles or pelicans may cause these species to rely more heavily on seabirds as prey (Votier et al. 2008, Elliot et al. 2011). Eagles also had region-wide impacts on colonial nesting waterbirds in 2011, causing failure of the largest known Caspian Tern colony in the Columbia River estuary (Collar 2013).

At the central coast site, the number and type of primary and secondary predators increased over time (2007 – 2013). Overall, secondary predators were responsible for

greater reproductive loss than primary predators, and degree of colony evacuation best predicted reproductive loss in this study. Reproductive success declined with an increase in predation rate over 7 years, and predation extended into chick rearing during the latter part of this study allowing secondary predators access to both eggs and chicks.

Contributions and future directions

This study provides novel contributions to research on top-down effects of native, avian predators at seabird breeding colonies along the Pacific coast of North America. Historic datasets on murre and eagles enabled the investigation of associations between species over time and space. Data collection in 2012 demonstrated the feasibility and limitations of using remote video cameras to collect predation and disturbance data of murre colonies from points on the mainland, compared to data collected by trained observers. Video enabled us to gain concurrent, comparable data on the mechanisms of disturbance among sites. Observers were able to quantify the effects of primary and secondary predators, and obtain estimates of reproductive success.

This study makes an important step toward filling knowledge gaps in the role of top-down forcing in seabird ecology. By documenting an association between Bald Eagle density and the distribution and abundance of Common Murres over time, there is some evidence for large-scale redistribution of a colonial nesting seabird in the presence of a recently recovered, native avian predator. Frequency, magnitude, timing and duration of colony disturbance are important factors influencing murre colony productivity. Work at individual seabird colonies in Oregon suggests the effects of both primary and secondary

predators are likely to increase if the Bald Eagle population continues to expand south along the coast. It is still unclear whether this process is a natural rebalancing of predators and prey as the predator population recovers, or whether eagles have recovered into a modified ecosystem, with fewer choices of alternative prey. Additionally, fluctuations in ocean conditions affecting prey availability (Brodeur et al. 2005, Peterson et al. 2006) may cause murre to be less resilient at times to predation and disturbance, thus creating varying dynamics between predator and prey (Furness 2007, Gladics et al. 2014).

Future studies on the effects of Bald Eagles on Common Murres would benefit from additional years of complete population census information for each species as they remain in flux. Unfortunately, 2007 is the last year when Bald Eagle nest territory data were collected and 2006 marks the last census of Common Murres conducted in Oregon. At least for murre population data, the Oregon Coast National Wildlife Refuge has conducted annual aerial surveys of seabird colonies within the state since 1988. With over 20 years of archived colony photographs, it would be beneficial to re-assess the index colonies being counted given redistribution of murre, especially on the north coast. It is also important to understand more about coastal Bald Eagle diets. Stable isotope analysis of feather or tissue samples from museum specimens and contemporary birds could provide some insight into changes in diets over time, particularly the proportion of diets made up of seabirds (Hobson and Clark 1992).

Estimates of reproductive success at murre breeding sites and eagle predation on the north, central and south coast in multiple years would be beneficial for tracking

changes in the impacts of predators over time. As eagles approach carrying capacity, density dependent mortality may occur, along with fluctuations in both murre and eagle populations on the coast. This study provides a snapshot of three murre breeding sites during a single season. Without longer term studies at multiple locations it will be very difficult to predict how increasing eagle populations will effect murre reproductive output and future population trends.

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