AN ABSTRACT OF THE THESIS OF

Caleb S. Spiegel for the degree of Master of Science in Wildlife Science presented on November 12, 2008.

Title: Incubation Patterns, Parental Roles, and Nest Survival of Black Oystercatchers (Haematopus bachmani): Influences of Environmental Processes and Potential Disturbance Stimuli

Abstract approved:

Susan M. Haig

Shorebirds display great variation in mating systems and breed in dynamic environments that are increasingly subject to human threats worldwide. In order to adequately assess productivity and demography of shorebird populations, it is important to understand factors that influence patterns of parental care and reproductive success. The Black Oystercatcher (Haematopus bachmani) is a shorebird species of concern and an indicator of the health of intertidal ecosystems. Much information on breeding biology is lacking for the species, though it is reported to regularly experience low reproductive success and may be vulnerable to human disturbance during nesting. This thesis examines relationships among natural and human processes related to incubation and nest success of Black Oystercatchers in a high density breeding area of Alaska, experiencing increasing human recreational activity.
In 2005 and 2006, oystercatcher nests were continuously monitored with video cameras to investigate the association of cyclical (time of day, tide, ambient temperature, seasonality) and stochastic (natural/human disturbance) processes with incubation patterns (nest attendance, incubation bout length, incubation recess rate) and sex roles. Review of over 3,000 hours of footage from 13 molecularly sexed nesting pairs revealed complimentary bi-parental care with differing roles between sexes. Females allocated more to nest attendance and had longer incubation bout lengths, indicating a greater investment in incubation compared to males. Males responded more frequently to nest area disturbance stimuli compared to females, indicating that males invest more in nest defense. Incubation patterns were also influenced by tide stage and height, ambient temperature, and disturbance stimuli. Incubation bout lengths nearly doubled at night, independent of sex. Longer nocturnal bouts may minimize parental activity near the nest during periods of increased predation risk when incubation duty changes could reveal the presence of nests to nocturnal predators.

Video footage was also used to document the types and frequencies of human and predator stimuli, and extreme weather and tide episodes encountered near oystercatcher nests, and the effect of these potential disturbance stimuli on incubation behavior and nest success. Nearly 800 potential disturbance stimulus events were documented within 25 m of video monitored nests. Other bird species were the most frequently observed type of potential disturbance, but were largely ignored by incubating oystercatchers. Oystercatchers were most frequently disturbed (as evidenced by displacement from a nest) by conspecifics and humans, with nests left unattended for longer periods following human disturbance than any other disturbance type. Although
infrequent, a high proportion of mammal observations also resulted in oystercatchers flushing from their nests. Changes in incubation behavior due to disturbance were not found to affect nest success, nor did nest success decrease with proximity to areas of frequent human recreational activity. Nocturnal nest predation by mustelids and nighttime flood tides accounted for six of seven nest failures recorded on video, even though nights were disproportionately short during the study. Thus, future shorebird breeding studies should assess causes of nest failure from latent nocturnal causes, rather than just obvious diurnal causes.

With the analysis of extensive nest observation data this study identified natural and anthropogenic processes that affected incubation patterns of an uncommon shorebird species, specially adapted to a dynamic nesting environment. Results elucidate factors influencing oystercatcher life history and lay the groundwork for further investigation into the effects of human disturbance on nest success and demography of the Black Oystercatcher. Future research should investigate nest success in breeding areas experiencing higher levels of disturbance, include post-hatching breeding stages, and be conducted over multiple breeding seasons.
INCUBATION PATTERNS, PARENTAL ROLES, AND NEST SURVIVAL OF BLACK OYSTERCATCHERS (*HAEMATOPUS BACHMANI*): INFLUENCES OF ENVIRONMENTAL PROCESSES AND POTENTIAL DISTURBANCE STIMULI

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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.

Caleb S. Spiegel, Author
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CONTRIBUTION OF AUTHORS

Dr. Susan M. Haig procured funding, assisted with project planning, supervised data analyses and data interpretation, and performed extensive editing of all chapters.

Dr. Michael I. Goldstein developed primary research goals, obtained additional funding, assisted with project planning and data collection, provided field equipment, supervised field logistics, and edited all chapters. Ms. Manuela Huso oversaw the design and implementation of statistical analysis of chapter 2, helped interpret research findings, and performed additional editing of all chapters.
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In memory of my grandmother Helen, an extraordinary woman who marveled at the birds outside her kitchen window.
INCUBATION PATTERNS, PARENTAL ROLES, AND NEST SURVIVAL OF BLACK OYSTERCATCHERS (*HAEMATOPUS BACHMANI*): INFLUENCES OF ENVIRONMENTAL PROCESSES AND POTENTIAL DISTURBANCE STIMULI

1. INTRODUCTION

1.1. INTRODUCTION

Coastal ecosystems are unique interfaces between marine and terrestrial environments which support high concentrations of biodiversity at many trophic levels (DeVogelaere 2004, Vitousek et al. 1997, Lotze and Milewski 2004). Relationships among highly adapted organisms in intertidal zones demonstrate the complexity and diversity of these ecosystems, where slight changes in environmental conditions or species composition can vastly alter functioning of the entire system (Marsh 1986, Lindberg et al. 1998, Lohrer and Whitlach 2002). Shorebirds (Order: Charadriiformes) are recognized as indicators of human-induced environmental change in coastal ecosystems (Piersma and Lindström 2004). Most species are restricted to wetlands for much of their lives and many utilize coastal habitats extensively. Thus, shorebirds are particularly affected by coastal degradation and include some of the most imperiled avian taxa (Haig et al. 1998, Brown et al. 2001, Şekercioğlu et al. 2004). Shorebirds face human-derived threats such as destruction and recreational overuse of critical habitats, marine pollution, climate change, and introduced predators and competitors

Incubation is a particularly important aspect of parental care in birds (Skutch 1957) which is influenced by physiological requirements of developing embryos and attending parents, and constrained by variability in weather conditions, food availability, and threats within the breeding environment (Skutch 1949, Afton 1980, Smith et al. 2007). Natural threats to shorebird nests include predators (Byrd et al. 1997, Sanders and Maloney 2002), severe weather (Hartwick 1974, Goss-Custard et al. 1995), conflict with conspecifics (Ens et al. 1996, Bruinzeel and van de Pol 2004), and tidal flooding (Lauro and Nol 1993, Calf and Underhill 2005). Human activity can promote or intensify effects of naturally-occurring disturbances. For example, frequent flushing of incubating birds by humans may increase the conspicuousness of a nest to predators and its susceptibility to predation (Skutch 1949). Interactions between human and natural disturbance can make it difficult to isolate human impacts on populations (Krebs 1994). A comprehensive understanding of the way natural factors influence reproductive behavior and success is necessary before assessing the affect of human activity on shorebird populations and adequately addressing conservation needs.

Black Oystercatchers (*Haematopus bachmani*) are conspicuous, long-lived shorebirds specially adapted to life in rocky intertidal zones along the west coast of North America (Andres and Falxa 1995). They play a key predatory role in intertidal zones (Marsh 1986, Hahn and Denny 1989) and are considered an indicator species (USDA 2002), along with other members of the genus (Leseberg et al. 2000). Black
Oystercatchers do not breed until four years of age (Hazlitt and Gaston 2002), and regularly experience reproductive failure (Hazlitt 2001). Species with long generation times and frequent reproductive failure may be particularly vulnerable to disturbance (Şekercioğlu et al. 2004). With an estimated world population of fewer than 11,000 individuals (Morrison et al. 2006) and specialized habitat requirements, Black Oystercatchers are listed as a “species of high concern” within the Canadian and U.S. National Shorebird Conservation Plans (Donaldson et al. 2000, Brown et al. 2001). Many aspects of the species’ reproductive ecology, including the roles of the two sexes in parental care, and the influence of temporal and environmental factors on breeding behavior, are not well understood.

1.2. SPECIES LIFE HISTORY

*H. bachmani* is one of eleven extant species of oystercatchers (Hockey 1996). An additional island endemic species, the Canarian Black Oystercatcher (*H. meadewaldoi*) is presumed extinct as a result of human activity (Hockey 1987). Oystercatchers are members of the Order Charadriiformes, Family Haematopodidae, and Genus *Haematopus* (Hayman et al. 1986). Genetic evidence suggests that oystercatchers are most related to the families Ibidorhynchadae, Recurvirostridae, and Himantopodidae (ibisbills, avocets, and stilts), each evolving from a common plover-like ancestor during the Eocene epoch (Baker et al. 2007). Oystercatcher species, which have a near-global distribution (Hayman et al. 1986), can be morphologically divided into two different plumage groups, pied (black and white), which generally inhabit
sandy coastlines, and melanistic (all black), which generally inhabit rocky shorelines (Andres and Falxa 1995, Hockey 1996).

North America has two species of oystercatcher, the pied American Oystercatcher (*H. palliatus*) and the melanistic Black Oystercatcher, whose ranges are geographically isolated except for a small area of overlap in Baja California, Mexico, where interbreeding infrequently occurs (Jehl 1986). In 1973, *H. bachmani* and *H. palliatus* were considered subspecies of the Eurasian Oystercatcher (*H. ostralegus*) (Nol and Humphrey 1994, Andres and Falxa 1995). However, the American Ornithologists’ Union (1983) later re-classified *H. bachmani* as a distinct species. No prehistoric evidence of Black Oystercatchers has been found in western North America (Andres and Falxa 1995). However, five million year old *Haematopus* fossils have been found in the southeastern U.S. (Nol and Humphrey 1994).

Black Oystercatchers range along the entire Pacific Coast of North America, from the Aleutian and Pribilof islands of Alaska south to central Baja California, Mexico (Eley 1976, Andres and Falxa 1995). Over half of the population occurs in Alaska during the breeding season, with over 10% in Prince William Sound (Andres 1998a, Tessler et al. 2007). In the southern part of their range, Black Oystercatchers are thought to maintain year-round territories (Andres and Falxa 1995). Recent satellite telemetry has determined that some Alaskan breeders migrate thousands of kilometers to central and southern British Columbia during winter (M. Johnson, USGS Forest and Rangeland Ecosystem Science Center, in prep.). Wintering habitat use is poorly understood for the species (Gill et al. 2004, Tessler et al. 2007). While large flocks
have been reported in parts of Alaska during winter (Andres and Falxa 1995), only 25% of Prince William Sound’s breeders are thought to remain over-winter (Andres 1998a).

In the northern parts of their range adult Black Oystercatchers have entirely jet-black plumage, while further south browner abdominal feathers are present (Andres and Falxa 1995). Bills are long (68 - 81 mm), straight, and bright red-orange. Adults have yellow irises, and eye rings that are a similar color to the bill (Hayman et al. 1986, Andres and Falxa 1995). Oystercatchers have thick, pale pink legs (Hayman et al. 1986). Chicks are born with gray and dull-black down plumage, and a white abdomen. Full pre-juvenile molts leave grayish-brown body feathers, remaining partially downy until > 28 days of age. Two complete molts take place within the first two years, leaving varying amounts of brown, gray, and black body feathers, before adult jet-black plumage is attained. Second year birds are most reliably distinguished by bill and iris color, which are paler than those of adults (Andres and Falxa 1995). Black Oystercatchers range in mass from 500 to 700 grams, and range from 420 mm to 480 mm in total length (Andres and Falxa 1995, Andres 1998a). Females are larger than males, and possess a longer bill with a more drooped tip, although considerable overlap exists in both metrics (Andres and Falxa 1995).

Black Oystercatchers largely avoid vegetated habitats and are most abundant on islands, islets, and gravel beaches (Andres 1998b, Gill et al. 2004), regularly utilizing low-sloping or level substrates for feeding (Andres and Falxa 1995). Oystercatchers feed primarily in the mid-intertidal zone where high concentrations of mussels and limpets are preferred prey (Hahn and Denny 1989, Andres and Falxa 1995). Despite
their common name, Black Oystercatchers rarely consume oysters (Andres and Falxa 1995). Most foraging occurs at low tides (Andres and Falxa 1995), although Hartwick (1978) noted that extreme low tides are periods of diminished food availability for oystercatchers due to intertidal drying. Black Oystercatchers have broad bills with a flattened tip, specialized for detaching gastropods from rocks and severing the adductor muscles of bivalves (Andres and Falxa 1995, Hockey 1996). They influence the distribution of their invertebrate prey, strongly affecting intertidal community composition (Marsh 1986). As with other oystercatcher species (Velhurst et al. 2001), feeding areas may be defended, especially during the breeding season when chick provisioning increases resource demands (Hartwick 1978).

Productive breeding sites may be limited for Black Oystercatchers; thus, they display a high level of mate and nest site fidelity (Andres and Falxa 1995, Hazlitt and Butler 2001, Bruinzeel et al. 2004). Although few data exist for *H. bachmani*, extra-pair copulations are rare in other *Haematopus* species (Ens 1992). In most of their range, Black Oystercatchers establish vigorously defended breeding territories beginning in mid-March (Webster 1941, Andres 1998a). In early May, both members of a pair assist with nest construction, when a depression in the ground is excavated and lined with rock flakes, pebbles, and shell fragments (Andres and Falxa 1995). Initial clutch size averages three eggs across the species’ range, but may be as small as one (L’Hyver and Miller 1991, Andres and Falxa 1995). Following the failure of an initial nesting attempt replacement clutches may be laid, often with fewer eggs (Andres and Falxa 1995). Incubation occurs for an average of 27.5 days (pers. obs.), and both members of the pair incubate (Andres and Falxa 1995). During hatching and early
brooding, offspring have been reported to face heightened risk from disturbance and predation (Groves 1984, Hazlitt and Butler 2001).

Chicks are capable of walking within 12 hours of hatching (pers. obs.). Mobile chicks are often led up to hundreds of meters from the nest to foraging grounds where adults present them with food and teach them to feed on invertebrate prey items (Groves 1984). Juveniles are generally capable of flight within 38 days of hatching, but remain dependant on adults for feeding for several months, possibly after leaving the breeding grounds (Groves 1984, Andres and Falxa 1995). Immature oystercatchers may take three years to develop proficient foraging skills (Andres and Falxa 1995). As with other oystercatchers species (Kersten and Brenninkmeijer 1995), high over-winter mortality in the year after hatching may constrain population growth. However, post-fledging information for Black Oystercatchers is limited. After hatch year adults become less susceptible to causes of mortality, such as predation, and live over 15 years (Andres and Falxa 1995). Members of other *Haematopus* species are known to live for over 40 years in the wild (Ens et al. 1996).

### 1.3. STUDY OBJECTIVES

Harriman Fjord, in northwest Prince William Sound, hosts one of the highest concentrations of breeding Black Oystercatchers in Alaska (Tessler et al. 2007). Productivity is low in the area, with many nests failing to depredation and tidal flooding (Brown et al. 2004). Although causes of low reproductive success have not been studied in detail, Harriman Fjord is more accessible to recreational tourism than much of coastal Alaska, and human use peaks when oystercatchers are incubating and rearing
young. Thus, it is theorized that human recreation, such as camping and kayaking, could affect oystercatcher breeding behavior and success (Brown et al. 2004).

The primary goal of this thesis is to identify and understand natural and anthropogenic factors affecting incubation patterns and nest success in Harriman Fjord. Identifying the causes of low reproductive success and understanding the impacts of disturbance can be challenging because failure events are rarely witnessed and adverse affects of disturbance on reproductive behavior may not necessarily result in reduced fitness (Larivière 1999, Gill et al. 2001). Further, reproductive behavior can be influenced by several proximate factors interacting simultaneously in the environment.

The first objective of this thesis is to determine how individuals allocate time to incubation (chapter 2). Variations in incubation patterns and contributions to incubation attendance are examined by sex, time of day, tide cycle, ambient temperature, and the occurrence of disturbance near nests. Before trying to determine whether incubation is affected by particular types of disturbances, it is essential to understand natural processes influencing incubation. This thesis provides an understanding of gender roles, and other natural factors influencing incubation in a species for which minimal information is available, using extensive observation of adult activity at the nest, facilitated by video monitoring.

The next thesis objectives are to identify the types and frequencies of human and natural activities observed near nesting oystercatchers and document their affects on incubation behavior and reproductive success (chapter 3). Video nest monitoring is one of the most reliable ways to identify disturbances to incubation behavior and threats to nest success (Larivière 1999, Pietz and Granfors 2005).
As human use of coastal ecosystems increases, an understanding of factors influencing shorebird breeding becomes increasingly timely. Results of this work will improve knowledge of life history and identify factors that affect reproductive behavior and success of Black Oystercatchers. This study elucidates several previously unrecognized factors that should be considered in future studies examining the relationships between parental behavior and the impact of human activities on the productivity and demography shorebird populations.


Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430-455.


2. FACTORS AFFECTING INCUBATION PATTERNS AND SEX ROLES OF BLACK OYSTERCATCHERS (*HAEMATOPUS BACHMANI*) IN ALASKA

2.1. ABSTRACT

Understanding factors that influence parental behavior is fundamental to animal ecology and informed conservation practices. Egg care is an aspect of avian parental behavior proximally influenced by a variable environment. This work examines relationships of cyclical (time of day, tide, temperature, seasonality) and stochastic (natural/human disturbance) processes with incubation patterns (attendance, bout lengths, recess rates) of the Black Oystercatcher (*Haematopus bachmani*), a shorebird of conservation concern. Continuous video monitoring of 13 molecularly sexed breeding pairs revealed behaviors poorly documented in the genus. Analyses of 3,177 h of video footage indicated greater nest attendance (54% vs. 42%, *P* < 0.018) and longer incubation bout lengths among females (88 min vs. 73 min, *P* < 0.004), a near doubling of nocturnal bout length, independent of sex (*P* < 0.001), and an influence of tide cycle and ambient temperature on incubation patterns. Incubation bouts interrupted by disturbance were > 50% shorter than un-disturbed bouts (*P* < 0.001). Incubating males departed nests more frequently in response to nest-area disturbance stimuli than females, reflecting the greater role of males in nest defense (*P* < 0.001). Thirty-two percent of video monitored nests failed, primarily due to egg predation by nocturnal mammals, implying higher night-time risk of egg loss. Findings suggest that the sexes exhibit different, but complimentary incubation patterns, facilitating efficient incubation
in a dynamic, fluctuating environment. This study emphasizes the importance of considering patterns of nest behavior and natural disturbances in studies examining the impacts of anthropogenic disturbance.

2.2. INTRODUCTION

Behavior undertaken by an individual that increases the fitness of its offspring and proportion of genetic material it contributes to a population (genetic “fitness”) may be defined as parental care (Emlen and Oring 1977, Clutton-Brock 1991). Animals have finite resources to invest in reproduction within a lifetime (Wittenberger 1981). Thus, a tradeoff exists between the time and energy an individual may invest in current versus future care of offspring (Trivers 1972, Dawkins and Carlisle 1976). Different patterns of parental care evolve in populations as individuals are selected for maximized lifetime reproductive success within social, ecological, and environmental constraints (Williams 1966, Cresswell et al. 2003). Constraints may be highly variable, however, resulting in diverse parental care strategies within and among taxa (Maynard Smith 1977, Clutton-Brock 1991). Understanding factors that influence and regulate patterns of parental care provides a basis for evaluating the effect of disturbance on productivity of wildlife populations, informing conservation efforts (Sabine et al. 2008).

Incubation is a fundamental component of parental care exhibited by most avian species (Skutch 1957). Avian eggs require extensive protection from environmental extremes and predation; newly hatched young are often dependent on adults for provisioning and thermoregulation (Oring 1982). Consequently, shared parental care is
often necessary for breeding success (Lack 1968), facilitating social monogamy in most avian species (Orians 1969). Incubation patterns are driven by physiological requirements of developing embryos and self-maintenance needs of attending parents, under the constraints of cyclically and stochastically fluctuating weather conditions, food availability, and predation risk in the breeding habitat (Skutch 1949, Afton 1980, Smith et al. 2007). Incubation patterns also may be affected by territorial interactions with conspecifics where high quality breeding habitat is limited (Pierce 1997, Møller 2003, Bruinzeel and van de Pol 2004), and may change as the breeding season progresses (Purdy 1985, Pierce 1997, Palestis 2005). While some studies have reported that energetic expenditures are minimal during incubation (Walsberg 1983, Monaghan and Nager 1997), others have shown that costs can be high (Williams 1996), particularly when eggs are thermoregulated at extreme ambient temperatures.

Shorebirds (suborder: Charadrii) exhibit the greatest variation among avian mating systems (Oring and Lank 1982, Reynolds and Székely 1997), have a worldwide distribution (Hayman et al. 1986), and often breed in dynamic environments (Elphick et al. 2001). Therefore, they make ideal subjects for understanding variations in incubation patterns related to parental care strategies and environmental influences. Timing and constancy of shorebird incubation may be influenced by interactions of several proximate factors such as ambient temperature extremes (Cantar [sic] and Montgomerie 1985, Cresswell et al. 2003), tide height and tidal stage (Nol 1984, Thibault and McNeil 1995), predation risk (Larsen et al. 1996, Smith et al. 2007), portion of the 24 h circadian period (Kosztolányi and Székely 2002, Wallander 2003),
and seasonality (Ashkenazie and Safriel 1979, Cuervo 2003). The degree to which parental care is shared between the sexes also influences shorebird incubation patterns (Norton 1972, Kosztolányi et al. 2003). Most shorebirds depend on aquatic ecosystems for much of their lifecycles (Haig et al. 1998), and are at particular risk from anthropogenic alteration of coastal habitats (Morrison et al. 2006, Bart et al. 2007). A working knowledge of parental care patterns is a prerequisite for evaluating the effects of anthropogenic activities on breeding behavior and reproductive success of shorebirds (Weston and Elgar 2005, Sabine et al. 2008).

Oystercatchers (Haematopus spp.) are large shorebirds with a worldwide distribution (Hockey 1996a). Individuals display a high degree of mate and nest-site fidelity (Hockey 1996a, Heg et al. 2003). Oystercatcher chicks are unique among precocial shorebirds in requiring parental feeding for several months after hatching (Lind 1965, Norton-Griffiths 1968), necessitating extended bi-parental care (Hockey 1996a). Thus, extra-pair mating is uncommon (Heg et al. 1993), as it could lead to reproductive failure, which may increase the likelihood of divorce, and fail to benefit either pair member (Cezilly and Nager 1995). As open ground nesters, oystercatchers experience a high rate of egg and chick mortality, largely from predation (Hockey 1996b). Oystercatchers are thought to compete for productive nest sites and aggressive conspecific interactions are common (Bruinzeel and van de Pol 2004). Males are reported to assume more vigilance and defense behaviors, while females incubate more (Nol 1985, Kersten 1996, Banks and Patterson 2002). Complimentary sex roles may facilitate nest protection (Nol 1985). Most oystercatcher foraging opportunities occur
during low tides when invertebrate prey are accessible (Hulscher 1996). Thus, tide
cycle has been reported to influence incubation patterns (Nol 1985, Hockey 1996b, but
see Kersten 1996). Unlike many other shorebirds (Kosztolányi and Székely 2002,
Cresswell et al. 2003), incubation patterns and sex roles of oystercatchers are thought to
be similar between daytime and nighttime (Purdy and Miller 1988), though few data are
available. The effect of ambient temperature on oystercatcher incubation patterns also
has not been well studied, though temperature influences incubation in other shorebirds

The melanistic Black Oystercatcher (H. bachmani) is specially adapted to rocky-
intertidal habitat along the west coast of North America (Andres and Falxa 1995). It
plays a key predatory role in intertidal zones (Marsh 1986, Hahn and Denny 1989) and,
as with other oystercatcher species (Leseberg et al. 2000), is considered a management
indicator of rocky intertidal zones (USDA 2002). With fewer than 11,000 individuals
in the population, (Morrison, et al. 2006) and specialized habitat requirements, the
Black Oystercatcher is listed as a “species of high concern” in the Canadian and U.S.
Several aspects of Black Oystercatcher ecology and life history are poorly understood,
including incubation behavior and parental care, and warrant further study (Andres and

Here I describe incubation patterns and sex roles of Black Oystercatchers
nesting in Prince William Sound, Alaska. My objective was to understand how
environmental factors influenced incubation behaviors of each sex. Variations in
incubation patterns and attendance were examined by sex, portion of the 24 h circadian period (hereafter “time of day”), tidal height and stage, ambient temperature, occurrence of disturbance, stage of incubation, and seasonality. With continuous video monitoring of nests, I assessed incubation patterns on a fine scale generally unattainable using other observational techniques. Extensive documentation of nest activity across all hours and weather conditions gave a complete picture of factors influencing incubation patterns. I also was able to isolate nest departures caused by disturbance, which may otherwise have confounded interpretations of how environmental factors influence incubation patterns and nest success (Weston and Elgar 2005).

2.3. METHODS

2.3.1. Study Area

Research was conducted in Harriman Fjord, Alaska (northwest Prince William Sound; 60° 58’N, 148° 26’W to 61° 7’N, 148° 9’W; Fig. 2.1), a 3 x 20 km mountainous tidal fjord in Chugach National Forest. Tides are extreme, reaching 6 m at their peak (NOAA 2007). Spring and summer weather is frequently cool, wet, and breezy; temperatures ranged from 0° to 18°C during study seasons (Harriman Fjord weather stations, USDA Forest Service, unpubl. data). Black Oystercatchers utilize gravel-sand beaches, alluvial outwash areas, tidal flats, and rock islets for nesting and foraging during breeding. Suspected oystercatcher nest predators in Harriman Fjord include Glaucous-winged Gulls (*Larus glaucescens*), Bald Eagles (*Haliaeetus leucocephala*), Northwestern Crows (*Corvus caurinus*), river otters (*Lutra canadensis*), American

Harriman Fjord is readily accessible by boat from the Port of Whittier (< 200 km from Anchorage), exposing it to a higher intensity of human recreational use than many oystercatcher breeding areas in Prince William Sound, particularly during the peak of oystercatcher nesting (Brown et al. 2004). Thus, the U.S. Forest Service began annual breeding censuses of Black Oystercatchers in Harriman Fjord in 2000, and initiated a monitoring and banding program there in May 2004 (Brown et al. 2004). Territorial oystercatcher pairs (25-29) have been documented in Harriman Fjord annually between May and August (Brown et al. 2004, Spiegel et al. 2006). With an uncommonly high density of nesting Black Oystercatchers, Harriman Fjord has been the site of several recent collaborative projects investigating movement, productivity, and behavior of the species (Tessler et al. 2007).

### 2.3.2. Site Surveys, Nest Checking, and Adult Capture

From early May to late July in 2005 and 2006, weekly oystercatcher surveys were conducted by motor-raft at high to mid tides. Potential breeding habitat (including gravel, cobble, or sand beaches; rocky islets; and cliff ledges) was scanned with 10x40 binoculars and suspected nesting areas were searched on foot. Nests found with one egg were assumed to have been initiated that day. Egg flotation was used to approximate initiation dates of nests found with more than one egg (Mabee et al. 2006). Nests were checked every 3 to 7 days until chick fledging, or failure. Unbanded adult oystercatchers were captured using noose mats, walk-in traps, mist nets, and leg snares.
(Benson and Suryan 1999, Mehl et al. 2003, Gratto-Trevor 2004). Each bird was given a unique color combination of plastic leg bands and a numbered USGS metal band. Fifteen $\mu$l of blood was obtained from the metatarsal vein of each adult, following American Ornithologists’ Union approved guidelines (Oring et al. 1998). Blood samples were molecularly sexed using CHD-Z/CHD-W (Griffiths et al. 1998). Molecular sexing was considered to be the most reliable method for determining sex because Black Oystercatchers are monomorphic in plumage, and considerable overlap exists in size metrics (Andres and Falxa 1995). Bird capture and handling was limited to $<1$ h, and was not attempted until approximately seven days after clutch initiation. No nests were abandoned after capture; incubation typically resumed soon after release.

2.3.3. Video Nest Monitoring

Twenty-two active oystercatcher nests were continuously monitored with weatherproof twin micro-camera and digital video units (SeeMoreWildlife Technologies, Homer, AK; Fig. 2.2) from seven days post-clutch initiation until approximately three days post-hatch (usually around 31 days post-clutch initiation), or nest failure. A camouflaged “close-up” camera was placed 15 cm above ground level, 1 m from each nest, facilitating color-band identification. A second “distance” camera was located 5 m from each nest and 1 m high, providing a wide-angle view of activity surrounding a nest, including stimuli that could cause disturbance. Infrared diodes permitted recording in darkness without disturbing a pair or attracting predators. A digital video recorder (DVR) with a 300 GB hard drive stored footage from both cameras with time and date stamps. The DVR was located 50 m from a nest,
minimizing researcher disturbance during hard drive exchanges and maintenance. Each unit was powered by three 40-watt solar panels, connected to two 100 amp-hour deep cycle batteries, via a voltage regulator.

Video units were similarly configured at each nest when possible (Fig. 2.2), with both cameras facing the water (downslope) and fields of view intersecting at a similar angle (roughly 120°). However, differences in slope and terrain at some nest sites led to variation in detection probabilities of distant activity (> 25 m from the nest). This was especially true during darkness. Each camera unit was placed at a nest randomly chosen from a running list of active nests. Nests were added to the list seven days post-clutch initiation and removed from the list when they failed or neared hatch. True randomization was not possible because 1) only four video units were available, 2) nesting activity was synchronous, 3) nests failed unpredictably, 4) nests on steep cliffs could not support video units, and 5) camera placement was delayed for seven days after laying of the initial egg to avoid nest desertion risk from excessive disturbance (Sanders and Maloney 2002, Williams and Wood 2002). Over 25% (22 of 87) of nests found in Harriman Fjord during 2005 and 2006 were video monitored (Fig. 2.1). Sampling constraints and occasional power failures during prolonged overcast periods resulted in uneven monitoring times among nests, necessitating the use of first nest and re-nest attempts from different pairs to obtain sufficient sample sizes for analyses.

2.3.4. Video Data Extraction

Video footage was viewed on 43 cm color monitors in 4x real time and slowed to real time whenever movement was seen at or near the nest. Footage from close-up
and distance cameras was viewed simultaneously, using a split-screen display, which enabled efficient data collection without missed activity. Oystercatchers were identified by colored leg band combination. Date and time were recorded (to the nearest 1 min) whenever an oystercatcher settled on or departed a nest. Each uninterrupted sitting period, beginning with an oystercatcher settling on a nest, was considered an incubation bout. Footage at each nest was reviewed from camera deployment until the first egg hatched, or nest failure occurred. Incubation bouts in progress at the start or end of a footage segment (incomplete bouts) or during a capture were removed from the dataset.

When an incubating bird departed a nest, ending an incubation bout, footage was slowed to half-time to attempt to determine the reason it departed (hereafter: “departure cause”). Departure cause was considered either an “incubation duty switch”, occurring when a departure was initiated by appearance of an incubator’s mate (within 30 s of departure), or a “disturbance”, when an inter-specific, intra-specific, or environmental (such as tidal flooding) stimulus was observed near a nest within 30 s of departure. Incubators often flushed due to humans and large mammals well before these disturbances were detectable in camera fields of view. Thus, these stimuli were assumed to be responsible for departure if detected on camera up to 10 min after a bird flushed, if it was likely they were in the vicinity before detection (see McGowan 2004).

Departure cause could not be conclusively assigned to > 1/4 of departures because of limitations in video fields of view. In these cases I examined the behavior of departing birds to determine whether departure may have been caused by an undetected disturbance in the area. Agitated flights directly off the nest were more frequently
associated with observed disturbances than with incubation duty switches (>60% vs. <3%). The percentage of agitated flight departures for undetected causes was nearly identical to the percentage for observed disturbances, but far higher than the incidence associated with observed incubation duty switches. Further, the same individual returned to the nest following a departure for an undetected cause a similar percentage of the time as following an observed disturbance (40% vs. 35% departures with incubator returning), suggesting that these were motivated by disturbances near the nest, rather than duty switches. Thus, for purposes of analyses, known and suspected disturbances were combined. Duty switches initiated after the same individual returned to the nest following a departure due to disturbance were omitted from bout length analyses because they were not representative of full, undisturbed bouts. Departure times of <30 s were not recorded if the same individual returned to the nest.

After receiving identical training in standardized data collection procedures, six observers extracted data from over 4,200 h of video footage. Each observer reviewed different portions of footage from each nest, ensuring that potential observer biases were spread out among nests. I randomly spot-checked data for consistency one to three times during review of each nest, detecting no substantial differences among observers.

2.3.5. Environmental and Temporal Variables

Time of day was categorized into “daytime” and “nighttime” in relation to sunset and sunrise times at Harriman Fjord, adjusted for daylight savings time (U.S. Naval Observatory 2007). Throughout each study season, the ratio of nighttime to
daytime ranged from 25:75 in early May and late July to 20:80 during the summer solstice. If over 50% of an incubation bout occurred during daytime or nighttime, it was considered to have occurred during that time of day category. When an incubating bird recessed from the nest for any reason, that recess was considered to have occurred during daytime or nighttime according to the exact time of departure.

I obtained regional tide height measurements in six min intervals (observed “Mean Lower Low Water”, Cordova Tide Station, NOAA 2007), and interpolated readings for each min of both study seasons. In addition to obtaining tide heights, I divided tides into four tide stage categories of equal duration: (FH) falling and high - end of high slack tide falling until median tide in an outgoing cycle; (FL) falling and low - from median tide falling until end of lowest slack tide in the cycle; (RL) rising and low - end of lowest slack tide, rising until median tide in an incoming cycle; (RH) rising and high, from median tide rising until end of highest slack tide in the cycle.

Ambient air temperature was measured at 10 min intervals, using temperature sensors placed approximately 0.5 m off the ground, and HOBO® Micro-station dataloggers (Onset Corporation, USA). Measurements were interpolated to produce a reading every min during each study season. Temperature was logged at two locations in Harriman Fjord (Fig. 2.1) to accurately represent microclimatic differences at nests throughout the study area.

Incubation day was defined as number of days elapsed since clutch initiation. Nests found after clutch completion were backdated from camera-documented hatch dates, to the laying of the first egg, assuming a 27.5 day incubation period, the average
incubation period of nests where both clutch initiation and hatch dates were observed ($n = 9$, SD = 1.0). This estimate is similar to other Black Oystercatcher studies (Purdy 1985, Andres and Falxa 1995). Stage of incubation period was divided between early incubation (incubation day 7 to 17) and late incubation (incubation day 18 to 28).

Differences in incubation patterns relative to the time elapsed in the breeding season were examined by distinguishing first nest from re-nest attempts as indicators of seasonality. Nest attempt was a valid representation of seasonality because attempts were largely synchronous during both years of the study, with nearly all first nests laid during May and early June, and nearly all re-nests laid in mid June and early July.

2.3.6. Data Analyses

I examined variation in three incubation pattern metrics: incubation attendance, average incubation bout length, and incubation recess rate, relative to several cyclical and stochastic explanatory factors. Incubation attendance was the proportion of total nest observation time during which an individual sat on the nest. Combined male and female attendance was the proportion of total nest observation time during which eggs were incubated. Bout length was the mean length of an uninterrupted incubation period for each individual (in min). Recess rate was the total number of nest departures by an incubating individual, divided by the total number of hours it was observed; a standardized rate comparable among birds with different amounts of observation time.

Differences in incubation attendance relative to time of day (daytime vs. nighttime), nest attempt (first nest vs. re-nest), year (2005 vs. 2006), and stage of incubation (incubation day 7-17 vs. incubation day 18-28) were modeled separately
using mixed model analysis of variance (ANOVA; PROC MIXED, SAS Version 9.1, SAS Institute, Inc., Cary, North Carolina). Additionally, I determined how attendance varied between sexes, and whether relationships between attendance and each explanatory variable differed between sexes, by including sex and interactions with sex in each of the four models. Explanatory variables and interactions with sex were modeled as fixed effects, with additional variables identifying nests included as random effects to account for suspected lack of independence within nest pairs. Incubation patterns could be compared between stages of incubation by examining differences between day 7-17 and day 18-28 for each nest, or by time of day by examining differences between nighttime and daytime within each nest. Thus, incubation attendance models including stage of incubation, or time of day relationships were structured as completely randomized strip-plot ANOVAs, with stage or time categories in a first strip, and sex in a second strip within each nest replicate. Alternatively, incubation patterns could be compared between nest attempts by comparing all first nests with all re-nests, and between years by comparing 2005 nests with 2006 nests. Thus, incubation attendance models, including nest attempt or year, were structured as a completely randomized split-plot ANOVA, with nest replicates grouped by first nests vs. re-nests, or 2005 vs. 2006, then split by sex.

Differences in mean incubation bout length between stage of incubation, time of day, nest attempt, and year categories were examined in four additional models using mixed models ANOVA. In addition to investigating how these relationships varied by sex and interactions with sex, I determined whether differences in mean bout length
varied by departure cause (incubation duty switch vs. disturbance), and whether relationships between bout length and other explanatory variables varied by departure cause (by including interactions with departure cause). Explanatory variables and two- and three-way interactions of sex, departure cause, and the others were modeled as fixed effects, with additional variables identifying nests included as random effects to account for suspected lack of independence within nesting pairs. Models including stage of incubation as an explanatory variable were structured as completely randomized block strip plots, including stage of incubation as a first strip, sex as a second strip, and departure cause as a strip within each interaction of stage and sex. Models including time of day were similarly structured, with time of day substituted for stage of incubation. All strips were nested within each nest replicate. Models including either nest attempt or year were structured as completely randomized split-split-plots, with nest replicates grouped by either nest attempt or year, then split by sex, with an additional split by departure cause within each sex.

Differences in recess rate by stage of incubation, time of day, nest attempt, year, sex, and departure cause were examined with the same method used to analyze relationships with bout length. Differences in recess rate were further examined among tide stages (FH, FL, RL, RH), employing a mixed model ANOVA. Comparisons of recess rates could be made among the four tide stage categories within each nest. Thus, this model was structured as completely randomized block strip plot, which included tide stage as a first strip, sex as a second strip, and departure cause as a strip within each interaction of tide and sex. Strips were nested within each nest replicate.
Analyses were conducted on nest means of incubation attendance, incubation bout length, and recess rate. Six of 22 video monitored nests considered to have insufficient coverage (< 100 h per nest) were omitted from all analyses to avoid inclusion of biased means. An additional three nests were omitted from analyses because the sexes of pair members were unknown. Thus most models included 13 nests in analyses. However, in analyses examining relationships of incubation patterns with stage of incubation, six of the remaining 13 nests with known sex pairs and sufficient hours of observation were omitted because they were not monitored during substantial portions of early or late incubation stages. Seven of 13 nests with known sex pairs and sufficient hours of observation were omitted from analyses relating time of day and incubation bout length because an insufficient number of bouts were obtained in all departure cause categories during disproportionately short nights at high latitude.

Bout length and recess rate were loge transformed when responses did not satisfy assumptions of normality and homoscedascity, as assessed graphically (residual vs. fit and normal QQ plots). High leverage outliers remaining after transformations were omitted from analyses (indicated in tables). Although number of hours and bouts differed among nests included in analyses, residuals plots indicated that estimated precision was similar among nests in all models.

Disparity in sample sizes across explanatory variables of interest precluded the efficient use of model selection tools, such as Akaike’s Information Criteria (Burnham and Anderson 1998). Any global model would have been restricted to the sample of nests for which information for all explanatory variables was available. While few
nests \((n = 6)\) had a sufficient number of nighttime incubation bout observations to include in time of day comparisons, nest attempt information was available to use in incubation bout length models for all nests with sufficient video coverage of known sex birds \((n = 13)\). Potential information gained by examining relationships of all variables of interest with separate models outweighed the loss in sample size and power that would have occurred if data were restricted to constraints of model selection. However, it is cautioned that multiple statistical tests compound the chance of confidence intervals failing to contain a “true” parameter value.

I predicted that incubation bout lengths would be positively related to tide heights, because higher tides may restrict access to intertidal foraging resources. After controlling for the confounding influence of disturbance by omitting disturbed bouts, I examined the relationship between incubation bout length and the highest tide height observed during a bout. I used a regression coefficient analysis technique, similar to the method described in Meredith and Stehman (1991), to account for a suspected lack of independence among nest pairs. A linear relationship between tide and bout length was assumed. The overall mean highest tide observed across bouts was subtracted from highest tide recorded during each bout in order to center the explanatory variable. For every nest, bout length was regressed against centered highest tide, sex, and an interaction of sex and tide, resulting in an intercept and slope coefficient for each bird. Each intercept value was interpreted as the mean bout length for an individual at the average highest tide observation during bouts, and each slope was interpreted as the rate of change in bout length relative to the change in highest observed tide. Repeated
measures ANOVA was used to determine whether intercept or slope parameters varied systematically by sex. Coefficient estimates for all individuals were modeled as repeated measures (by nest) in a mixed models ANOVA that included sex, parameter, and a sex by parameter interaction as fixed effects, and nest as a random effect. Covariance was unstructured in this model, permitting differences in magnitudes of variance in coefficient parameters, because a significant difference in parameter means was expected. A significant interaction term would indicate that at least one parameter differed with sex. A non-significant interaction term, with a significant sex term would indicate that the difference in intercepts between females and males was the same as the difference in slopes between females and males. I also tested the prediction that incubation bout lengths, constrained by cold conditions, were inversely related to temperature, using the same regression coefficient analysis technique to examine the relationship between bout length and lowest temperature observed during a bout.

Suspecting that colder temperatures may occur disproportionately at night, I examined whether mean temperatures observed during video monitoring differed between daytime and nighttime, using a two-sample $t$-test. If a significant difference was detected, a relationship found between temperature and incubation bout length could be confounded with the relationship between time of day and bout length. While not predicted, I further examined whether mean tide heights observed during video monitoring differed between daytime and nighttime, using a two-sample $t$-test, to see if tide height was confounded with time of day.
I used the Mayfield method to obtain nest survival estimates (Mayfield 1961, 1975) and confidence intervals (Johnson 1979) for video and non-video monitored nests, to investigate whether monitoring affected nest success. Non-video monitored nests failing before the mean number of days post-clutch initiation when cameras were deployed (day 11) were omitted from the analysis to account for the average interval between clutch initiation and commencement of video monitoring. Including these nests in analyses would have inflated survival rate estimates of video monitored nests. I assumed homogeneity in survival probability across days of incubation and assigned nest failure times to the midpoint between checks if failure date was unknown.

Estimates from all models are reported as means with exact 95% confidence intervals from a \( t \)-distribution, unless indicated. Analyses involving explanatory variables included in multiple models are presented as a range of estimates and confidence intervals. \( \log_e \) transformed estimates and confidence limits were back-transformed for reporting, unless indicated. All tests were significant at \( \alpha = 0.05 \).

2.4. RESULTS

2.4.1. Video Nest Documentation, Nest Failure, and General Incubation Patterns

I reviewed 4,280 h of footage from 22 nests (11 per season; Fig. 2.1), documenting 3,398 incubation bouts. Seven of 22 (32%) nests failed during incubation, four from nocturnal mammalian predation (2 American mink, 1 pine marten, 1 wolverine), one from diurnal mammalian predation (black bear), and two from tidal flooding during a spring tide event. The Mayfield daily survival estimate for video

monitored nests was 0.970 (95% CI: 0.948-0.992), nearly identical to the survival estimate for non-video monitored nests (0.970, 95% CI: 0.955-0.985, n = 27 nests). No mortality of video monitored adults was observed during either field season. No behavioral differences were witnessed between video monitored and non-video monitored pairs, nor was there evidence that cameras were detected by pairs, or attracted other animals to a territory.

Sufficient coverage was obtained to examine general patterns of incubation behavior at 16 nests. Nests were attended an average of 96% of the time (± 3% SD), with a mean incubation bout length among all individuals lasting 78 min (± 20 SD). A mean of 0.78 incubation recesses occurred per hour (± 0.16 SD), or nearly 19 (± 4 SD) recesses per 24 h period. Data were further subdivided by sex using 13 molecularly-sexed nesting pairs (3,177 h of footage) to examine differences in incubation patterns between sexes (Table 2.1). Subsequent results are based on these pairs, unless noted.

2.4.2. Incubation Attendance

Incubation attendance was higher for females than males (P < 0.018 all models; Table 2.2); mean female attendance was 0.53-0.55 (95% CI range: 0.47-0.53 to 0.57-0.59, depending on model), while mean male attendance was 0.41-0.43 (95% CI: 0.37-0.39 to 0.43-0.49, depending on model). Sex differences were greater for re-nests than for first nests (P = 0.005 for ‘sex x attempt’ interaction; Table 2.2).

No significant difference in overall incubation attendance was detected between daytime and nighttime, after accounting for sex (P = 0.90, n = 13 nesting pairs; Table 2.2), nor was there evidence that incubation attendance varied between 2005 and 2006
(P = 0.623, Table 2.2), first or re-nests (P = 0.789, Table 2.2), or early (day 7 through 17 post-clutch initiation) and late (day 18 through 28 post-clutch initiation) stages of incubation (P = 0.940, Table 2.2), after accounting for sex. Low sample sizes prevented examination of time of day differences in attendance between males and females within separate years, nest attempts, or stages of incubation.

2.4.3. Incubation Bout Length

Median incubation bout length of females (88-90 min, 95% CI range: 77-78 to 99-106 min depending on model) was 21-24% longer (95% CI range: 8-36 to 11-40%, depending on model) than bout length of males (73 min, 95% CI range: 62-64 to 82-85 min, depending on model) in models including the full set of 13 nests (P < 0.004; Fig. 2.3). A non-significant difference in bout length between sexes in models with smaller sample sizes (P = 0.093 - 0.102; Table 2.2) was likely a result of low power to detect a difference, rather than lack of a difference.

The median length of incubation bouts ending due to disturbance (56-73 min, 95% CI range: 49-61 to 63-87 min, depending on model) was 52-70% shorter (95% CI range: 34-72 to 51-92%, depending on model) than bouts ending with an incubation duty switch (94-110 min, 95% CI range: 84-92 to 106-132 min, depending on model), regardless of sex (P < 0.001 in all models; Table 2.2; Fig. 2.3). This indicated a strong relationship between disturbance and incubation patterns of both pair members.

Mean incubation bout length was 81% longer (95% CI: 56 to 110%) during nighttime (120 min, 95% CI: 96 to 150 min) than during daytime (67 min, 95% CI: 53 to 83 min), independent of sex or departure cause (P < 0.001; Table 2.2; Fig. 2.3).
Short nights during spring and summer, at the high latitude of our study area, resulted in only six nests with a sufficient sample of nighttime bouts to warrant inclusion in the model examining time of day.

Differences in incubation bout length between sexes or disturbance causes did not vary by year, nest attempt, or stage of incubation (Table 2.2). No difference in incubation bout length was detected between first and re-nest attempts ($P = 0.942$, Table 2.2), nor between early and late stages of incubation ($P = 0.640$, Table 2.2). However, median bout length was 38% longer (95% CI: 12 to 69%) in 2006 (94 min, 95% CI: 82 to 108 min) than in 2005 (68 min, 95% CI: 59 to 79 min) independent of sex and departure cause ($P = 0.006$, Table 2.2).

A strong positive relationship was found between incubation bout length and the highest tide height observed during a bout, as indicated by a significant slope estimate ($t_{36} = 4.4$, $P < 0.001$; Fig. 2.4A). Bout lengths were estimated to be 20% longer (95% CI: 10 to 30%) for each additional 1 m in the level of highest tide height observed during a bout. This relationship did not vary between males and females, nor was a sex-based difference detected in the mean incubation bout length across highest observed tides; as indicated by a non-significant interaction between sex and the parameter for intercept and slope from regression models ($F_{1, 36} = 1.0$, $P = 0.336$, $n = 13$ nests), and a lack of significant difference in the sex parameter ($F_{1, 36} = 0.3$, $P = 0.598$). Tide heights were significantly higher at night ($P < 0.001$). Thus, the relationship between tide height and bout length could have been an artifact of longer bouts occurring at night when higher tide heights were more frequent.
A significant inverse relationship was found between incubation bout length and lowest temperature observed during a bout, as indicated by a slope estimate significantly different than zero \((t_{36} = -2.8, P = 0.008; \text{Fig. 2.4B})\). However, the effect of the relationship was minor, as evidenced by a shallow slope. Bout lengths were only estimated to be 3% (95% CI: 1 to 5%) longer for each 1°C reduction in lowest temperature observed during a bout. This relationship did not vary between males and females, nor was a sex-based difference detected in the mean incubation bout length across lowest observed temperatures; as indicated by a non-significant interaction between sex and the parameter for intercept and slope from regression models \((F_{1,36} = 1.8, P = 0.185, n = 13 \text{ nests})\) and a lack of significant difference in the sex parameter \((F_{1,36} = 1.3, P = 0.273)\). Significantly colder temperatures occurred at nighttime \((P < 0.001)\). Thus, the relationship between temperature and bout length could have been an artifact of longer bouts occurring at night when cold temperatures were most frequent.

### 2.4.4. Incubation Recess Rate

The female incubation recess rate was lower than the male rate. The median number of female recesses per hour (0.26-0.35, 95% CI: 0.21-0.29 to 0.31-0.42, depending on model) was 19-23% lower (95% CI range: 1-3 to 33-39%, depending on model) than the number of male recesses per hour (0.33-0.46, 95% CI: 0.28-0.39 to 0.40-0.52, depending on model) in models including all 13 nests \((P < 0.044; \text{Table 2.2})\). This corroborated the finding of longer female incubation bout lengths, as fewer recesses result in longer, uninterrupted bouts.
The difference between female and male incubation recess rates resulted from a difference between sexes in the rate of incubation bouts ending due to disturbance, rather than due to incubation duty switches ($P < 0.040$ for a departure cause x sex interaction; Table 2.2). While no significant difference between sexes was detected in the rate of recesses for incubation duty switches ($P > 0.600$), there was a highly significant difference between sexes in the rate of recesses due to disturbance ($P < 0.001$). The median rate of recesses due to disturbance was 37-38% lower (95% CI range: 11-20 to 51-58%, depending on model) for females (0.31-0.35 recesses per h, 95% CI: 0.25-0.26 to 0.38-0.44, depending on model) than males (0.49-0.59 recesses per h, 95% CI: 0.40-0.51 to 0.59-0.70, depending on model), denoting that males responded more to disturbance stimuli than females. Overall, the rate of recesses due to disturbance was greater than the rate of recesses for incubation duty switches ($P < 0.018$; Table 2.2), largely due to a higher frequency of male bouts ending due to disturbance. Much of the discrepancy between males and females in the rate of disturbance-caused departures can be attributed to an extremely high male disturbance departure recess rate during 2005 (0.81 recesses per h, 95% CI: 0.69 to 0.94), compared with recess rates for other sex, departure cause, and year combinations (as indicated by a significant interaction of ‘year x sex x departure cause’, $P = 0.002$; Table 2.2; Fig. 2.5). This resulted in a significantly higher overall recess rate in 2005 than 2006 ($P = 0.007$, Table 2.2).

The high rate of male disturbance recesses in 2005 corresponded with a higher female rate of recesses for incubation duty switches in the same year (0.42 recesses per
h, 95% CI: 0.29 to 0.55 in 2005, compared with 0.28 recesses per h, 95% CI: 0.16 to 0.40 in 2006; Fig 2.5). During 2005 females may have compensated for a high disturbance recess rate of their mates by regularly replacing disturbed males at the nest. Thus, females would be more frequently on the nest for duty switches when males returned after a disturbance recess. This supposition is supported by the finding that males were more likely to be relieved by their mate after a departure attributed to disturbance than were females ($\chi^2 = 8.3, P = 0.004$). Male recess rate for duty switches was correspondingly low in 2005 (0.28 recesses per h, 95% CI: 0.15 to 0.40), indicating that most male recesses were initiated by responses to disturbance in 2005.

The mean recess rate was 91% greater during daytime than during nighttime, independent of sex and departure cause ($P < 0.001$; Table 2.2), supporting the finding of far shorter diurnal incubation bouts. The 95% confidence interval ranged from 49 to 143% due to high variability in recess rate by nest (especially at night). Results were similar for 2005 and 2006, and for first nests and re-nests.

No significant difference in recess rates were detected among the four tide stages ($P = 0.066$; Table 2.2). However, the relationship was near-significant, owing to differences in the recess rates during the low-incoming (RL) tide stage (0.38 recesses per h, 95% CI: 0.31 to 0.47) versus the high-outgoing (FH) tide stage (0.28 recesses per h, 95% CI: 0.23 to 0.34). Although differences in recess rates by tide stage were not significant, the finding of increased recess rates during lower tide stages agreed with the finding of longer bout lengths during higher tides.
Recess rates were not significantly different between first nests and re-nests \( (P = 0.913) \), nor between early and late stages of incubation \( (P = 0.629, \text{Table 2.2}) \).

2.5. DISCUSSION

Where bi-parental care is necessary for reproductive success, natural selection favors efficient, long-term pair bonds, and synchronization of care activities within pairs (Emlen and Oring 1977). Balancing self-maintenance needs with constant incubation is difficult without the benefit of shared attendance (Norton 1972). Such high attendance is rarely possible in shorebirds with uniparental care (Cantar [sic] and Montgomerie 1985). Similarly, this study found that bi-parental participation in incubation facilitated a high level of nest attendance, as reported in other oystercatcher studies (range: 0.90 - 0.98, Helbing 1977, Nol 1985, Purdy and Miller 1988).

Incubating males recessed more frequently in response to disturbances than did females, resulting in shorter male incubation bouts and lower male nest attendance. Females often replaced males at the nest after a disturbance that caused the male to depart. Nol (1985) reported similar findings in American Oystercatchers \( (H. palliatus) \), concluding that cumulative energy investment in breeding was nearly equal between sexes, but resource allocation differed. Males expended more energy in territory defense and flight, balancing initially costly female investment in egg-laying. Nol proposed that complimentary sex roles had evolved to maximize energetic efficiency, with smaller males more suited to chase flights (lighter wing loadings), and larger females more suited to maintaining egg temperatures. This hypothesis may explain
incubation patterns of Black Oystercatchers at Harriman Fjord. However, while males left the nest due to disturbance at a far higher rate than females in 2005, rates were similar between sexes during 2006. It is possible that males recess for disturbances at a higher rate than females only when high numbers of disturbance stimuli are encountered, as more potential disturbance stimuli (particularly humans and conspecifics) were observed near nests at Harriman Fjord in 2005 than 2006 (see chapter 3). However, additional study is required to assess whether males typically assume the dominant role in nest defense.

Findings from this work indicate that disturbance stimuli greatly influence incubation patterns in Black Oystercatchers. Well over half of nest departures were attributed to disturbance stimuli. Disturbed bouts were half as long as bouts ending with undisturbed duty switches. Incubators were regularly observed leaving a nest to chase conspecific and interspecific intruders in their breeding territory, including much larger birds and mammals (C.S. Spiegel, unpubl. data). I suggest that oystercatchers employ a “guard and chase” strategy in response to high levels of nest area intrusion (Helbing 1977, Nol 1985), rather than a “conceal and hide” strategy common in many smaller shorebirds (Thibault and McNeil 1995, Pierce 1997, Weston and Elgar 2005). Oystercatchers are among the largest representatives of the order Charadriiformes (Hockey 1996a). Adults have low mortality rates (Hockey 1996b), with few predators posing serious risks. Conversely, oystercatcher species have conspicuously large eggs, experiencing frequent nest and chick depredation (Andres and Falxa 1995, Hockey 1996b). A guard and chase strategy is adaptive under these life history conditions. Bi-
parental care with shared sex roles facilitates guarding and chasing, allowing flexible responses to stochastic disturbance events under fluctuating environmental constraints, without compromising an individual’s self-maintenance needs, or preventing nearly continuous nest attendance.

Access to intertidal oystercatcher foraging resources is limited during high tides (Hulscher 1996, Hockey 1996b). In Harriman Fjord incubation bout length was positively related to the height of the highest tide observed during a bout. This relationship indicates that individuals spend more time engaged in continuous incubation when high tides render foraging conditions unsuitable. There was suggestive, but inconclusive evidence that recess rates were higher during low, incoming tidal stages than during high, outgoing stages, implying that activity levels increase during tide stages when intertidal resources are available. Peak foraging activity of incubating Black Oystercatchers reportedly occurs within an hour of low tide (Helbing 1977).

Temperature extremes are known to influence avian incubation schedules (Conway and Martin 2000), especially in ground-nesting shorebirds (Cantar [sic] and Montgomerie 1985, Cresswell 2003 et al.). Low temperatures can impede embryo development and drain adult energy reserves during long bouts, constraining incubation scheduling (Conway and Martin 2000). Ambient temperatures at Harriman Fjord were frequently between 4° and 7° C during the study; a temperature which would preclude embryo development while eggs were unattended (Webb 1987). Although longer incubation bouts occurred in conjunction with lower ambient temperature observations,
temperature was probably not the direct cause of longer bouts because: 1) recesses were rarely long enough to result in substantial temperature changes of slow-cooling, high-volume oystercatcher eggs, even during low temperatures (Webb 1987), 2) bi-parental care permitted frequent incubation switches between mates, limiting times during temperature extremes when incubation would prohibit pair members from being able to engage in self-maintenance activities, and 3) eggs of shorebirds breeding in high latitudes have unusually high tolerances to cooling (Norton 1972, Cantar [sic] and Montgomerie 1985). The relationship between ambient temperature and incubation bout length may be related to variation in bout lengths by time of day, since lower temperatures were associated with nighttime periods.

While changes in incubation patterns have been documented in shorebirds relative to time of day (Thibault and McNeil 1995, Kosztolányi and Székely 2002), information is limited (Warnock and Oring 1996), especially for oystercatchers. Purdy and Miller (1988) reported that incubation bout durations of Black Oystercatchers were similar during daytime and nighttime. However, data were collected from a small sample of breeding pairs, observed during only three nights. In contrast, I determined that nocturnal incubation bouts were nearly twice as long as diurnal bouts, with correspondingly lower nighttime recess rates. Reduction in suitable foraging opportunities at night could have led to the observed incubation patterns, as fewer foraging opportunities would decrease feeding motivated recesses. This seems counterintuitive because access to intertidal food resources is primarily regulated by height and stage of the tide, rather than the time of day (Hulscher 1996). However, in
many areas with semidiurnal tides, particularly those with high declinations, tidal amplitudes within a day are uneven (Hicks 2006). Such “diurnal inequality” is common in Harriman Fjord and results in higher high tides during nighttime than during daytime (NOAA 2007). Thus, the relationship between time of day and incubation patterns may be related to tide cycle and food availability. Subsequent studies of tidally regulated shorebirds should consider the influence of diurnal inequality if divergent nocturnal foraging patterns are detected.

Increased predation risk also could explain the differences in incubation patterns between daytime and nighttime. Skutch (1949) theorized that increased parental activity near nests led to higher rates of failure and would be selected against. Although empirical tests of this prediction have produced conflicting conclusions (Roper and Goldstein 1997, Martin et al. 2000), experiments have confirmed that nest activity levels may vary in response to perceived predation risk (Ghalambor and Martin 2002). Despite disproportionately short nights during research in Harriman Fjord oystercatcher nest failure was primarily caused by nocturnal or crepuscular mustelid predators, known to supplement their diets with eggs (Feldhamer et al. 2003). Video observation confirmed an increase in mammalian activity near nests at night (see chapter 3). Thus, the species composition of active predators in Harriman Fjord changed at night, potentially posing higher risks. In agreement with Skutch’s (1949) hypothesis, this may imply that selection has favored oystercatchers with lower nocturnal recess rates, and longer bouts. Other oystercatcher studies also have noted a preponderance of nocturnal nest predation (McGowan 2004, Sabine et al. 2006), particularly on mainlands
accessible to mammals. Mink, the nocturnal nest predator species most frequently documented on video at Harriman Fjord, regularly prey on large adult waterbirds (Sullivan, 1996). Therefore, nocturnal bout changes also could be perilous to adult oystercatchers, which would have a harder time detecting stealthy predators in darkness. Because oystercatcher activity decreased at night throughout the study site, fewer interactions with other nesting pairs would be expected. Fewer conspecific interactions would result in fewer recesses due to disturbance, and increased nocturnal bout lengths.

Sample sizes of nests included in incubation attendance, bout length, and recess rate analyses were small when separated by stage of incubation, nest attempt, and year, possibly resulting in insufficient power to detect differences. Thus, caution should be used in interpreting these results. Further, analyses did not include an assessment of incubation patterns from clutch initiation through day six of incubation, and thus failed to detect differences during the earliest stages of incubation. Despite these limitations, video monitoring permitted the collection of an extensive and largely continuous record of incubation behavior, providing strong evidence for several associations. Video documentation arguably produces the most complete assessment of incubation activity. Future studies of oystercatcher incubation could utilize more recording units simultaneously to alleviate issues associated with small sample sizes. This is increasingly feasible as camera and digital video recording technology becomes more efficient and cost-effective (Sabine et al. 2005, Pierce and Pobprasert 2007). Based on the outcome of a recent American Oystercatcher video study (Sabine et al. 2008) it is now evident that cameras could be placed at nests prior to seven days post-clutch
initiation without adverse effects providing a more complete picture of early incubation activity. Because limitations in camera field of view prevented certainty of causes for 25% of departures, future video studies should also use field observers to systematically verify that assumed disturbance recesses are motivated by disturbance stimuli.

Disturbance stimuli were strongly related to incubation patterns, illustrating the importance of considering influences of natural and human disturbance stimuli in studies of breeding shorebird behavior (as in Sabine et al. 2008). Both types of disturbance likely play a part in the evolution of parental behavior. Proximate behavioral responses to disturbance stimuli do not necessarily reflect the impact they have on a population, however (Gill et al. 2001). Relationships between behavioral responses to disturbance and survival and fecundity must be examined. Black Oystercatchers are ideal study organisms for assessing these relationships because they frequently and conspicuously interact with stimuli in the nest area. While the number of failed nests documented with video in Harriman Fjord was too small for analyzing differences in nest survival based on individual responses to stimuli, data were sufficient to assess how the type of stimulus and its proximity to a nest affected Black Oystercatcher incubation behavior, laying the groundwork for assessing threats to productivity in the species (see chapter 3).

Understanding behavioral changes induced by environmental and temporal variation is a crucial prerequisite to evaluating the effects of human disturbance on poorly known species and implementing conservation measures, if needed. Incubation
patterns of Black Oystercatchers nesting in Harriman Fjord varied depending on temporal and environmental processes, while incubation attendance remained high and constant across nesting pairs. Analyses were conducted on an uncommonly extensive and continuous dataset of incubation behavior. This study identifies incubation patterns that enable pairs to efficiently care for nests in a dynamic environment experiencing disturbance and predation risks, tidal fluctuations, and weather extremes.

2.6. ACKNOWLEDGMENTS

I thank the U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, USDA Forest Service, and National Fish and Wildlife Foundation for funding. I am particularly indebted to my academic advisor, Dr. Susan Haig, for guidance, encouragement, and patience, and to Dr. Michael Goldstein for insight and support. This work would not have been possible without the statistical guidance of Manuela Huso. Invaluable logistics, planning, and field work were provided by B. Brown, R. Crandall, A. Poe, B. Venable, and other staff and volunteers of the Chugach National Forest’s Glacier Ranger District. I also am exceptionally grateful to my hardworking technicians B. Cline and E. Krantz for their dedication in and out of the field. B. Guzzetti kindly contributed extra field assistance and performed molecular sexing for the project. I appreciate advice and field time provided by D. Tessler, and the generous volunteer efforts of students and teachers of Rowland St. Marks School, and Babkin Charters. I thank J. Bridges, B. Carroll, D. Gagliasso, E. Krantz, S. Peterman, and B. Powers of Oregon State University (OSU) for reviewing thousands of hours of video. I
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2.7. LITERATURE CITED


Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430-455.


Table 2.1. Number of hours of camera observation at each nest used in incubation analyses for Black Oystercatchers in Harriman Fjord, Alaska, 2005-2006 ($n = 13$ nests).

<table>
<thead>
<tr>
<th>Nest</th>
<th>Hrs obs. $^a$</th>
<th>Nest attempt</th>
<th>Incubation coverage $^b$</th>
<th>Year</th>
<th># bouts / sex</th>
</tr>
</thead>
<tbody>
<tr>
<td>101-05</td>
<td>360.7</td>
<td>First</td>
<td>7 to 28</td>
<td>2005</td>
<td>124 / F</td>
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<td></td>
<td></td>
<td>158 / M</td>
</tr>
<tr>
<td>109-05</td>
<td>351.2</td>
<td>Re-nest</td>
<td>10 to 28</td>
<td>2005</td>
<td>143 / F</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>156 / M</td>
</tr>
<tr>
<td>110-05</td>
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<td>Re-nest</td>
<td>17 to 27</td>
<td>2005</td>
<td>64 / F</td>
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<td></td>
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<td>2006</td>
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<td>22 to 28</td>
<td>2006</td>
<td>40 / F</td>
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<td></td>
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<td></td>
<td>37 / M</td>
</tr>
</tbody>
</table>

$^a$Includes unattended periods.

$^b$Days after laying 1st egg (mean clutch initiation to hatch duration = 27.5 days).
Table 2.2. Mixed models ANOVA results for analyses of incubation attendance, bout length, and recess rates among Black Oystercatchers in Harriman Fjord, Alaska, 2005 - 2006.

<table>
<thead>
<tr>
<th>Model</th>
<th>Variables</th>
<th>Attendance</th>
<th>Incubation Bout Length</th>
<th>Incubation Recess Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$n^a$ $F$ $df^b$ P</td>
<td>$n^a$ $F$ $df^b$ P</td>
<td>$n^a$ $F$ $df^b$ P</td>
</tr>
<tr>
<td>Time of Day c</td>
<td>Time of day</td>
<td>13 &lt; 0.1 1,12 0.900</td>
<td>6 101.6 1,5 &lt; 0.001</td>
<td>13 34.7 1,10 &lt; 0.001</td>
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<tr>
<td></td>
<td>Sex</td>
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<td>4.0 1,5 0.102</td>
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<td></td>
<td>Departure cause (DC)</td>
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<td>50.6 1,5 &lt; 0.001</td>
<td>11.9 1,10 0.001</td>
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<td>Time of day x sex</td>
<td>1.6 1,12 0.233</td>
<td>1.0 1,20 0.371</td>
<td>0.2 1,44 0.685</td>
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<td>Time of day x DC</td>
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<td>3.0 1,20 0.099</td>
<td>3.0 1,44 0.092</td>
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<td>Sex x DC</td>
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<td>0.1 1,20 0.818</td>
<td>3.6 1,44 0.064</td>
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<td>Time of day x sex x DC</td>
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<td>&lt; 0.1 1,20 0.951</td>
<td>0.1 1,44 0.722</td>
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<td>Incub. Stage d</td>
<td>Incubation stage</td>
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<td>Stage x DC</td>
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<td>2.4 1,24 0.132</td>
<td>0.2 1,24 0.707</td>
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-continued-
Table 2.2. Continued. Mixed models ANOVA results for analyses of incubation attendance, bout length, and recess rates among Black Oystercatchers in Harriman Fjord, Alaska, 2005 - 2006.

<table>
<thead>
<tr>
<th>Model</th>
<th>Variables</th>
<th>Attendance</th>
<th>Incubation Bout Length</th>
<th>Incubation Recess Rate</th>
</tr>
</thead>
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<td></td>
<td>$n^a$</td>
<td>$F$</td>
<td>df$^b$</td>
</tr>
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<td>1,11</td>
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<td>1,11</td>
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$^a$ $n$ = number of nests.

$^b$ df = numerator degrees of freedom, denominator degrees of freedom.

$^c$ Seven nests omitted from time of day model for incubation bout length due to insufficient data during nighttime; Outlying observations from two individuals from different nests (one male, one female) omitted from time of day model for incubation recess rate.

$^d$ Six nests omitted from all incubation stage models due to insufficient data within an incubation stage.
Figure 2.1. (A) Location of Prince William Sound in Alaska. (B) Location of Harriman Fjord study area within Prince William Sound. (C) Locations of video monitored, and non-video monitored Black Oystercatcher nests by year, and locations of temperature stations within the study area.
Figure 2.2. Video monitoring configuration showing (A) close-up camera position (1 m from nest), (B) distance camera position (5 m from nest), and (C) power source and digital video recorder (50 m from nest).
Figure 2.3. Differences in mean duration of incubation bouts in Black Oystercatchers due to time of day, sex, and cause of departure, with 95% confidence interval bars. (a) estimates from nest attempt model with 13 nests, (b) estimates from year model with 13 nests. Estimates are back-transformed from the natural log scale.
Figure 2.4. Regression lines for the relationship of each male \((n = 13)\) and female \((n = 13)\) Black Oystercatcher incubation bout length with (A) highest tide observation during a bout, and (B) lowest temperature observation during a bout. Bouts ending due to disturbance are not included. Bold lines indicate mean of all individual regression lines.
Figure 2.5. Mean Black Oystercatcher incubation recess rate by year, sex, and departure cause, with 95% confidence interval bars.
3. THE INFLUENCE OF POTENTIAL NEST AREA DISTURBANCE ON BLACK OYSTERCATCHER INCUBATION AND NEST FAILURE IN ALASKA

3.1. ABSTRACT

Demographic patterns of avian populations cannot be adequately understood without identification of anthropogenic and natural factors that adversely affect reproductive behavior and success. In this study, Black Oystercatcher (*Haematopus bachmani*) nests were continuously video monitored to document the types and frequencies of natural and human stimuli occurring near birds incubating in an area of Alaska which experiences regular recreational use. The study further assessed whether stimuli disrupted incubation activity and affected nest success in this shorebird of conservation concern. Nearly 70% of 791 stimulus events observed in within 25 m of a nest were other bird species. Incubating oystercatchers departed in response to an average of 31% (± 21% SD) of stimuli observed within 25 m of nests, and an average of 44% (± 23% SD) of stimuli observed within 5 m of nests. A significantly greater proportion of conspecifics and humans (over 65%) disrupted incubation than did other bird species (under 15%; $P < 0.001$), when observed within 25 m of nests. While nearly 50% of mammals observed within 25 m of nests disrupted incubation, they were uncommonly observed in nest areas. A smaller percentage of incubation disruptions were attributable to humans (21% ± 10% SD) than conspecifics (41% ± 10% SD). Nests were left unattended for longer periods following human disruption of incubation (14 min ± 8 min SD) than following disruption by any other type of stimuli.
Unexpectedly, daily survival rates of nests within 200 m of shoreline used for camping or other human recreation activities was higher than in other areas, and nest failure was not related to an increased rate of humans or other stimuli observed near nests. Because disturbance intensity may have been too low to reduce nest success, future work should be conducted in breeding areas experiencing higher levels of human disturbance.

3.2. INTRODUCTION

Most shorebird species depend on aquatic ecosystems for much of their lifecycles (Haig et al. 1998) and face risks from expanding human uses of coastal habitats (Şekercioğlu et al. 2004, Morrison et al. 2006, Bart et al. 2007). This results in habitat destruction (Yasué and Dearden 2006), introduction of exotic species (Dowding and Murphy 2001, Jackson et al. 2004), and conflicts with recreational activities (Ruhlen et al. 2003, McGowan and Simons 2006). An understanding of natural and anthropogenic factors that affect behavior and reproductive success in shorebirds is important because these factors can have adverse impacts on demography and population persistence (Weston and Elgar 2005, Sabine et al. 2008). This information also is valuable for understanding selective processes that shape reproductive strategies (Ricklefs 2000, Ghalambor and Martin 2002).

Identifying causes of nest failure is rarely straightforward. While predation has often been identified as a primary cause of avian nest loss (Ricklefs 1969, Martin 1992), predation events are infrequently witnessed and predators are seldom identified with
certainty (Lariviére 1999). Human disturbance can also indirectly promote reproductive failure by inducing adverse behavioral changes in breeding birds, but the mechanisms are often difficult to document (Gill et al. 2001).

Skutch (1949) predicted that increased parental activity at nests would attract predators and leave offspring exposed to higher levels of predation. While studies testing the ‘Skutch hypothesis’ have produced mixed conclusions (Roper and Goldstein 1997, Martin et al. 2000), it has recently been invoked to explain detrimental effects of human disturbance on shorebird reproduction (McGowan and Simons 2006, Smith et al. 2007). Humans have been further implicated in indirectly promoting nest and chick failure by attracting predator populations to breeding areas (Tjørve and Underhill 2008), displacing breeding pairs (Morse et al. 2006), and interfering with parental care (Ruhlen et al. 2003). The effects of disturbance are dependent on a variety of interacting factors, including the type and intensity of disturbance (Frid and Dill 2002, Tarlow and Blumstein 2007), parental response (Montgomerie and Weatherhead 1988, Whittaker and Knight 1998), and breeding habitat (Hockey 1982, Vermeer et al. 1992).

Three of the world’s 11 oystercatcher species (Family Hematopodidae) have fewer than 5,000 individuals in their populations, and several others have less than 15,000 (Hockey 1996a, Morrison et al. 2006). Population trends vary by species, but, in many cases, are not well studied (Hockey 1996a,b). Adult oystercatchers are long-lived and generally have high annual survivorship (Andres and Falxa 1995, Hockey 1996b). However, reproductive success is low and variable among year, site, and species (Hockey 1996b). Predation by birds and mammals is a predominant cause of nest and
chick failure (Andres and Falxa 1995, Sabine et al. 2006, Tjørve and Underhill 2008). Tidal flooding and adverse weather also are responsible for considerable nest loss (Hartwick 1974, Lauro and Nol 1993, Nol 1989, Calf and Underhill 2005, Morse et al. 2006). Human coastal use likely contributed to the extinction of the Canarian Black Oystercatcher (H. meadewaldoi; Hockey 1987), and historic hunting and egg collecting (Jehl 1985, Nol and Humphrey 1994), pollution (Lambeck et al. 1996, Andres 1997), and introduction of exotic predators (Byrd et al. 1997, Dowding and Murphy 2001) have had adverse impacts on other oystercatcher species. As recreational tourism has increased over the last decades (Flather and Cordell 1995), recent studies have examined the impacts of recreational activity on oystercatcher reproductive behavior and success (Leseberg et al. 2000, McGowan and Simons 2006, Morse et al. 2006).

Black Oystercatchers (H. bachmani) are adapted to rocky-intertidal habitat along the western coast of North America (Andres and Falxa 1995). As a key predator within intertidal zones (Marsh 1986, Hahn and Denny 1989) they are considered a management indicator species for rocky intertidal ecosystems (USDA 2002). With fewer than 11,000 individuals in the population (Morrison et al. 2006) and specialized habitat requirements, the Black Oystercatcher is listed as a “species of high concern” in the Canadian and U.S. National Shorebird Conservation Plans (Donaldson et al. 2000, Brown et al. 2001). While research has shown that predation contributes to low reproductive success, several aspects of the species’ ecology and life history are poorly understood, including the extent to which natural and human stimuli affect breeding behavior and productivity (Andres and Falxa 1995, Tessler et al. 2007).
Over half of Black Oystercatchers breed in Alaska (Tessler et al. 2007), with particularly high nesting concentrations found in Prince William Sound and other portions of the state’s south-central coastline (Andres 1998). This area is a popular destination for backcountry recreational activities, particularly during the peak of oystercatcher nesting season (Brown et al. 2004, Morse et al. 2006). In 2004, Black Oystercatcher productivity was monitored in Harriman Fjord, northwestern Prince William Sound, an area of high breeding density for the species (Tessler et al. 2007). Only two of 25 nesting pairs hatched young (Brown et al. 2004). River otter (*Lutra canadensis*) depredation and tidal flooding were suspected as the primary causes of low reproductive success. However, further work was warranted because failures were not witnessed (Brown et al. 2004) and it was unknown whether recreation and research activities increased the probability of nest failure.

In 2005 and 2006, I studied incubation patterns, sex roles, and behavior of Black Oystercatchers nesting in Harriman Fjord using continuous video monitoring. Results of this work indicated that incubation patterns were affected by disturbances near the nest, predation risk varied between daytime and nighttime, and oystercatchers employed complimentary sex roles to facilitate vigorous nest defense (see chapter 2). Here I expand upon these findings, examining how different stimuli affect incubation behavior and whether behavioral responses affect nest success. Objectives of my study included: (1) identify natural and human stimuli having the potential to disturb incubation activity near oystercatcher nests, (2) quantify associated behavioral responses of birds disrupted from incubation, and amounts of time nests were left unattended following disruption,
(3) investigate whether increased parental activity at nests related to decreased nest success, and (4) determine whether nest survival was lower for nests closer to recreational shoreline use and camping activity within the study area. Results will inform conservation practices pertaining to this rare shorebird and other similar species.

3.3. METHODS

3.3.1. Study Area

Research was conducted in Harriman Fjord, Alaska (northwest Prince William Sound; 60° 58’N, 148° 26’W to 61° 7’N, 148° 9’W; Fig. 2.1), a 3 x 20 km mountainous tidal fjord in Chugach National Forest. Tides are extreme, reaching 6 m at their peak (NOAA 2007). Black Oystercatchers utilize gravel-sand beaches, alluvial outwash areas, tidal flats, and rock islets for foraging and nesting. Suspected predators of oystercatcher nests include Glaucous-winged Gulls (*Larus glaucescens*), Bald Eagles (*Haliaeetus leucocephalus*), Northwestern Crows (*Corvus caurinus*), river otters, American minks (*Mustela vison*), black bears (*Ursus americanus*), and wolverines (*Gulo gulo*; Andres and Falxa 1995, Morse et al. 2006, Tessler et al. 2007). Harriman Fjord is readily accessible by boat from the Port of Whittier (< 200 km from Anchorage), exposing portions of it to a higher intensity of human recreational use than many other oystercatcher breeding areas in Prince William Sound, particularly during the nesting season (Brown et al. 2004). In 2000, the U.S. Forest Service began annual breeding censuses of Black Oystercatchers in the area and initiated a banding and monitoring program in Harriman Fjord in May 2004 (Brown et al. 2004). Twenty-five
to 29 territorial oystercatcher pairs have nested at the site annually from May to August (Brown et al. 2004, Spiegel et al. 2006).

3.3.2. Site Surveys, Nest Monitoring, and Adult Capture

From early May to late July in 2005 and 2006, weekly oystercatcher surveys were conducted by motor-raft at high to mid tides. Potential oystercatcher breeding habitat (including gravel, cobble, or sand beaches; rocky islets; cliff ledges) was scanned with 10x40 binoculars, and nesting areas were searched on foot. Nest locations were recorded with a Global Positioning Systems (GPS) unit. Nests found with one egg were assumed to have been initiated that day. Egg flotation was used to approximate initiation dates of nests found with more than one egg (Mabee et al. 2006). Nests were checked every three to seven days until chick fledging or failure. If nest failure was discovered, the nesting area was examined for convincing evidence of cause including eggshell fragments (Mabee et al. 2006), predator tracks, or scat, suggesting predation; or tidal debris above the nest bowl, suggesting tidal flooding.

Unmarked adult oystercatchers were captured using noose mats, walk-in traps, or leg snares (Benson and Suryan 1999, Mehl et al. 2003, Gratto-Trevor 2004), and banded with unique UV stable plastic color band combinations. Fifteen μl of blood was obtained from the metatarsal vein of each adult, following American Ornithologists’ Union approved guidelines (Oring et al. 1998). Blood samples were molecularly sexed using CHD-Z/CHD-W (Griffiths et al. 1998). Molecular sexing is the most reliable method to determine sex because Black Oystercatchers are monomorphic in plumage and considerable overlap exists in size metrics (Andres and Falxa 1995). Captures were
limited to less than one hour and were not attempted until at least seven days after clutch initiation. No nests were abandoned after capture, with incubation typically resuming soon after release.

3.3.3. Human Recreational Use Surveys

Harriman Fjord was surveyed for human recreational use approximately every three days throughout the field season. While this monitoring method did not yield a precise number of recreationists, it identified areas within the field site most regularly experiencing shoreline use or camping activity. Serendipitous observations of human activities also occurred during daily site surveys and nest monitoring. Locations of humans using the shore were recorded with a GPS unit, along with the date, time and type of shoreline use. Evidence of overnight camping also was noted.

3.3.4. Video Nest Recording

Oystercatcher nests \((n = 22)\) were continuously monitored with weatherproof video units (SeeMoreWildlife Technologies, Homer, AK; Fig. 3.2) from seven days post-clutch initiation through three days post-hatch (around 31 days post-clutch initiation), or nest failure. A camouflaged “close-up” camera was placed 15 cm above ground level, 1 m from a nest, facilitating color-band identification. A second “distance” camera was located 5 m from a nest, 1 m high, providing a wide-angle view of oystercatcher activity and potential disturbance stimuli in the nest vicinity. Infrared diodes permitted recording in darkness without disturbing a pair or attracting predators. A digital video recorder (DVR) with a 300 gigabyte hard drive stored footage from both cameras. The DVR was located 50 m from a nest, minimizing researcher disturbance.
during hard drive exchanges and maintenance. Each unit was powered by three 40-watt solar panels connected to two 100 amp-hour deep cycle batteries, via a voltage regulator.

Video units were similarly configured at each nest (Fig. 3.2), with both cameras facing downslope and fields of view intersecting at a similar angle (roughly 120°). However, differences in slope and terrain at each nest site led to variation in observation probabilities of stimuli > 25 m from the nest. Stimuli > 25 m from the nest also were harder to observe during darkness. Each camera unit was placed at a nest randomly chosen from a running list of active nests. Nests were added to the list seven days post-clutch initiation and removed from the list when they failed or neared hatch. True randomization was not possible because (1) only four video units were available, (2) nesting activity was synchronous, (3) nests failed unpredictably, (4) nests on steep cliffs could not support video units, and (5) camera placement was delayed for seven days after clutch initiation to avoid nest desertion risk from excessive disturbance (Sanders and Maloney 2002, Williams and Wood 2002). Over 25% (22 of 87) of nests found in Harriman Fjord during 2005 and 2006 were video monitored (Fig. 3.1). Sampling constraints and occasional power failures during prolonged overcast periods resulted in uneven monitoring times among nests, necessitating the use of both first and re-nesting attempts from different pairs to obtain sufficient sample sizes for analyses.

3.3.5. Video Data Extraction

Video footage was viewed on 43 cm color monitors in 4x real time and slowed to real time whenever movement was observed. Footage from close-up and distance
cameras was viewed simultaneously using a split-screen display that enabled efficient data collection without overlooking activity. When an oystercatcher settled on or departed a nest, the date and time was documented from a time-date stamp embedded in footage (to the nearest 1 min) and color-banded oystercatchers were identified. Each uninterrupted sitting period was considered an “incubation bout”. Identities of all stimuli having the potential to disrupt an incubation bout by causing an incubating bird to depart the nest (hereafter “potential disturbance stimuli”) also were recorded, noting the time they entered and exited camera fields of view. To assure that unexpected causes of disturbance were not discounted, I defined potential disturbance stimuli liberally as any inter- or intra-specific activity, or environmental perturbation (including waves and tidal flooding), observed within camera fields of view. The estimated distance of closest approach to a nest by each potential disturbance stimulus was recorded and grouped into three distance categories: all distances, within 25 m, and within 5 m of a nest. Incubation bouts or potential disturbance stimulus events in progress at the start or end of a footage segment were removed from the dataset.

When incubation bouts ended, footage was slowed to half time to attempt to determine the reason the incubating bird left the nest. Departures prompted by a potential disturbance stimulus observed in footage within 30 s (before or after) were considered to be “flushed” by disturbance. Incubators often flushed in response to humans and large mammals well before they were observable in camera fields of view. Thus, these stimulus types were assumed to be responsible for departure if observed up to 10 min after a bird flushed, if they had likely been in the nest area before observation
The cause of over one-quarter of departures could not be conclusively identified because of video field of view limitations. These departures were not included in analyses. The primary behavior of a bird immediately after being flushed was identified as aggression, retreat, aggression-retreat, or undetermined. Aggression included nest defense, chasing or mobbing the disturbance stimulus, and distraction and piping displays near the nest. Retreat included running or flying from the disturbance stimulus, crouching, and hiding. Aggression-retreat included aggression and retreat behaviors in response to the same disturbance stimulus. Undetermined responses to disturbance stimuli were ambiguous or could not be observed clearly. The amount of time a nest was left unattended following each disturbance flush also was recorded.

I distinguished daytime and nighttime in relation to true sunset and sunrise times in Harriman Fjord, adjusted for daylight savings time (U.S. Naval Observatory 2007). Throughout study seasons, the ratio of nighttime to daytime ranged from 25:75 in early May and late July to 20:80 during the summer solstice. If over 50% of an incubation bout fell during daytime or nighttime, the incubation bout was considered to have occurred during that time of day. When an incubating bird departed from the nest for any reason, that departure, defined as a “recess”, was considered to have occurred during daytime or nighttime according to the exact time of departure.

After receiving identical training in standardized data collection procedures, six observers extracted data from over 4,200 h of video footage. Each observer reviewed different portions of footage from each nest, ensuring that any observer biases were
spread out among nests. I randomly spot-checked data for consistency one to three
times during review of each nest and detected no substantial differences among
observers.

3.3.6. Data Analyses

The frequency with which potential disturbance stimuli were observed near 22
video monitored oystercatcher nests was obtained by dividing the number of times a
particular stimulus type was observed in the footage by the number of hours the nest
was monitored, resulting in an hourly “observation rate”. Observation rate was
assumed to be a rough approximation of the frequency that a type of stimulus was
encountered by an incubating oystercatcher. Potential disturbances were divided into
five “stimulus types”: conspecifics (extra-pair oystercatchers), other bird species,
humans, mammals, and other (including boats larger than a kayak, aircraft, nest
flooding, waves caused by glacial calving, wind, or boat wakes, and unidentifiable
stimuli). Since there was extreme variation among observers in the accuracy of stimuli
observations in video beyond 25 m of nests, observation rates were only calculated for
stimuli observed within 25 m of nests. The mean observation rate for each potential
disturbance stimulus type was calculated. To avoid the inclusion of biased means in
estimates, six nests with an insufficient amount of monitoring time (< 100 h) were
omitted from calculations. Six additional nests were omitted from calculations because
vegetation obstruction or poor camera angles interfered with stimulus detection beyond
5 m of nests. Thus, ten nests were used to calculate mean observation rates.
Because stimuli closer to nests were probably observed at a different rate, and theorized to affect incubation behavior differently, I also calculated the mean observation rate for each potential disturbance stimulus type occurring within only 5 m of nests. At this distance to the nest, vegetation obstruction and poor camera angles did not interfere with detection of stimuli, and six nests removed for observation rate calculations within 25 m of nests were included in calculations (n = 16 nests used).

The occurrence of particular stimuli was thought to vary depending on the time of day (see chapter 2). Thus, I examined whether there was a difference in the mean observation rate of each stimulus type between daytime and nighttime. Comparisons were made using paired one-sample t-tests. Non-parametric tests were used where assumptions of normality and homoscedacity were not met (Wilcoxon signed-rank test, S-Plus 7.0 for Windows, Insightful Corp.; Ramsey and Schafer 2002).

I calculated the mean proportion of observations in each of five stimulus types observed within 25 m of nests that causing incubating oystercatchers to “flush” from nests. Nests with a low number of stimulus observations within a stimulus category (< 3) were omitted from the calculations to avoid inclusion of biased means in estimates. Because the number of observations of each stimulus type varied among nests, more nests were omitted from certain stimulus categories than from others, resulting in different nest sample sizes (n = 4-13 nests) used to calculate the proportion of each stimulus type that caused flushing.

Each stimulus type was included in a generalized linear mixed model (PROC GLIMMIX, SAS Version 9.1, SAS Institute, Inc., Cary, North Carolina) with a
binomial response distribution (“flushed” vs. “didn’t flush”) among stimulus types to test whether differences existed among the proportion of observations of conspecifics, other bird species, and humans within 25 m of nests that caused flushing. An overdispersion parameter was included in the model and allowed to vary uniquely by stimulus type to control for potentially uneven overdispersion in response variance among stimulus types. Variables identifying nests were included as random effects to account for suspected lack of independence across stimulus types by nest. The analysis was restricted to six nests which had ≥ 3 observations in each stimulus category. Too few nests had ≥ 3 observations of “mammal” or “other” stimulus types to include them in the model.

Theorizing that the response of an incubating oystercatcher to stimuli may vary depending on the time of day, I examined whether there was a difference between daytime and nighttime in the mean proportion of stimuli that caused flushing, when observed within 25 m of nests. Time of day comparisons were made using all stimuli combined (n = 11 nests) because there were too few nests with ≥ 3 observations in a stimulus category to examine them separately. A non-parametric Wilcoxon signed-rank test was used for this analysis because assumptions of normality were not met.

To examine whether a particular disturbance within a stimulus category had a greater chance of flushing an incubating oystercatcher than another type within the same category, three of the five potential disturbance stimulus categories were sub-divided into potential “sub-stimulus” categories. Other bird species and mammal stimuli were sub-divided into “predatory” or “non-predatory” sub-stimuli, depending on
whether they were suspected of preying on Black Oystercatcher nests, as assessed from the primary literature or field observation (Hartwick 1974, Vermeer et al. 1992, Andres and Falxa 1995, Hazlitt and Butler 2001, Feldhamer et al. 2003, Morse et al. 2006, Tessler et al. 2007). Human stimuli were subdivided into “research” or “recreation”. The mean proportion of each sub-stimulus type observed within 25 m of a nest that caused flushing was calculated. Differences between proportions of two sub-stimulus types, within each of three stimulus categories, were compared using Wilcoxon signed-rank tests, because assumptions of normality were not met.

Following every flush attributable to a conspecific, other bird species, human, or mammal stimulus, the behavioral response of the flushing bird to the stimulus was categorized as: aggression, retreat, combined aggression and retreat, or undeterminable (when the response could not be well seen in footage). For each oystercatcher monitored, the proportion of each behavioral response exhibited was calculated as a percentage of all behavioral responses to a stimulus type. Percentages of behaviors were averaged across nests, and separated by sex. Nests with an insufficient number of flushes in a stimulus category (< 3) were omitted to avoid the inclusion of biased means in estimates. This resulted in different nest sample sizes (n = 3-14 nests) used in calculations for each stimulus type. Responses to stimuli observed on video at any distance from nests (not just within 25 m) were included in calculations if the stimulus was known to have caused flushing, because these observations were not susceptible to detection biases.
To learn whether different types of disturbance disrupted incubation for differing amounts of time, I calculated the mean number of minutes nests were left unattended following flushes caused by conspecific, other bird, human, or mammal stimulus types, and predator vs. non-predator or recreation vs. research sub-stimulus types observed at any distance from nests (not just within 25 m). Estimates of the time a nest was left unattended following a particular stimulus or sub-stimulus type were restricted to nests with ≥3 flushes caused by that stimulus or sub-stimulus.

I compared recess rates of depredated nests with that of successful nests (hatching at least one egg) using a two-sample $t$-test (S-Plus 7.0 for Windows, Insightful Corporation) to determine whether nest depredation was related to greater parental activity at a nest (Skutch 1949). Recess rate was defined as the total number of departures of incubating birds from a nest (due to disturbance, mate switches, and unknown causes), divided by the number of hours the nest was observed. This metric was assumed to be a valid representation of parental activity at a nest. To determine whether nest depredation was related to an increased presence of particular potential disturbance stimuli near nests, I compared observation rates of conspecific, other bird species, human, and mammal stimuli, within 25 m of nests, between depredated and successful nests using two-sample $t$-tests. A non-parametric alternative (Wilcoxon rank sum test, S-Plus 7.0 for Windows, Insightful Corp.) was used where assumptions of normality and homoscedacity were not met. Recess rate and observation rate calculations for successful nests were restricted to day 6-14 post-clutch initiation to roughly standardize the timing and duration of observations between depredated and
successful nests. To avoid inclusion of biased means, 9 of 22 nests were omitted from analyses because they were not thoroughly monitored (< 50 footage) during day 6-14 post-clutch initiation. Additionally, two nests failing from flooding and two more with obstructed camera fields of view were also omitted from analyses. This resulted in a sample size of nine nests (5 hatched, 4 depredated). Because of the small sample size, I had to combine nests from both study years into analyses. However, there was no reason to expect the relationships to vary between years.

To identify whether nests in the vicinity of recreational shoreline use had a lower survival probability, I obtained distances between documented human shoreline use and oystercatcher nests using ArcMap software (ESRI 2002). I then used the Mayfield method to calculate daily nest survival estimates (Mayfield 1961, 1975) and confidence intervals (Johnson 1979) of nests within 200 m of human recreational shoreline use (see Morse 2005) during nest building or incubation, and nests where human use was not observed during that period (Figure 3.1). Additionally, I obtained daily survival estimates of nests within 200 m of camping activity during incubation, and nests where camping was not observed during incubation (Figure 3.1). Because there was no difference in nest survival between video monitored and non-monitored nests (see chapter 2), they were pooled for analyses \( n = 79 \). Nest survival was calculated separately between nest attempts and between years to determine if differences attributed to human use may have been confounded by attempt or year. Daily survival of oystercatcher nests in Alaska may vary depending on tidal nest flooding (Morse et al. 2006). Thus, 13 nests that failed due to flooding were omitted
from analyses, to satisfy analysis assumptions of homogeneity in nest survival probability throughout the incubation period (Mayfield 1961, 1975).

Estimates are reported as means ± SD, unless indicated. All tests were considered significant at $\alpha = 0.05$.

3.4. RESULTS

3.4.1. Potential Disturbance Stimuli Documented with Video

During 2,976 h of footage collected at 16 nests with unobstructed fields of view, a total of 791 potential disturbance stimuli were observed within 25 m of nests. Other bird species, particularly gulls and ducks, accounted for 67% of all observations. Far fewer conspecifics, humans, and mammals were observed (Table 3.1). There were over twice as many observations of researchers than recreationists (Table 3.1). There also were far more observations of non-predatory mammals (particularly deer) than predatory mammals (Table 3.1). River otters and black bears were the most common of six “predatory” mammals observed. Waves made up the majority of other stimuli.

Ten nests with unobstructed fields of view and sufficient amounts of coverage ($\geq 100$ h) were included in observation rate estimates of stimuli within 25 m of nests. An average of $0.27 \pm 0.22$ potential disturbance stimuli were observed per hour of footage reviewed. Other bird species were observed at a rate of $0.19 \pm 0.19$ per hour. Conspecifics were observed more frequently within 25 m of nests than humans, mammals, or other stimulus types, but over six times less frequently than other bird species (Table 3.2).
Fewer conspecifics, other birds, humans, or mammals were observed within 5 m of nests than within 25 m of nests (Table 3.2). The average observation rate of potential disturbance stimuli within 5 m of nests was $0.09 \pm 0.13$ per hour of footage reviewed ($n = 16$ nests).

Within 25 m of nests, other bird species were observed 65% more during daytime than nighttime (95% CI: 3 to 160%, $P = 0.40$; Table 3.2). The rate of other birds observed within 5 m of nests did not significantly vary between daytime and nighttime ($P = 0.29$). Humans were only observed during daytime within 5 m or 25 m from nests. Significant differences in observation rates between daytime and nighttime were not detected for other stimulus types, potentially because of low power to detect differences due to small sample sizes and high variability among nests, rather than a true lack of a difference.

### 3.4.2. Responses of Incubating Oystercatchers to Potential Disturbance Stimuli

An average of $31\% \pm 21\%$ of all potential disturbance stimuli observed within 25 m of nests ($n = 14$ nests with $\geq 3$ stimulus observations included in estimate) caused incubating birds to flush. A significant difference was detected among the proportions of conspecific, other bird, and human stimuli that caused flushing at six nests (with $\geq 3$ observations of each stimulus type), included in analysis, after accounting for variation by nest ($F_{2,10} = 60.4$, $P < 0.001$). A significantly lower proportion of other bird species caused flushing than the proportion of conspecifics ($t_{10} = -10.5$, $P < 0.001$) or humans ($t_{10} = -5.3$, $P < 0.001$) that caused flushing (Figure 3.3). No difference was found between the proportions of conspecifics and humans that caused flushing ($t_{10} = -0.2$, $P =$
0.871). However, conspecifics were observed more frequently, and thus were responsible for the greatest percentage (41% ± 10%) of all flushes observed.

Within 25 m of nests (n = 11 nests with ≥ 3 observations of stimuli at night), no difference was detected in the proportion of all potential disturbance stimuli that caused flushing in daytime compared with nighttime (Z = -1.0, P = 0.307, after removing human stimuli to control for the absence of human activity at night). However, the mean proportion of observations of human recreational stimuli that caused flushing was greater than the proportion of human researcher stimuli that caused flushing (Table 3.3). Fewer predatory bird species caused flushing than non-predatory species within 25 m of nests.

An average of 44% ± 23% of all potential disturbance stimuli within 5 m of nests (n = 16 nests) caused flushing. A greater proportion of conspecific, human, and mammalian stimuli caused flushing within 5 m of nests than they did within 25 m of nests (Table 3.3). Conversely, a greater proportion of other bird species observed within 25 m of nests caused flushing than the proportion observed within 5 m of a nest. Most other bird species that ventured within 5 m of nests, particularly shorebirds, were tolerated by incubating oystercatchers.

Incubating oystercatchers that were flushed from nests (n = 14 nests with ≥ 3 flushes observed) responded to disturbance stimuli with a similar incidence of aggression (39 ± 14%) and retreat (40 ± 12.7%; Figure 3.4). Responses of flushed oystercatchers sometimes occurred rapidly, off-camera. Thus, behavioral responses to 20% ± 15% of disturbances were undeterminable. Flushing oystercatchers retreated
from 84% ± 17% of human disturbances ($n = 5$ nests), and 91% ± 15% of mammalian disturbances ($n = 3$ nests), displaying aggression < 1% of the time. Conversely, 80% ± 17% of conspecific disturbances ($n = 9$ nests) elicited an aggressive response. Responses to disturbances by other bird species ($n = 8$ nests) were mixed: 24% ± 14% aggressive, 31% ± 26% retreat, and 43% ± 26% undeterminable. While both sexes usually retreated from human and mammalian disturbance (Figure 3.4), the mean percentage of aggression toward conspecifics and other bird species was higher for males than females, (97% ± 6% vs. 79% ± 16%, and 46% ± 17% vs. 7.2% ± 11.3% respectively). The only documented aggression toward mammals was initiated by males (Figure 3.4).

Nests were left unattended for an average of 8 min ± 5 min after a disturbance caused an incubating oystercatcher to flush (Figure 3.5, “all stimuli”). Nests were left unattended longer following human disturbance (14 min ± 8 min) than any other disturbance stimulus type. Unattended nest times were particularly long following researcher disturbance (20 min ± 12 min; Figure 3.5), potentially because some research activities (e.g., capture) occurred for sustained periods. Nests were left unattended for shorter periods after flushes due to non-predatory bird species than after flushes due to any other disturbance stimulus type (Figure 3.5).

### 3.4.3. Causes of Nest Failure

Seven of 22 video monitored oystercatcher nests failed, five from predation and two from tidal flooding. Six of seven failures occurred during nighttime which accounted for only 5 of 24 h of each day during the study period. Four video monitored
nests were depredated during nighttime by nocturnal species of mustelids (2 American mink, 1 marten, 1 wolverine), and one was depredated during daytime by a black bear (Figure 3.6). Nocturnal nest predators were rarely seen in video footage except during predation events. Each mustelid nest predator ran a rapid, direct approach to a nest, generally flushing the incubating oystercatcher well before coming into the camera’s field of view. In all four instances of nest predation by mustelids, the incubating oystercatcher retreated and did not attempt to defend the nest. Individuals of the same predator species were observed consuming eggs in different ways. During a 2006 nest depredation, a mink consumed eggs at a nest over a 15-min period, leaving behind numerous shell fragments at the nest. In 2005, another mink carried whole eggs from a nest, removing each in rapid succession. Whole eggs were carried away by predators in three instances. Each instance coincided with a high tide event. When field researchers found no eggshells at the nest they erroneously concluded that nest failure was caused by tidal flooding, until video footage was reviewed.

Tidal flooding of four nests was recorded on camera (Figure 3.6), two resulting in nest failure. All flooding occurred at night, during extremely high tide levels. Oystercatchers generally continued to incubate while rising tides inundated nests, departing only after water levels submerged the nest bowl. When eggs were displaced from a nest bowl by marginal flooding but were not swept away, nesting pairs re-built the nest bowl, rolled the eggs back into the nest using their bills, and re-initiated incubation. Eggs were observed being rolled for over 1 m. A similar process was witnessed at all four flooded nests (two of which failed the following night during a
higher peak tide), with incubation re-commencing within four hours. Two nests that failed due to tidal flooding were lost to the peak spring tide event during the 2005 nesting season, which took place between 0100 and 0300. This tidal event also likely caused failure of five other nests not recorded on video. In 2006, two nests experienced non-lethal nest flooding when tide water covered nests but was not high enough to sweep eggs away. Incubation resumed at both nests. While one of these nests later failed due to predation, the other successfully hatched. One non-lethal flood event was amplified by a series of waves, likely produced by glacial calving. Waves produced by boat wakes were not responsible for flooding of any video monitored nests.

3.4.4. Incubation Recess Rates, Stimulus Observation Rates, and Nest Failure

No significant difference in mean recess rate was detected between depredated and hatched nests, during day 6 and 14 post clutch-initiation (Table 3.4). Likewise, no significant difference was found in observation rates of conspecifics, other birds, humans, mammals, or all combined stimulus types between hatched and depredated nests, during day 6 and 14 post clutch-initiation (Table 3.4).

3.4.5. Human Recreation Use and Daily Nest Survival

The Mayfield daily survival estimate for all nests of known fate monitored in Harriman Fjord in 2005 and 2006 was 0.948 (95% CI: 0.934 to 0.962). The probability of a nest surviving to hatch, assuming a mean incubation period of 27.5 d (the average incubation period for nine video monitored nests where clutch completion and hatch dates were observed), was nearly identical in 2005 (24%, 95% CI: 14 to 41%) and 2006 (22%, 95% CI: 12 to 40%). After removing confounding effects of flood-induced
failure (nest survival probabilities remained nearly identical between years), daily survival estimates were slightly higher for nests within 200 m of shoreline used by humans during nest building or incubation (0.969, 95% CI: 0.944 to 0.993) than for nests where human use was not detected within 200 m (0.955, 95% CI: 0.940 to 0.970; Figure 3.7). Daily survival estimates were substantially higher for active nests within 200 m of sites where camping activity occurred (0.988, 95% CI: 0.972 to > 0.999) than for active nests not within 200 m of camping activity (0.951, 95% CI: 0.935 to 0.966; Figure 3.7). Because of restricted sample sizes, first nests and re-nests were pooled for analyses. While re-nests had a slightly lower daily survival rate than first nests, pooling data across attempt was not expected to influence comparisons because equal proportions of first nest and re-nest attempts were included in human use and non-use categories (44% of observations per category were re-nests).

3.5. DISCUSSION

Responses of nesting birds to potential disturbance stimuli should vary depending on the costs and benefits of current reproductive investment weighed against residual reproductive value in the form of self-maintenance and survival (Trivers 1972, Dawkins and Carlisle 1976, Montgomerie and Weatherhead 1988). Costs are influenced by the type, frequency, and intensity of potential disturbance stimuli (Frid and Dill 2000). Oystercatcher nesting behavior can be affected by humans, conspecifics, predators, and weather-related stimuli (Nol 1985, Purdy and Miller 1988, Leseberg et al. 2000, Banks and Patterson 2002). Increased disturbance in their nest
area, particularly from human sources, may reduce oystercatcher reproductive success (Toland 1999, Tjørve and Underhill 2008), potentially by enhancing the risk of nest predation (McGowan and Simons 2006).

In Harriman Fjord several types of natural and anthropogenic stimuli were observed near oystercatcher nests at different rates, some resulting in disruption of incubation activity and eliciting behavioral responses. Depredated nests did not experience a higher rate of human or natural disturbance stimuli than successful nests, nor was nest depredation associated with increased parental activity near nests. Unexpectedly, daily nest survival was higher near human shoreline activity. Most nest failures were caused by infrequently observed nest predators and flooding during spring tide events. Continuous video monitoring was crucial for obtaining these results, which likely would have been missed with conventional nest monitoring.

The frequency with which an incubating oystercatcher was disrupted from incubation by a particular potential disturbance stimulus depended on the rate with which the stimulus was observed near the nest, and the proportion of those observations that caused a bird to flush. Thus, the propensity of a stimulus to disturb an incubating oystercatcher is likely contingent on the frequency a stimulus is encountered (Whittaker and Knight 1998), and the perceived risk of the stimulus by the incubating bird (Frid and Dill 2002). At Harriman Fjord conspecifics accounted for the majority of all flushes by incubating oystercatchers. They were observed frequently relative to all other stimuli besides other birds and caused flushing nearly every time they were seen. Conversely, other bird species, although observed over six times more than
conspecifics, infrequently prompted flushing, even when close to the nest (≤ 5m). While humans nearly always caused an incubating bird to flush when observed, they were not observed frequently, and never during nighttime. Mammal species also caused routine flushing, but were infrequent.

Incubating oystercatchers evidently perceived risks from sub-stimuli within the same stimulus type differently, as indicated by proportions which caused a flush. For example, predatory birds (primarily gulls and raptors) prompted flushing at three times the rate of non-predatory birds (primarily duck and shorebird species). Predatory bird species are probably recognized as threats to nests. Gulls are reported to be primary predators of Black Oystercatcher eggs and chicks, and poor reproductive success has been associated with proximity to gull colonies (Hartwick 1974, Vermeer et al. 1992, Hazlitt 2001). A greater proportion of human recreation activity prompted a flush than did researcher activity. This could have been a result of the concerted effort of researchers to minimize activity when in a nest vicinity. However, some research activity was particularly intrusive (eg., capture). It is also possible that habituation to researchers may be occurring at some nests (Baudains and Lloyd 2007) because research activity around nests was observed more frequently than recreation activity. Still, results suggest that different types of human activity may be perceived differently by incubating oystercatchers. In contrast to our findings, other studies have shown that oystercatcher incubation and nest area attendance decreases similarly in response to human recreation and research activities (Verboven et al. 2001, Morse 2005, McGowan and Simons 2006).
Behavioral responses of incubating birds to stimuli that caused flushing varied depending on the stimulus and sex of the incubating bird. Oystercatchers responded to over 80% of conspecific disturbances with aggression. Conspecifics are known to elicit aggressive responses from incubating oystercatchers (Purdy and Miller 1988, Sabine 2008), which are particularly protective of productive breeding sites that they defend for many years (Bruinzeel and van de Pol 2004). In contrast, nearly 85% of flushes caused by humans resulted in an oystercatcher retreating or hiding and no aggressive reactions to humans were observed. Nests were left unattended longer following human disturbance than any other disturbance type, especially after research activities such as camera installation and bird capture. Most oystercatchers also retreated or hid from mammals, and aggressive responses were rare. While the effects of mammal presence on incubation patterns are poorly documented for Black Oystercatchers, mammals are a frequent predator of oystercatcher nests and chicks on a mainland, where the abundance and diversity of mammals is unrestricted (Vermeer et al. 1992, Morse et al. 2006). While adult mortality of Black Oystercatchers is low (Andres and Falxa 1995), some mammalian predators encountered in Harriman Fjord are known to prey upon large incubating birds (Feldhamer et al. 2003). Quick retreat from a potentially life-threatening stimulus, such as a predatory mammal or human, is expected to be selected for in long-lived species, such as Black Oystercatchers, which have a high residual reproductive potential.

After being flushed from a nest, male oystercatchers more often responded to disturbance stimuli with aggression than did females. Males were especially aggressive
in response to disturbance from conspecifics (97% of responses), and only males attacked mammals. These findings suggest that males may play a more active role in nest defense (chapter 2, Nol 1985, Purdy and Miller 1988).

Although potential disturbance stimuli were found to affect incubation behavior, there was no evidence that these stimuli adversely affected nest success. Disturbance can indirectly promote nest failure by increasing the rate with which incubating birds flush, thereby increasing the chance that a nest location will be revealed to predators (McGowan and Simons 2006). However, oystercatcher nest predation was not found to relate to a higher rate of human or other potential disturbance stimuli observed near nests. This study also failed to find support for the hypothesis that increased parental nest activity resulted in a greater incidence of nest predation (Skutch 1949), although, low nest sample sizes (especially of failed nests) may have prevented differences in parental activity levels, or observation rates of stimuli from being detected between failed and hatched nests. Further, behavioral responses to disturbance may not always indicate direct fitness consequences (Gill et al 2001, Lind and Cresswell 2005).

Mammalian predation accounted for failure of five of 22 video monitored nests, despite mammals being observed in video footage less frequently than any other stimulus type. Throughout the study the four species responsible for depredations, primarily nocturnal mustelids, were only observed on video 13 times. Five of these observations culminated in nest predation. Other studies of oystercatchers have also reported a high proportion of nest and chick failure from nocturnal mammal depredation (e.g., Sabine et al. 2006). In Alaska, Morse et al. (2006) observed Black Oystercatcher
nests being preyed upon by stealthy mammal species such as wolverine. Data from my study suggest that prior assessments of productivity at Harriman Fjord may have underestimated the impact of nocturnal mammalian predators (Brown et. al 2004).

Determining the cause of nest failure from nest remains is difficult and may be biased toward commonly observed or obvious failure sources (Larivière 1999, Liebezeit and Zack 2008). In Harriman Fjord, researchers falsely identified the cause of nest failure at three depredated nests as tidal flooding, when depredations failed to leave eggshell evidence and high tides were predicted. Prior studies of Black Oystercatchers have indicated that birds (particularly gulls) can be a primary source of egg and chick loss (Nysewander 1977, Hazlitt 2001). However, in Harriman Fjord no video monitored nests failed due to avian predation. It is possible that studies identifying nest failure based on indirect evidence may have inaccurately assigned responsibility for failures to birds because avian nest predators tend to be conspicuous and diurnally active (Andres and Falxa 1995). However, most prior studies were conducted on islands where eggs are a more widely utilized food source for avian predators, and mammals are scarce (Vermeer et al. 1992).

Two of 22 video monitored nests failed due to nocturnal tidal floods. Tidal flooding has been implicated in substantial nest losses in other oystercatcher studies (Lauro and Nol 1993, Nol 1989, Morse et al. 2006). While the extent of nest loss to tidal flooding may vary annually, some oystercatcher pairs regularly nest within reach of extreme high tides. However, the timing and magnitude of extreme tidal events varies from year to year (NOAA 2007). Thus, a clutch laid in the same location may
survive to hatch in some years, but not others. Video observations support this hypothesis, as extreme spring tide flood events caused nest failure in 2005, while lower spring tide floods in 2006 did not cause nest failure. Occasional nest success in areas intermittently flooded by spring tide events would prevent natural selection from acting against their use. Nesting within flood zones also may be influenced by competition for productive nest territories (Bruinzeel and van de Pol 2004), encouraging high nest site fidelity (Hazlitt and Butler 2001) despite occasional risk of flooding.

There was no evidence that the occurrence of nest flooding was elevated by human activity. It has been suggested that wake waves generated by large tour boats in Prince William Sound could be responsible for flooding nests during high tides (Tessler et al. 2007). However, most nests risked flooding only during peak spring tide events, which occur primarily at night along the Pacific coast of North America (NOAA 2007, California DFG 2008). As tour boat operations in Harriman Fjord rarely occur at night, boat wake flooding is probably rare.

Human activity has been linked to lowered reproductive success in oystercatchers (Sabine et al. 2006, Tjørve and Underhill 2008). Unexpectedly, daily nest survival in Harriman Fjord was higher within 200 m of recreational use or camping. This result could have been an artifact of study methodology, since the number of nests monitored near human activity was far smaller than those monitored away from such activity. Alternatively, recreational activity near active oystercatcher nests may have increased nest success by repelling common nest predator species, such as mink, that may be sensitive to human disturbance (Sutherland 2007). A controlled
study would be needed to better understand the relationship between current levels of human recreational activity and oystercatcher nest success in Harriman Fjord.

Despite the positive association found between recreation and nest success in Harriman Fjord, caution is advised in concluding that human disturbance cannot adversely affect oystercatcher reproductive success and productivity. Black Oystercatchers have likely evolved the ability to persist with a considerable amount of disturbance because they nest in dynamic, open shoreline environments, experiencing regular intrusions by conspecifics and other bird species. However, beyond a certain threshold of frequency or intensity, added human disturbance pressures could begin to affect productivity. McGowan and Simons (2006) found that increased all-terrain vehicle activity caused increased flushing of incubating American Oystercatchers, likely promoting nest predation on the Outer Banks of North Carolina. Typical of most backcountry areas in Alaska, Harriman Fjord encounters less frequent and less intensive human recreation. At Kenai Fjords National Park in Alaska, Morse et al. (2006) failed to find a relationship between human use and nest success. While neither Kenai Fjords, nor Harriman Fjord may currently experience enough human recreational use to affect nest success, shoreline recreation is increasing in Alaska (Morse et al. 2006). To understand the effects of more intense human disturbance on reproductive success of Black Oystercatchers, studies could be conducted in southern portions of the breeding range which presently experience greater human pressures (Tessler et al. 2007).

Human disturbance may affect productivity in ways that were not immediately detectable in my study. Prior research has stressed the importance of chick mortality in
contributing to low productivity levels of Black Oystercatchers (Groves 1984, Hazlitt and Butler 2001). Video nest monitoring was insufficient for documenting behavior and failure during the chick stage because chicks are highly mobile, often leaving a nest within 24 h of hatching (Andres and Falxa 1995). However, to understand the full effects of human or natural disturbance on reproductive success it is recommended that chicks be intensively monitored after they depart the nest. Although beyond the scope of this study, radio-tracking may be an effective way to monitor chick survival (S. Schulte, North Carolina State University, pers. comm.).

Short-term reproductive failure may not predict demographic effects on a population, especially in long-lived species (Frid and Dill 2002). For oystercatchers, which may live over 40 years (Ens et al. 1996) and experience naturally high rates of reproductive failure, relatively low average annual fecundity may be sufficient to maintain stable populations (Hockey et al. 1996b, Davis 1999). Thus, long term monitoring is crucial to understanding oystercatcher demography and threats to populations. My study was too short to fully evaluate the impact of human activity on oystercatcher populations in Harriman Fjord. Thus, extended monitoring of known pairs is warranted, particularly if intensity of human use changes at the site.

Video monitoring provided an extensive, continuous record of human and natural activities occurring near Black Oystercatcher nests, facilitating a better understanding of the affects of potential disturbance stimuli on incubation behavior and nest failure. Conventional nest monitoring is often restricted to daytime and, thus, may fail to accurately identify major threats to nest success. My results demonstrate that
causes of nest failure cannot always be determined from post-failure evidence; latent
causes of nest failure should be considered. Video documentation arguably produces
the most complete picture of natural processes occurring in the nest environment. Use
of two cameras per nest allowed a large coverage area to be monitored around nests,
and proximity of stimuli to nests to be estimated. Future studies may be enhanced by
deploying video units at more nests simultaneously to alleviate sample size issues. This
is increasingly feasible as camera and digital video recording technology becomes more
efficient and cost-effective (Sabine et al. 2005, Pierce and Pobprasert 2007).

Understanding the effects of disturbance on reproductive behavior and success
of shorebird populations is important for assessing their persistence and conservation
needs. This study elucidates factors to be considered when instituting future research
and management practices involving Black Oystercatcher disturbance and nest success.
Past studies have been hindered by incomplete knowledge of the types, frequencies, and
impacts of potential disturbance stimuli near nests. At Harriman Fjord continuous
video monitoring was used to collect an uncommonly extensive record of Black
Oystercatcher nesting and document the most frequent causes of incubation disruption
and nest failure. Consideration should be given to nocturnal failure risks and
infrequently observed nest predators as primary natural causes of nest failure. Further,
the oystercatcher population at Harriman Fjord should be monitored over the long term,
and research should be extended into other breeding areas in the species range which
experience higher human activity levels.
3.6. ACKNOWLEDGEMENTS

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3.7. LITERATURE CITED


Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430-455.


Table 3.1. Stimulus types as a percentage of all stimulus observations \((n = 791)\), percentage of a stimulus type made up by sub-stimulus type, and the composition of each sub-stimulus type detected in Black Oystercatcher nest video footage within 25 m of a nest \((n = 16 \text{ nests})\) during the 2005 and 2006 breeding seasons, Harriman Fjord, AK.

<table>
<thead>
<tr>
<th>Stimulus type</th>
<th>Sub-stimulus type</th>
<th>Sub-stimulus composition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bird (66.8%)</td>
<td>Duck (42.2%)</td>
<td>Harlequin ((\text{Histrionicus histrionicus}; &gt;75%))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Common Merganser ((\text{Mergus merganser}))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Scoter ((\text{Melanitta spp.}))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unidentified species</td>
</tr>
<tr>
<td>Gull (35.4%)</td>
<td></td>
<td>Glaucous-winged Gull ((\text{Larus glaucencens}; &gt;75%))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mew Gull ((\text{Larus canus}))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Black-legged Kittiwake ((\text{Rissa tridactyla}))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unidentified species</td>
</tr>
<tr>
<td>Shorebird (7.0%)</td>
<td></td>
<td>Spotted Sandpiper ((\text{Actitis macularia}; 65%))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wandering Tattler ((\text{Heteroscelus incanus}; 24%))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Semipalmated Plover ((\text{Charadrius semipalmatus}; 3%))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unidentified species (8%)</td>
</tr>
<tr>
<td>Raptor (6.3%)</td>
<td></td>
<td>Bald Eagle ((\text{Haliaeetus leucocephalus}; &gt;99%))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unidentified species</td>
</tr>
<tr>
<td>Other (9.1%)</td>
<td></td>
<td>Passerine spp. (Family: Emberizidae; 46%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Arctic Tern ((\text{Sterna paradisaea}; 10%))</td>
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<tr>
<td></td>
<td></td>
<td>Pigeon Guillemot ((\text{Cepphus Columba}; 10%))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unidentified species (mostly distant seabirds; 34%)</td>
</tr>
<tr>
<td>Conspp. (10.7%)</td>
<td></td>
<td>---</td>
</tr>
<tr>
<td>Human (7.3%)</td>
<td>Recreation (31.0%)</td>
<td>Includes humans in kayaks along shoreline</td>
</tr>
<tr>
<td></td>
<td>Research (69.0%)</td>
<td>Includes humans in rafts along shoreline</td>
</tr>
</tbody>
</table>
Table 3.1. Continued. Stimulus types as a percentage of all stimulus observations \((n = 791)\), percentage of a stimulus type made up by sub-stimulus type, and the composition of each sub-stimulus type detected in Black Oystercatcher nest video footage within 25 m of a nest \((n = 16\) nests) during the 2005 and 2006 breeding seasons, Harriman Fjord, AK.

<table>
<thead>
<tr>
<th>Stimulus type ((% \text{ of all stimuli}))</th>
<th>Sub-stimulus type ((% \text{ of stimulus type}))</th>
<th>Sub-stimulus composition (in order of abundance; % of sub-stimulus)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mammal ((7.5%))</td>
<td>Non-predatory ((69.5%))</td>
<td>Sitka deer ((Odocoileus hemionus; 63.4%))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Porcupine ((Erethizon dorsatum; 14.6%))</td>
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<tr>
<td></td>
<td></td>
<td>Hoary marmot ((Marmota caligata; 9.8%))</td>
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<tr>
<td></td>
<td></td>
<td>Small rodent ((Rodentia spp.; 7.3%))</td>
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<tr>
<td></td>
<td></td>
<td>Sea otter ((Enhydra lutris; 4.9%)^a)</td>
</tr>
<tr>
<td>Predatory ((30.5%))</td>
<td>River otter ((Lutra Canadensis; 33.3%))</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Black bear ((Ursus americanus; 27.8%))</td>
<td></td>
</tr>
<tr>
<td></td>
<td>American mink ((Mustela vison; 22.2%))</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wolverine ((Gulo gulo; 11.1%))</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Marten ((Martes americana; 5.6%))</td>
<td></td>
</tr>
<tr>
<td>Other ((7.7%))</td>
<td>Wave ((93.4%))</td>
<td>Boat wake caused ((66.7%))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Glacier calving caused ((26.3%))</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unidentified cause ((7.0%))</td>
</tr>
<tr>
<td>Tidal flooding ((6.6%))</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>

^aWhile sea otters have been reported as potential oystercatcher egg predators (Andres and Falxa 1995), there is considerable evidence that sea otters eat primarily marine invertebrates and rarely, if ever, feed on land (Schneider 1994). Sea otters were never observed out of the water, or within 25 m of a nest in Harriman Fjord. Thus, it is highly unlikely that they consume oystercatcher eggs.
Table 3.2. Mean observation rates (# observations per h video footage) of potential disturbance stimuli recorded within 25 m of Black Oystercatcher nests \((n = 10)\), and within 5 m of Black Oystercatcher nests \((n = 16)\), in Harriman Fjord, Alaska, during 2005 and 2006. Daytime and nighttime rates are listed separately. Nests with < 3 observations in a stimulus category, or limited fields of view within 25 m of nests are omitted from estimates. Means are \(\pm\) SD.

<table>
<thead>
<tr>
<th>Stimulus</th>
<th>w/in 25m of nest</th>
<th>w/in 5m of nest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Other birds</td>
<td>0.194 ± 0.185</td>
<td>0.060 ± 0.125</td>
</tr>
<tr>
<td></td>
<td>Daytime</td>
<td>0.219 ± 0.217</td>
</tr>
<tr>
<td></td>
<td>Nighttime</td>
<td>0.103 ± 0.103</td>
</tr>
<tr>
<td>Conspecifics</td>
<td>0.029 ± 0.030</td>
<td>0.010 ± 0.012</td>
</tr>
<tr>
<td></td>
<td>Daytime</td>
<td>0.031 ± 0.031</td>
</tr>
<tr>
<td></td>
<td>Nighttime</td>
<td>0.020 ± 0.034</td>
</tr>
<tr>
<td>Humans</td>
<td>0.018 ± 0.014</td>
<td>0.010 ± 0.011</td>
</tr>
<tr>
<td></td>
<td>Daytime</td>
<td>0.022 ± 0.017</td>
</tr>
<tr>
<td></td>
<td>Nighttime</td>
<td>no encounters</td>
</tr>
<tr>
<td>Mammals</td>
<td>0.014 ± 0.019</td>
<td>0.005 ± 0.008</td>
</tr>
<tr>
<td></td>
<td>Daytime</td>
<td>0.010 ± 0.018</td>
</tr>
<tr>
<td></td>
<td>Nighttime</td>
<td>0.028 ± 0.039</td>
</tr>
<tr>
<td>Other</td>
<td>0.016 ± 0.035</td>
<td>0.001 ± 0.002</td>
</tr>
<tr>
<td></td>
<td>Daytime</td>
<td>0.018 ± 0.043</td>
</tr>
<tr>
<td></td>
<td>Nighttime</td>
<td>0.008 ± 0.018</td>
</tr>
</tbody>
</table>
Table 3.3. Proportion of observations of a potential disturbance stimulus or sub-stimulus type associated with the flush of incubating Black Oystercatchers video monitored in Harriman Fjord, Alaska, during 2005 and 2006. Estimates are reported for observations within two distances from nests. Nests with < 3 observations in a stimulus or sub-stimulus category, or limited fields of view within 25 m of nests are not included in estimates. Means are presented ± SD.

<table>
<thead>
<tr>
<th>Stimulus / sub-stimulus</th>
<th>w/in 25m of nest (# nests)</th>
<th>w/in 5m of nest (# nests)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Other birds</td>
<td>0.146 ± 0.242 (13)</td>
<td>0.072 ± 0.097 (12)</td>
</tr>
<tr>
<td></td>
<td>0.076 ± 0.164 (9)</td>
<td>0.029 ± 0.076 (7)</td>
</tr>
<tr>
<td>Non-predatory&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.210 ± 0.297 (9)</td>
<td>0.132 ± 0.143 (6)</td>
</tr>
<tr>
<td>Predatory&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conspecifics</td>
<td>0.708 ± 0.187 (7)</td>
<td>0.758 ± 0.229 (5)</td>
</tr>
<tr>
<td>Humans</td>
<td>0.679 ± 0.315 (7)</td>
<td>0.900 ± 0.167 (6)</td>
</tr>
<tr>
<td></td>
<td>0.833 ± 0.289 (3)</td>
<td>1.000 ± 0.000 (2)</td>
</tr>
<tr>
<td></td>
<td>0.504 ± 0.270 (6)</td>
<td>0.825 ± 0.236 (4)</td>
</tr>
<tr>
<td>Mammals</td>
<td>0.483 ± 0.125 (5)</td>
<td>0.792 ± 0.144 (4)</td>
</tr>
<tr>
<td></td>
<td>0.393 ± 0.376 (3)</td>
<td>0.875 ± 0.177 (2)</td>
</tr>
<tr>
<td>Predatory</td>
<td>0.571 ± --- (1)</td>
<td>1.000 ± 0.000 (2)</td>
</tr>
<tr>
<td>Other&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.250 ± 0.215 (4)</td>
<td>--- (0)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Duck, shorebird, seabird, and passerine species

<sup>b</sup>Gull and raptor species

<sup>c</sup>Lack of observation within the ‘other’ stimulus category precluded an estimate within 5 m of nest.
Table 3.4. Incubation recess rates, and mean observation rates of potential disturbance stimulus types encountered within 25 m of Black Oystercatcher nests. Recess rates and stimulus observation rates of hatched nests are compared with recess rates and stimulus observation rates of depredated nests. Data were obtained from nests video monitored from day 6 - 14 post clutch initiation, in Harriman Fjord, Alaska during 2005 and 2006. Only nests with ≥ 50 hours of observation during this period are included (n = 5 hatched, 4 depredated nests). Means are presented ± SD.

<table>
<thead>
<tr>
<th></th>
<th>Hatched nests</th>
<th>Predated nests</th>
<th>$t, Z$ stat$^a$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recess rate</td>
<td>0.80 ± 0.08</td>
<td>0.79 ± 0.11</td>
<td>$t = 0.2$</td>
<td>0.880</td>
</tr>
<tr>
<td>Observation rates</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All stimuli</td>
<td>0.18 ± 0.19</td>
<td>0.30 ± 0.25</td>
<td>$Z = -0.4$</td>
<td>0.749</td>
</tr>
<tr>
<td>Other birds</td>
<td>0.07 ± 0.06</td>
<td>0.19 ± 0.25</td>
<td>$t = -0.3$</td>
<td>0.811</td>
</tr>
<tr>
<td>Conspecifics</td>
<td>0.02 ± 0.01</td>
<td>0.02 ± 0.02</td>
<td>$t = -0.2$</td>
<td>0.884</td>
</tr>
<tr>
<td>Humans</td>
<td>0.04 ± 0.05</td>
<td>0.01 ± 0.02</td>
<td>$Z = 0.9$</td>
<td>0.391</td>
</tr>
<tr>
<td>Mammals</td>
<td>0.04 ± 0.04</td>
<td>0.03 ± 0.03</td>
<td>$Z &lt; 0.1$</td>
<td>&gt; 0.999</td>
</tr>
</tbody>
</table>

$^a$ Statistical comparisons between hatched and predated nests were performed with two sample $t$-tests ($t$-statistic), or Wilcoxon rank sum tests ($Z$-statistic) where data were non-normal.
Figure 3.1. (A) Location of Prince William Sound in Alaska. (B) Location of Harriman Fjord study area within Prince William Sound. (C) Locations of video monitored and non-video monitored nests within the study area, by year. Camping sites documented within 200 m of an active nest are indicated with a tent symbol. Any recreational shoreline use documented within 200 m of an active nest is indicated with black dotted outline.
Figure 3.2. Video monitoring configuration showing (A) close-up camera position (1 m from nest), (B) distance camera position (5 m from nest), and (C) power source and digital video recorder (50 m from nest).
Figure 3.3. Proportion of observations of other birds, conspecifics, and humans, within 25 m of a nest associated with the flushing of an incubating Black Oystercatcher. Data were obtained from six of 22 nests monitored with video cameras in Harriman Fjord, Alaska, during 2005 and 2006 with sufficient sample sizes of detections within each potential disturbance stimulus category, and with adequate fields of view. Means and 95% confidence intervals are back-transformed from the logit scale.
Figure 3.4. Mean percentage of flush-causing disturbance stimuli responded to by incubating Black Oystercatchers with aggression, retreat, combined aggression-retreat, or undeterminable behaviors in Harriman Fjord, Alaska, during 2005 and 2006. Data were obtained from video monitored nests with \( \geq 3 \) flushes per disturbance stimulus category. Nest sample sizes used for calculations are listed above bars. Responses are separated by sex: (A) females, (B) males.
Figure 3.5. Mean number of minutes a Black Oystercatcher nest was left unattended following an incubator flush associated with a disturbance stimulus or sub-stimulus (within a stimulus). Data were obtained from nests filmed in Harriman Fjord, Alaska during 2005 and 2006, for which ≥ 3 disturbance flushes were observed per stimulus and sub-stimulus category. Nest sample sizes for each stimulus or sub-stimulus type are listed above bars. Means are reported ± SD.
Figure 3.6. Causes of Black Oystercatcher nest failure documented with video monitoring in Harriman Fjord, Alaska during 2005 and 2006. (A) nocturnal tidal flooding, (B) diurnal black bear predation, (C) nocturnal wolverine predation, (D) nocturnal American mink predation, and (E) nocturnal pine marten predation.
Figure 3.7. Mayfield daily survival estimates and 95% confidence intervals for Black Oystercatcher nests in Harriman Fjord, Alaska within 200 m of any observed human recreational shoreline activity (n nests = 14) compared with no observed human activity (n nests = 52), and within 200 m of camping activity (n nests = 9) compared with no camping activity (n nests = 57). Nests were pooled between 2005 and 2006, and between first and re-nest attempts.
4. CONCLUSION

This study identified natural and anthropogenic factors influencing incubation patterns and nest failure of the Black Oystercatcher, an uncommon and poorly-known shorebird, within an area of unusually high breeding density. Comprehensive analyses of incubation patterns, relative to environmental processes and nest area stimuli, were conducted using over 4,000 hours of incubation and nest area video footage collected around the clock, under variable weather conditions. Incubation behavior was influenced by several dynamic, interacting variables. Complimentary sex roles within pairs facilitated a balance between efficient nest care and self-maintenance needs under changing environmental conditions and stochastic disturbance events. Changes in incubation patterns were attributable to variables rarely considered for the species, such as time of day. Disturbance stimuli were found to influence incubation patterns, but were not associated with lower reproductive success. This work elucidates several aspects of Black Oystercatcher reproductive behavior and ecology which will enhance future study and conservation of the species.

4.1. BLACK OYSTERCATHER INCUBATION PATTERNS AND SEX ROLES

Analyses of incubation patterns suggested that female oystercatchers assumed a dominant role in incubation, and males assumed a dominant role in nest defense. Oystercatchers breed in exposed environments, subject to frequent intrusions by conspecifics and other bird species, and unpredictably harsh environmental conditions.
Under these conditions shared parental care is an efficient behavioral strategy which permits nearly continuous incubation by one member of the pair, while potential predators are chased or distracted by the other. Cyclical environmental processes, such as tide and ambient temperature, were found to influence incubation patterns to some degree. However, because shared incubation duties permitted ample feeding opportunities and temperatures were relatively mild, these factors were not as influential as the time of day, or occurrence of disturbance. Incubation bout length nearly doubled at night. Avian nest studies are rarely able to document changes in incubation behavior during darkness. This study emphasizes the importance of considering incubation behavior over the entire 24 h period, even at latitudes where nights may be disproportionately short during the breeding season. While several factors may have contributed to longer incubation bouts during nighttime, longer bouts corresponded to the much higher nocturnal predation rate. It is possible that longer incubation bouts at night are a response to a nocturnal shift in the composition of potential predators. A reduction in parental activity near the nest could prevent the attraction of more dangerous nighttime nest predators. Incubation bouts that were disturbed by a stimulus near the nest were far shorter than bouts ending with a normal exchange of incubation duties. This indicated that disturbances had an effect on incubation patterns, warranting a closer examination of the types of disturbances near nests, a quantification of associated behavioral responses to disturbance, and an analysis of the effects of disturbance on nest failure.
4.2. THE INFLUENCE OF DISTURBANCE ON INCUBATION BEHAVIOR AND NEST SUCCESS

Video was used to document over 3,500 observations of potential disturbance stimuli at 22 oystercatcher nests during incubation. While variation existed among nests, an average of 31% of potential disturbance stimuli observed within 25 m of a nest prompted an incubating oystercatcher to flush. Conspecifics and humans were the most common types of stimuli to prompt the flushing of an incubating oystercatcher. However, as humans were infrequently observed, conspecific disturbance accounted for the most flushes overall. Other bird species were observed near nests more than any other type of potential disturbance stimulus, but rarely caused incubating oystercatchers to flush. This indicates that the intensity of responses by incubating birds to potential disturbance stimuli varied greatly depending on the type of disturbance encountered. Thus, certain stimuli are probably viewed as a greater threat to individual or nest safety (e.g., humans and other terrestrial mammals), or to territory ownership (i.e., conspecifics). Different disturbance stimulus types produced different responses from flushed oystercatchers. For example, while conspecifics were almost always attacked by incubating oystercatchers, humans nearly always caused an incubator to flee, and nests were left unattended for longer periods after a human disturbance than after other types of disturbances.

Although disturbance affected incubation patterns, it was not associated with lowered nest success. Unlike more populated, developed portions of the Black Oystercatcher range further south, the intensity of human disturbance in Harriman Fjord
may be too low to induce nest failure. However, because human activity produced marked changes in incubation behavior, more intensive human use could affect oystercatcher reproductive success. Thus, I recommended that research be extended into areas of the Black Oystercatcher range where human activity levels are higher.

Causes of nest failure were identified for all failed, video monitored nests. Mammal depredation (primarily mustelid) and tidal flooding accounted for all nest failures. One nest was consumed by a marten, a previously unreported predator of oystercatcher nests. Six of seven failures occurred during nighttime which made up only 21% of the total number of hours that nests were monitored. Because evidence of nest fate was often unclear after nest failure events, conventional monitoring of nests would have failed to accurately identify causes of nest failure in at least three cases. This study illustrates the importance of 24 h nest monitoring for accurately identifying the causes of nest failure.

4.3. RECOMMENDATIONS FOR FUTURE STUDY

Understanding the effects of anthropogenic and natural disturbances on reproductive behavior and success is important for assessing population trends and conservation needs of shorebird populations. Conventional nest monitoring methods may fail to identify factors that affect nesting behavior, including the influence of time of day, and the presence of certain disturbance stimuli. Continuous video monitoring produces a more complete picture of factors influencing nesting behavior and nest success. This study identified causes of nest failure that were not widely suspected.
Conventional methods of determining nest failure often rely on anecdotal evidence and supposition. In these cases caution should be taken when assigning causes of nest failure. Observer biases toward frequently observed daytime events are likely, while unseen nocturnal causes of nest failure may never be suspected. Use of dual camera video units greatly enhanced the information that could be obtained from the nest area. However, the number of camera units that could be simultaneously deployed was limited, restricting the power of analyses to detect differences. Future shorebird incubation studies may be enhanced by deploying more video units to alleviate sample size limitations. This is increasingly feasible as camera and video technology becomes more efficient and cost-effective.

Limited camera fields of view prevented behavioral observations of off-duty members of incubating pairs. It is important to consider preceding and concurrent activities to fully understand the context and motivation for a particular breeding activity. While beyond the scope of this study, further work should document activity of pair members during recesses, to enhance understanding of nesting behavior. This could be accomplished by combining radio-tracking with video nest monitoring to determine relationships between shorebird incubation and foraging schedules, under disturbance pressures.

In Harriman Fjord, secretive nocturnal mammalian predators were responsible for the majority of nest depredations. A fuller understanding of demographics and behavior of potential nest predators is necessary and may be facilitated with predator radio-tracking studies, extensive predator sign surveys, or infrared-triggered camera
systems. Studies of predator assemblages may be important for understanding the extent and temporal variability of predation risk. This could have conservation implications should rates of nest failure increase at the study site.

Although most human activity observed near nests caused incubating oystercatchers to flush, affects on nest success were less conclusive. The mechanisms by which human activities reduce nest success are rarely straightforward. Thus, more study of the process is needed in Harriman Fjord and elsewhere. Behavioral responses to human disturbance may not have conservation significance unless they are associated with lower reproductive success.

While much nest loss occurred in Harriman Fjord, high rates of reproductive failure over a short monitoring period may not predict subsequent population declines, especially in a long-lived species like the Black Oystercatcher which may experience many opportunities to breed within a lifetime. Thus, this study may have been too short to adequately assess how nest failure affects population trends of Harriman Fjord oystercatchers. Thus, longer-term monitoring of oystercatcher populations at the site, and throughout the range, is warranted.


Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430-455.


