FACTORS AFFECTING INCUBATION PATTERNS AND SEX ROLES OF BLACK OYSTERCATCHERS IN ALASKA

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Abstract. Studies examining the effects of human disturbance on avian parental behavior and reproductive success are fundamental to bird conservation. However, many such studies fail to also consider the influence of natural threats, a variable environment, and parental roles. Our work examines interactive 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. We used 24-hr-per-day video monitoring of 13 molecularly sexed breeding pairs to systematically examine incubation, revealing previously undocumented information that may inform conservation practices for the genus. Seven of 22 video-monitored nests failed, primarily from egg depredation by nocturnal mammals. Analyses of 3177 hr of video footage indicated a near doubling of incubation-bout lengths at night, corresponding to the increased risk of nighttime egg predation. Females had higher overall nest attendance (54% vs. 42%) and longer mean incubation bouts than did males (88 min vs. 73 min). Uninterrupted incubation bouts were over twice as long as bouts interrupted by disturbance. Incubating males departed nests substantially more frequently because of nest-area disturbances than did females in one but not both years of our study. Our findings suggest that the sexes incubate in different but complementary patterns, facilitating efficient egg care in a dynamic environment with several nest threats. We emphasize the importance of considering natural influences when human threats to shorebird reproductive behavior and success are evaluated.

Key words: *Black Oystercatcher, disturbance,* Haematopus*, incubation behavior, nest failure, Prince William Sound, sex roles, video monitoring.*

Factores que Afectan los Patrones de Incubación y los Roles Sexuales en *Haematopus bachmani* en Alaska

Resumen. Los estudios que examinan los efectos de las perturbaciones humanas sobre el comportamiento parental de las aves y sobre su éxito reproductivo son fundamentales para la conservación de estas. Sin embargo, muchos de estos estudios no consideran la influencia de las amenazas naturales, de un entorno variable, ni las funciones parentales. Nuestro trabajo examina las relaciones interactivas entre procesos cíclicos (hora del día, marea, temperatura, estacionalidad) y procesos estocásticos (perturbaciones naturales/humanas) con los patrones de incubación (asistencia, duración de los eventos, tasas de receso) de *Haematopus bachmani*, un ave playera de interés para la conservación. Monitoreamos con cámaras de vídeo durante las 24 horas del día a 13 parejas reproductoras, cuyos sexos fueron determinados molecularmente, para examinar sistemáticamente la incubación, lo que reveló información previamente no documentada que puede ayudar a optimizar las prácticas de conservación para el género. Siete de los 22 nidos monitoreados por video fracasaron, principalmente por depredación de huevos por parte de mamíferos nocturnos. Los análisis de 3177 horas de video indicaron una casi duplicación de las longitudes de los eventos de incubación durante la noche, correspondiendo con un aumento del riesgo de depredación de los huevos durante estas horas. Las hembras en general atendieron más veces el nido (54% vs. 42%) y presentaron periodos de incubación significativamente más largos que los machos (88 min vs. 73 min). Los eventos de incubación no interrumpidos duraron más del doble del tiempo que los eventos interrumpidos por perturbaciones. Los machos que se encontraban incubando dejaron los nidos con mayor frecuencia debido a perturbaciones en el área del nido que las hembras en sólo uno de los dos años de nuestro estudio. Nuestros hallazgos sugieren que los dos sexos incuban con patrones diferentes pero complementarios, facilitando el cuidado eficiente de los huevos en un ambiente dinámico con varias amenazas a los nidos. Enfatizamos la importancia de considerar las influencias naturales cuando se evalúan las amenazas humanas sobre el comportamiento y el éxito reproductivo de las aves playeras.

INTRODUCTION

Avian behavior is often ignored in studies that address conservation. However, mitigating effects of human disturbance on bird species at risk requires knowledge of how parents care for their young, and how disturbance interacts with other environmental influences (Weston and Elgar 2005, Yasué and Dearden 2006, Sabine et al. 2008). Any behavior an individual engages in to increase its offspring's fitness may be considered parental care and, subject to genetic control, will be selected for at optimal levels (Emlen and Oring 1977, Clutton-Brock 1991).

Incubation is a form of parental care common to most birds. Eggs require protection from weather and predation (Skutch 1949, 1957). In shorebirds, which vary greatly in mating patterns (Oring and Lank 1982), the degree to which sexes share parental care influences incubation patterns (Norton 1972, Kosztolányi et al. 2003). Incubation also can be influenced by ambient temperature (Cantar and Montgomerie 1985, Cresswell et al. 2003), tides (Nol 1984, Thibault and McNeil 1995), predation risk (Larsen et al. 1996, Smith et al. 2007), time of day (Kosztolányi and Székely 2002, Wallander 2003), and seasonality (Ashkenazie and Safriel 1979, Cuervo 2003). In coastal areas, where human activity is often concentrated, human disturbance may adversely affect nesting shorebirds (Colwell 2010). As a result, many studies have assessed the effects of human disturbance on shorebird incubation, although few studies have examined human disturbance within the context of natural disturbance and other processes influencing incubation (e.g., Yasué and Dearden 2006, Sabine et al. 2008).

Oystercatchers (*Haematopus* spp.) are large shorebirds with a worldwide distribution. They nest in dynamic coastal environments where incubation is influenced by many natural processes (Hockey 1996a). Individuals' fidelity to mates and nest sites is high, and they compete for productive territories, prompting aggressive conspecific interactions (Hockey 1996a, Bruinzeel and van de Pol 2004). Oystercatchers have exposed ground nests, resulting in high rates of egg and chick predation and periodic nest flooding (Hockey 1996b). Biparental care and complementary sex roles counter the high risk of predation, with males assuming more vigilance and nest-defense behaviors, and females spending more time on eggs (Nol 1985, Kersten 1996). The tide cycle also may influence incubation patterns, the birds feeding most at low tide when invertebrates are accessible (Hockey 1996b, Hulscher 1996). Few studies have examined how other natural processes, such as time of day and weather, influence incubation patterns (but see Purdy and Miller 1988).

The melanistic Black Oystercatcher (*H. bachmani*) is adapted to rocky intertidal habitat along the North American west coast (Andres and Falxa 1995). It plays a key role as a predator in rocky intertidal ecosystems (Marsh 1986, Hahn and Denny 1989) and, like the other oystercatchers (Leseberg

et al. 2000), is considered a indicator of management needs within these habitats (USDA Forest Service 2002). With a world population of 11 000 (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) and may be highly vulnerable to human disturbance (Tessler et al. 2007). However, as several aspects of Black Oystercatcher ecology and life history, including parental care, are poorly understood, appropriate conservation strategies require more information (Andres and Falxa 1995, Tessler et al. 2007). In one of few studies to examine the effects of human disturbance on the Black Oystercatcher, Morse et al. (2006) found that extreme tides had a greater effect on nest survival than did human recreation, illustrating the importance of examining disturbance holistically.

Here we describe incubation patterns and sex roles of the Black Oystercatcher in Prince William Sound, Alaska. Our objective was to identify factors that influence incubation behaviors of each sex, including natural and human disturbance. We considered variation in incubation patterns and attendance by sex, portion of the 24-hr circadian period ("time of day"), tidal height and stage, ambient temperature, occurrence of disturbance, stage of incubation, seasonality, and year. With continuous video monitoring of nests, we assessed incubation patterns on a fine scale unattainable by other observation techniques. We also identified nest departures caused by disturbance to understand interactions between disturbance and other processes influencing incubation and nest success. Video documentation of nest activity through all hours and weather conditions provided a comprehensive understanding of factors influencing Black Oystercatcher incubation that is rarely obtained for most shorebirds.

METHODS

STUDY AREA

Our study site was Harriman Fjord, Alaska (northwest Prince William Sound; 60° 58′ N, 148° 26′ W to 61° 7′ N, 148° 9′ W), a 3 × 20-km tidal fjord in Chugach National Forest (Fig. 1). Peak tides in the fjord exceed 6 m (NOAA 2007). Spring and summer weather is cool (0° to 18° C during the study, USDA Forest Service, unpubl. data), wet, and breezy. Black Oystercatchers use gravel-sand beaches, alluvial outwashes, tidal flats, and rock islets for nesting and foraging. Suspected predators of oystercatcher nests in Harriman Fjord include the Glaucous-winged Gull (*Larus glaucescens*), Bald Eagle (*Haliaeetus leucocephalus*), Northwestern Crow (*Corvus caurinus*), river otter (*Lutra canadensis*), American mink (*Mustela vison*), black bear (*Ursus americanus*), and wolverine (*Gulo gulo*; Andres and Falxa 1995, Morse et al. 2006, Tessler et al. 2007).

Harriman Fjord is scenic, with easy boat access from the port of Whittier (<200 km from Anchorage), exposing
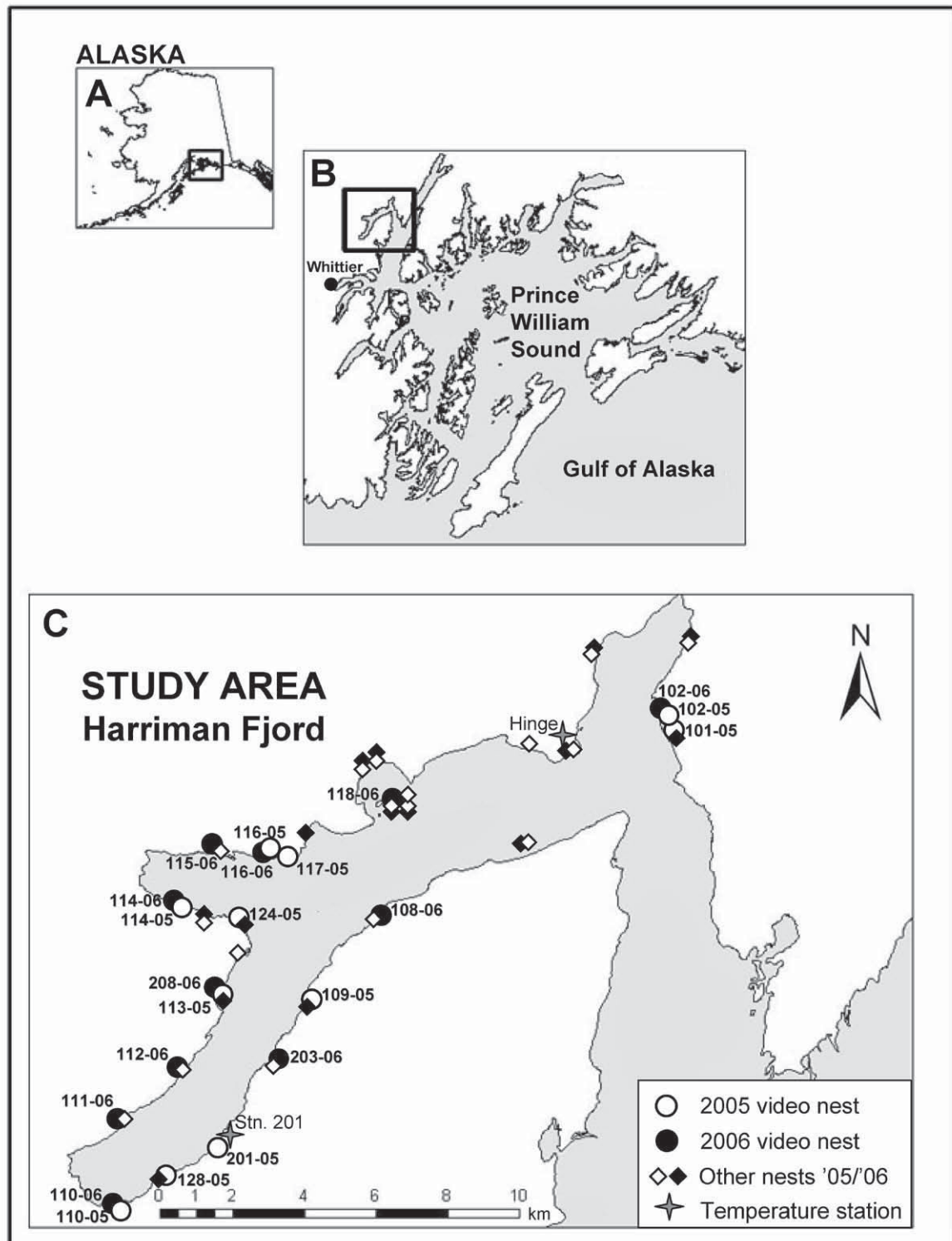
FIGURE 1. (A) Location of Prince William Sound in Alaska. (B) Location of Harriman Fjord study area in Prince William Sound. (C) Locations of video-monitored and non-video-monitored Black Oystercatcher nests by year and locations of temperature stations within the study area.

it to more human recreational use than many oystercatcher-breeding areas in Prince William Sound, particularly during the peak of nesting. This prompted the U.S. Forest Service to begin annual censuses of breeding Black Oystercatchers in Harriman Fjord in 2000 and to initiate a banding and monitoring program in 2004. Each year since 2004, the study area has supported one of the higher densities of breeding Black Oystercatchers in the species' range, with 25–29 nesting pairs present between May and August (Spiegel 2008, Poe et al. 2009).

SITE SURVEYS, NEST CHECKS, AND ADULT CAPTURE

From early May to late July in 2005 and 2006, we surveyed Harriman Fjord's shoreline from motorized rafts at least once per week for oystercatcher breeding activity during mid to high tides. We searched areas of probable nesting on foot. We assumed nests found with one egg were initiated that day and used egg flotation 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 the chicks fledged or the nest failed. We captured unbanded adults with walk-in traps and leg snares during trapping, temporarily replacing clutches with decoy eggs (Benson and Suryan 1999, Gratto-Trevor 2004). Each adult was given a unique combination of colored plastic leg bands and a numbered U.S. Geological Survey metal band. We drew 15 μL of blood from the metatarsal vein of each banded bird, following guidelines approved by the American Ornithologists' Union (Oring et al. 1998) and sexed the samples molecularly by CHD-Z/CHD-W (Griffiths et al. 1998). Capture was not attempted until 7 days after clutch initiation. No nests were abandoned after capture. Incubation typically resumed soon after the birds' release.

VIDEO NEST MONITORING

We continuously monitored 22 active oystercatcher nests with weatherproof twin micro-camera and digital video units from 7 days after clutch initiation until approximately 3 days after the eggs hatched or the nest failed (Spiegel 2008). We placed a camouflaged "close-up" camera 15 cm high, 1 m from each nest, allowing color-band identification. A "distance" camera was located 5 m from each nest and 1 m high, recording a wide angle 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 was located 50 m from a nest, storing footage from both cameras with time and date stamps, and powered by six 40-watt solar panels connected to two deep-cycle batteries, rated at 100 amp-hr.

We configured video units similarly at each nest, with both cameras facing downslope and fields of view intersecting at 120°. Detection of activity >25 m from some nests was reduced because of slope and terrain, especially during darkness. Cameras were set up at nests 7 days after the initial egg was laid to reduce risk of nest desertion (Sanders and Maloney 2002, Williams and Wood 2002). We placed each of four sets of cameras at a nest randomly chosen from a running list of active nests (Spiegel 2008). We recorded both first nests and replacement nests (of different pairs) to obtain samples large enough for analyses.

VIDEO DATA EXTRACTION

We viewed footage from close-up and distance cameras simultaneously on a split screen at a rate 4× real time, slowing whenever we saw movement at or near the nest. Oystercatchers were identified by leg-band combination. Date and time were recorded whenever an oystercatcher settled on or departed a nest. We considered each uninterrupted period of sitting, beginning with an oystercatcher settling on a nest, an incubation bout. We reviewed video of each nest from the cameras' deployment until the first egg hatched or the nest failed. We excluded from the dataset incubation bouts in progress at the start or end of a segment of video (incomplete bouts) or interrupted by a capture.

After receiving identical training, six observers recorded from the video number of incubation bouts per bird, length of each incubation bout, and reason each incubation bout ended. All observers reviewed footage from each nest, to spread observer biases among nests. C. Spiegel randomly spot-checked data for consistency one to three times for each nest, detecting no substantial differences among observers.

When an incubating bird departed a nest, ending an incubation bout, we slowed the video to half-time to determine the cause of departure. We considered the cause an "incubation-duty switch" if it was initiated by the appearance of an incubating bird's mate (within 30 sec of departure), or a "disturbance" if an interspecific, intraspecific, or environmental (e.g., tidal flooding) stimulus was observed near a nest within 30 sec of departure. Incubating birds often flushed because of humans and large mammals well before such disturbances were detectable in the video. We assumed these stimuli caused a departure if detected ≤10 min after a bird flushed if it was likely they were in the vicinity before detection (see McGowan 2004). The cause of 25% of departures was not evident because of the cameras' limited fields of view. In these cases we examined the departing bird's behavior to determine whether departure was caused by an undetected disturbance. Agitated flights directly off nests were more frequently associated with observed disturbances than with incubation-duty switches (>60% vs. <3%). The percentage of agitated flight departures for undetected causes mirrored the percentage for observed disturbances but was far higher than for observed incubation-duty switches. Furthermore, the percentage of times the same individual returned to the nest after a departure for an undetected cause was similar to that after an observed disturbance (40% vs. 35% of departures),

suggesting disturbance rather than duty switches motivated departures. Thus, for analyses, we coded undetected causes of departure as disturbances. We did not record departures of <30 sec if the same individual returned to the nest.

ENVIRONMENTAL AND TEMPORAL VARIABLES

We categorized time of day as "daytime" and "nighttime" in relation to sunrise and sunset at Harriman Fjord (U.S. Naval Observatory 2007). The ratio of nighttime to daytime during study seasons ranged from 1:3 to 1:4. If over 50% of an incubation bout occurred during daytime or nighttime, we assigned the bout to that time-of-day category. We categorized incubation departures as daytime or nighttime according to exact departure times.

For both seasons of the study we obtained regional tide heights at 6-min intervals (NOAA 2007) and interpolated them to the minute. We categorized tides into four stages of equal duration within a cycle: (1) outgoing tide from end of high slack until median tide, (2) outgoing tide from median tide until end of lowest slack, (3) incoming tide from end of lowest slack until median tide, and (4) incoming tide from median tide until end of highest slack.

During each season of the study we recorded ambient air temperature at 10-min intervals with temperature sensors and Hobo Micro-station dataloggers (Onset Computer Corporation, Bourne, MA) and interpolated it to the minute. Temperature was logged at two locations in Harriman Fjord to account for microclimatic differences (Fig. 1).

We defined incubation day as the number of days elapsed since clutch initiation. To estimate dates of laying of first eggs, we backdated nests found after clutch completion 27.5 days (the average incubation period at nests where we observed clutch initiation and hatching, $n = 9$, SD = 1.0) from camera-documented hatch dates. We defined the stage of incubation as early incubation (day 7–17) or late (day 18–28). We examined differences in incubation patterns within a season by distinguishing first and replacement nests. Nest attempt was a valid representation of seasonality as attempts were largely synchronous, with first clutches laid mid-May to early June and replacement clutches laid mid-June to early July.

STATISTICAL ANALYSES

To assess whether video monitoring affected nest success we used the Mayfield method to estimate nest survival (Mayfield 1961, 1975) and confidence intervals (Johnson 1979) for video- and non-video-monitored nests. To account for the diminished exposure time of video-monitored nests, we omitted non-video-monitored nests from analysis if they failed within 11 days of clutch initiation (average number of days from clutch initiation to when video monitoring of nests began). Including these nests in analyses would have inflated estimates of the rate of survival of video-monitored nests. We assumed uniformity of survival probability through incubation and

assigned nest failure to the midpoint between checks if the date of failure was unknown.

We evaluated average incubation-bout length, incubation-recess rate, and incubation attendance in relation to several explanatory variables. Bout length was the mean length (in minutes) of uninterrupted incubation by an individual. Recess rate was the total number of nest departures by an incubating individual, divided by the total number of hours it was observed. For all analyses, if the data did not conform to the model's assumptions of normality and homoscedascity, we ln-transformed incubation-recess rate and incubation-bout length. Incubation attendance was the proportion of total nest-observation time during which an individual incubated, with total attendance as the sum of incubation attendance of both members of the pair.

Using mixed-model analysis of variance (ANOVA; PROC MIXED, SAS 2004), we evaluated differences in mean incubation-bout length by time of day (daytime vs. nighttime), year (2005 vs. 2006), nest attempt (first nest vs. replacement nest), and stage of incubation (early vs. late) with four models. We also determined whether mean bout length varied by sex or by departure cause (incubation-duty switch vs. disturbance) and whether relationships between bout length and each of the other explanatory variables varied by sex and/or departure cause (two- and three-way interactions with sex and/or departure cause). We modeled all explanatory variables and two- and three-way interactions between sex or departure cause as fixed effects, with nest as a random effect to account for lack of independence of observations within nesting pairs. Models including time of day as an explanatory variable were structured as randomized-block strip-split plots, with nest as the block, time of day as a first strip, sex as a second strip, and departure cause as a split within each interaction of time and sex. Models including stage of incubation were similarly structured, with stage of incubation substituted for time of day. Models including year or nest attempt were structured as completely randomized split-split plots, with nest replicates grouped by either year or nest attempt, then split by sex, with an additional split by departure cause within each sex.

We evaluated differences in recess rate by time of day, year, nest attempt, stage of incubation, sex, and departure cause with the same method used to analyze relationships with bout length, examining differences in recess rate further by the four tide stages with mixed-model ANOVA. Recess rates could then be compared by tide stage within each nest. This model was structured as a completely randomized-block strip-split plot, with nest as a block and tide stage as a first strip, sex as a second strip, and departure cause as a split within each interaction of tide and sex.

We evaluated differences in incubation attendance by time of day, year, nest attempt, and stage of incubation in four additional models with mixed-model ANOVA. Additionally,

we determined how attendance varied by sex, and we determined whether relationships between attendance and each of the other explanatory variables differed by sex by including sex and interactions with sex in each of the four models. We modeled explanatory variables and interactions with sex as fixed effects, with nest as a random effect to account for lack of independence of observations of nesting pairs. In ANOVA models of incubation attendance, we modeled nests as random blocks with time of day or stage of incubation modeled as strip plots, with the time or stage category in a first strip and sex in a second strip within each nest replicate. We structured ANOVA models of incubation attendance including year or nest attempt as completely randomized split plots, with nest replicates grouped by year or first nests vs. replacement nests, then split by sex.

To avoid inclusion of biased means, we omitted six of 22 video-monitored nests considered to have insufficient coverage (<100 hr) from mixed-model ANOVA analyses. Three more nests were omitted from analyses because sexes of the pairs were unknown. Thus most models included pairs from 13 nests. However, in analyses examining relationships of incubation patterns with stage of incubation, six of the 13 nests with sufficient observation time and individuals of known sex were omitted because they were not monitored during much of the early or late incubation stages. Seven of 13 nests with sufficient observation time and birds of known sex were omitted from analyses examining differences in incubation-bout length by time of day because we recorded too few bouts during the short nights at Alaska's high latitude to examine the interaction with departure cause. Two high-leverage outliers remaining after ln-transformations (a female from 2005 and male from 2006) were also omitted from the time-of-day model in the recess-rate analysis.

Missing values for some potential explanatory variables precluded the efficient use of model-selection techniques. Any global model would have been restricted to the sample of nesting pairs for which information for all potential explanatory variables were available. Information gained by examining relationships among all variables of interest with separate models outweighed the loss in sample size and power from restricting data to the constraints of model selection. However, multiple statistical tests compounded the chance of confidence intervals failing to contain a parameter's "true" value.

We predicted that incubation-bout lengths should be positively related to tide heights because higher tides may restrict foraging birds' access to intertidal resources, reducing foraging trips. We also predicted that incubation-bout lengths should be inversely related to temperature, colder temperatures requiring eggs be incubated more continuously. To examine these predictions we used a regression-coefficient analysis (Meredith and Stehman 1991). We analyzed only the subset of bouts not interrupted by disturbance. For this subset, we mean-corrected tide height and temperature data to aid interpretation of the intercept coefficient. We fit a linear regression relationship of ln(bout length) to the explanatory variable (tide height or temperature) and estimated intercept and slope coefficients for each bird. The intercept may be interpreted as an individual's average ln-transformed bout length at the average highest tide (or average lowest temperature), the slope as the rate of change in an individual's bout length relative to the change in highest observed tide (or lowest observed temperature). To examine sex differences in bout-length relationships with tide height and temperature, we analyzed each of the regression coefficients by blocked ANOVA (PROC GLM, SAS 2004) with nest as the block and sex as the main effect.

Suspecting that colder temperatures were more frequent at night, we used a two-sample t-test to examine whether the mean temperature in Harriman Fjord during video monitoring differed by day or night. A significant difference would indicate that a relationship found between temperature and incubation-bout length could be confounded with time of day. Although we predicted no difference, we used a two-sample t-test to examine whether the mean tide height during video monitoring differed by day or night, to see if tide height was confounded with time of day.

We report estimates as means with 95% confidence intervals, unless indicated otherwise, and present analyses involving explanatory variables included in multiple models as a range of estimates and confidence intervals. For reported values, we back-transformed ln-transformed estimates and confidence limits, unless indicated otherwise. We consider test results significant at $\alpha = 0.05$.

RESULTS

VIDEO NEST DOCUMENTATION AND NEST FAILURE

We monitored 22 of 87 nests found in Harriman Fjord during 2005 and 2006 with video (11 per season, Fig. 1), and reviewed 4280 hr of video footage. Seven video-monitored nests (32%) failed, four from nocturnal mammalian predation [2 American mink, 1 marten (*Martes americana*), 1 wolverine], one from diurnal mammalian predation (black bear), and two from flooding by a spring tide. Mayfield estimates of daily survival of video-monitored nests (0.970, 95% CI: 0.948–0.992, $n = 22$ nests) and non-video-monitored nests of comparable exposure time (0.970, 95% CI: 0.955–0.985, $n = 27$ nests) were nearly identical. No adult mortality was observed during the study. We did not witness overt behavioral differences between video-monitored and non-video-monitored pairs, nor did we find that cameras were detected by the birds or attracted animals to a territory.

FACTORS INFLUENCING INCUBATION-BOUT LENGTH

We used a subset of 13 molecularly sexed nesting pairs (3177 hr of video) to examine differences in incubation

patterns between the sexes. We based subsequent results on these pairs, unless noted. Incubation bouts lasted an average of 78 min (± 20 SD). The median incubation bout was 21-24% longer (95% CI: 8–36 to 11–40%, depending on model) for females (88–90 min, 95% CI: 77–78 to 99–106 min, depending on model) than for males (73 min, 95% CI: 62–64 to 82–85 min, depending on model) in models including all 13 nests ($P < 0.004$; Fig. 2). A nonsignificant difference in bout length between the sexes in models based on smaller samples ($P = 0.09–0.10$; Table 1) was likely a result of low power to detect a difference rather than a lack of difference.

The median length of incubation bouts ending because of disturbance (56–73 min, 95% CI: 49–61 to 63–87 min, depending on model) was 52–70% shorter (95% CI: 34–72 to 51–92%, depending on model) than that of bouts ending with incubation-duty switches (94–110 min, 95% CI: 84–92 to 106–132 min, depending on model; $P < 0.001$ in all models; Table 1, Fig. 2), regardless of sex.

The median incubation bout was 81% longer (95% CI: 56–110%) during nighttime (120 min, 95% CI: 96–150 min) than during daytime (67 min, 95% CI: 53–83 min; $P < 0.001$; Table 1, Fig. 2), independent of sex or departure cause. Only six nests had enough nighttime bouts to be included in the model examining time of day, a result of the shortness of night during spring and summer in our high-latitude study area.

Incubation-bout length was positively related to the highest tide ($t_{12} = 6.1$, $P < 0.001$) and lowest temperature observed during a bout ($t_{12} = -2.8$, $P = 0.02$), independent of sex. Bouts were 20% longer (95% CI: 12–28%) for each additional 1 m in highest tide during a bout, regardless of sex, and 3% (95% CI: 1–5%) longer for each 1 °C reduction in lowest temperature during a bout.

We detected no difference in incubation-bout length between first nests and replacement nests or between the early and late stages of incubation (Table 1). However, the median bout length was 38% greater (95% CI: 12–69%) in 2006 (94 min, 95% CI: 82–108 min) than in 2005 (68 min, 95% CI: 59–79 min) independent of sex and departure cause ($P = 0.006$; Table 1).

FACTORS INFLUENCING INCUBATION-RECESS RATE

Incubating oystercatchers took a mean of 0.78 recesses per hour (± 0.16 SD) or nearly 19 recesses per 24 hr. In three of five models males and females had a difference in recess rates attributable to disturbance but not to incubation change ($P \leq 0.04$ for sex × DC in attempt, stage, tide models; Table 1). In these models, for females the median rate of recesses (0.31–0.35 hr^{-1}, 95% CI: 0.25–0.27 to 0.38–0.45) attributable to disturbance was 36–47% lower (95% CI: 10–25 to 49–63%, depending on model) than that for males (0.49–0.66 hr^{-1}, 95% CI: 0.40–0.51 to 0.59–0.85, depending on model). Females had a significantly lower recess rate than did males in the time-of-day model ($P = 0.04$), but the difference was
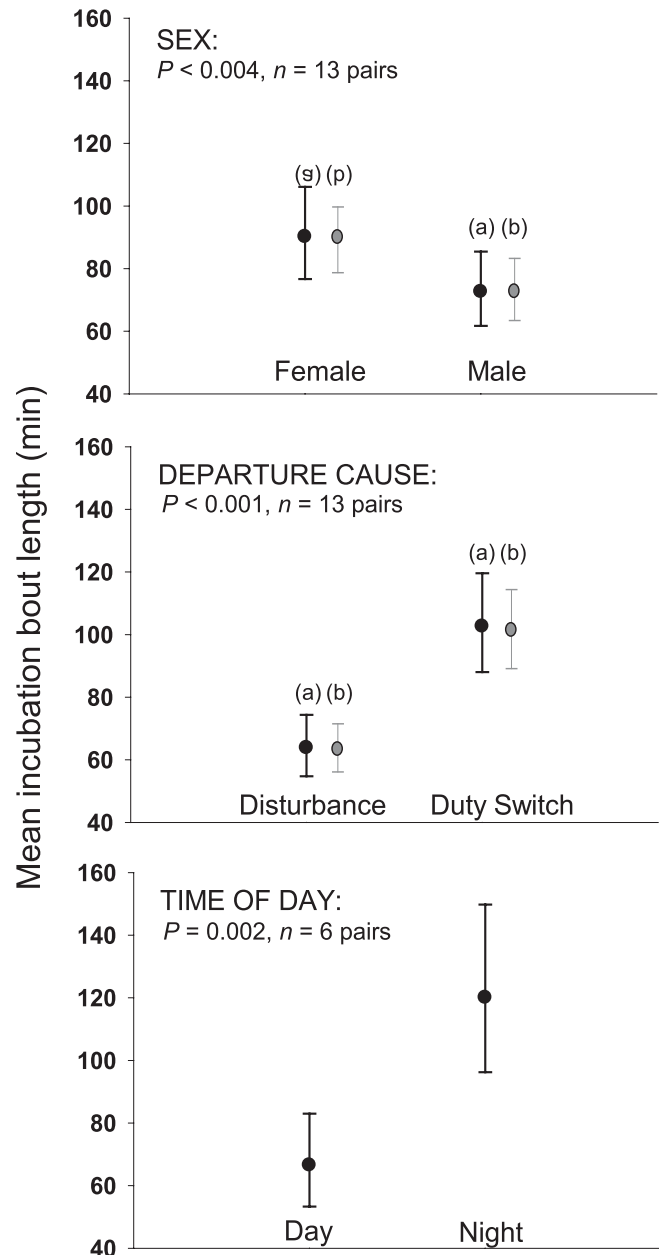

FIGURE 2.   Mean duration of incubation bouts of Black Oystercatchers in Prince William Sound, Alaska, by sex, cause of departure, and time of day; bars show 95% confidence intervals. (a) Estimates from nest-attempt model with 13 nests; (b) estimates from year model with 13 nests. Estimates are back-transformed from the natural log scale.

only marginally attributable to departures due to disturbance ($P = 0.06$ for "sex × DC," Table 1).

Much of the difference between the sexes in the rates of recesses due to disturbance was attributable to males' very high rate of disturbance-motivated departures in 2005 (0.81 recesses hr^{-1}, 95% CI: 0.69–0.94; significant interaction of year × sex × departure cause in the year model, $P = 0.002$; Table 1, Fig. 3). In 2006, the sexes' rates of recesses due to disturbance were more similar (Fig. 3).

TABLE 1.   Results of mixed-model ANOVA of incubation-bout length, incubation-recess rates, and nest attendance of Black Oystercatchers at Harriman Fjord, Alaska, 2005–2006. *P*-values in **bold** are significant at $\alpha = 0.05$.

		Incubation-pattern metric										
		Bout length				Recess rate				Attendance		
Model	Variables	n^a	F	df	P	n^a	F	df	P	n^a	F	df	P
Time of day[b,c]	Time of day	6	101.6	1,5	**<0.001**	13	34.7	1,10	**<0.001**	13	<0.1	1,12	0.90
	Sex		4.0	1,5	0.10		5.3	1,10	**0.04**		7.5	1,12	**0.02**
	Departure cause (DC)		50.6	1,20	**<0.001**		11.9	1,44	**0.001**		—	—	—
	Time of day × sex		1.0	1,5	0.37		0.2	1,10	0.69		1.6	1,12	0.23
	Time of day × DC		3.0	1,20	0.10		3.0	1,44	0.09		—	—	—
	Sex × DC		0.1	1,20	0.82		3.6	1,44	0.06		—	—	—
	Time of day × sex × DC		<0.1	1,20	0.95		0.1	1,44	0.72		—	—	—
Year[d]	Year	13	11.7	1,11	**0.006**	13	11.1	1,11	0.007	13	0.3	1,11	0.62
	Sex		13.4	1,11	**0.004**		6.3	1,11	0.03		45.1	1,11	**<0.001**
	Departure cause (DC)		78.1	1,22	**<0.001**		10.3	1,22	0.004		—	—	—
	Year × sex		1.4	1,11	0.26		0.7	1,11	0.41		2.5	1,11	0.14
	Year × DC		1.1	1,22	0.31		7.7	1,22	0.01		—	—	—
	Sex × DC		0.8	1,22	0.38		10.4	1,22	0.004		—	—	—
	Year × sex × DC		1.4	1,22	0.25		13.2	1,22	**0.002**		—	—	—
Nest attempt[d]	Nest attempt (attempt)	13	<0.1	1,11	0.94	13	<0.1	1,11	0.91	13	0.1	1,11	0.79
	Sex		16.8	1,11	**0.002**		2.6	1,11	0.13		75.3	1,11	<0.001
	Departure cause (DC)		80.4	1,22	**<0.001**		6.6	1,22	0.02		—	—	—
	Attempt × sex		2.8	1,11	0.12		0.4	1,11	0.55		12.3	1,11	**0.005**
	Attempt × DC		1.9	1,22	0.19		4.4	1,22	**0.05**		—	—	—
	Sex × DC		0.8	1,22	0.37		4.8	1,22	**0.04**		—	—	—
	Attempt × sex × DC		0.2	1,22	0.64		0.5	1,22	0.49		—	—	—
Incubation stage[b,e]	Incubation stage (stage)	7	0.2	1,6	0.64	7	0.3	1,6	0.63	7	<0.1	1,6	0.94
	Sex		4.0	1,6	0.09		1.2	1,6	0.31		10.4	1,6	**0.02**
	Departure cause (DC)		82.1	1,24	**<0.001**		10.3	1,24	0.004		—	—	—
	Stage × sex		<0.1	1,6	0.96		<0.1	1,6	0.89		0.9	1,6	0.38
	Stage × DC		0.3	1,24	0.57		0.4	1,24	0.51		—	—	—
	Sex × DC		2.2	1,24	0.15		16.5	1,24	**<0.001**		—	—	—
	Stage × sex × DC		2.4	1,24	0.13		0.2	1,24	0.71		—	—	—
Tide[b]	Tide	—	—	—	—	13	2.6	3,36	0.07	—	—	—	—
	Sex	—	—	—	—		6.6	1,12	0.03	—	—	—	—
	Departure cause (DC)	—	—	—	—		12.4	1,96	<0.001	—	—	—	—
	Tide × sex	—	—	—	—		0.5	3,36	0.66	—	—	—	—
	Tide × DC	—	—	—	—		1.1	3,96	0.36	—	—	—	—
	Sex × DC	—	—	—	—		9.4	1,96	**0.003**	—	—	—	—
	Tide × sex × DC	—	—	—	—		1.9	3,96	0.13	—	—	—	—

[a]*n* = number of nests.
[b]Randomized complete block ANOVA models.
[c]Seven nests omitted from time-of-day model for bout length because of insufficient data during nighttime; outlying observations from two individuals from different nests (one male, one female) omitted from time-of-day model for recess rate.
[d]Completely randomized design ANOVA models.
[e]Six nests omitted from all incubation-stage models because of insufficient data within an incubation stage.

Males' high rate of recesses in response to disturbance in 2005 corresponded with a high rate of females' recesses for incubation-duty switches in the same year (0.42 hr^{-1}, 95% CI: 0.29–0.55 in 2005, compared with 0.28 hr^{-1}, 95% CI: 0.16–0.40 in 2006; Fig. 3). During 2005 females may have compensated for the high rate of disturbance-motivated recesses by their mates. In replacing a mate that recessed frequently because of disturbance, a female would frequently be on the nest for a duty switch when the male returned to the nest. Accordingly, males were more likely to be relieved by their mate after a departure attributed to disturbance than
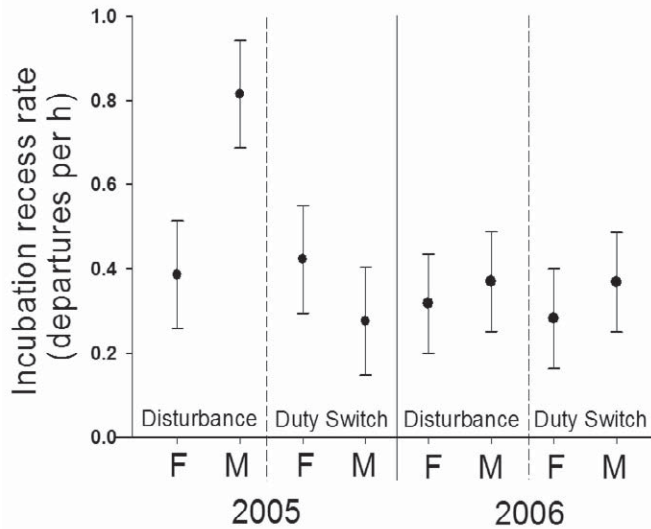
FIGURE 3. Mean Black Oystercatcher incubation recess rate in Prince William Sound, Alaska, by year, sex, and departure cause, with 95% confidence interval bars.

were females ($\chi^2 = 8.3$, $P = 0.004$). The rate of males' recesses for duty switches was low in 2005 (0.28 hr^{-1}, 95% CI: 0.15–0.40), as most of males' recesses were due to disturbance.

The mean recess rate was 91% greater (95% CI: 49–143%) during daytime than during nighttime, independent of sex and departure cause ($P < 0.001$; Table 1), supporting the finding of shorter daytime incubation bouts. Results between years and between nest attempts were similar. There were no significant differences in recess rates between first nests and replacement nests ($P = 0.91$) nor between the early and late stages of incubation ($P = 0.63$; Table 1).

FACTORS INFLUENCING INCUBATION ATTENDANCE

Nests were attended an average of 96% of the time they were monitored (± 3% SD). Incubation attendance was higher for females than males in all models (Table 1). Females' mean attendance ranged from 0.53 to 0.55 (95% CI: 0.47–0.59, depending on model), and males' ranged from 0.41 to 0.43 (95% CI: 0.37–0.49, depending on model) in all but the nest-attempt model. A significant interaction between attempt and sex ($P = 0.005$) in the nest-attempt model indicated that females' attendance was higher than males' attendance at first nests (0.13, 95% CI: 0.09–0.17) and that this difference was even greater for replacement nests (0.22, 95% CI: 0.16–0.28). Incubation attendance did not vary by time of day, year, or stage of incubation ($P > 0.63$, all models; Table 1).

DISCUSSION

Our study is the first to document effects of disturbance on the Black Oystercatcher's incubation patterns by 24-hr-per-day continuous video monitoring of nests. Continuous nest monitoring enabled us to record events at each nest exhaustively, to identify nest predators unequivocally, and to elucidate patterns of parental care, such as nocturnal incubation, rarely documented for shorebirds (Warnock and Oring 1996).

We suggest that, in response to frequent disturbance, oystercatchers employ a guard-and-chase strategy (Helbing 1977, Nol 1985) rather than the conceal-and-hide strategy common to many smaller shorebirds (Thibault and McNeil 1995, Weston and Elgar 2005). Disturbed bouts of incubation were less than half as long as bouts ending with duty switches. Incubating oystercatchers regularly left their nests to chase conspecific and heterospecific intruders, including much larger birds and mammals, from their territory (Spiegel 2008). Adult oystercatchers have low mortality rates and few major predators (Hockey 1996b). Conversely, they lay large, conspicuous eggs that are frequently depredated (Andres and Falxa 1995, Hockey 1996b). A guard-and-chase strategy is adaptive in such a life history. Biparental care with complementary sex roles facilitates guarding and chasing, allowing flexible responses to stochastic disturbances under fluctuating environmental constraints, without compromising individuals' needs for self-maintenance or reducing nest attendance. Accordingly, despite frequent nest disturbance, we found incubation attendance to be high, as reported for most oystercatchers (range 90–98%, Helbing 1977, Nol 1985, Purdy and Miller 1988).

We found that males' incubation bouts were generally shorter and their nest attendance lower than those of females. Nol (1985) reported similar results for the American Oystercatcher (*H. palliatus*), proposing that complementary sex roles evolved to maximize energetic efficiency; with smaller males, more suited to chase flights (lighter wing loading), regularly off the nest watching for disturbance and initiating territory defense, and larger females, more suited to maintaining egg temperatures, remaining on the nest during disturbances. This idea could explain why, in 2005, we found a substantially higher rate of disturbance-motivated recesses for males than for females. Males, assuming a larger role in nest defense, may have been more likely to respond to a disturbance while incubating. However, we observed a sex-based difference in the rate of disturbance-motivated recesses in only one of two years of the study. It is possible that males recess for disturbances at a rate higher than do females only when they encounter specific types of threatening stimuli at high frequencies or densities. We observed three times as many conspecific stimuli and nearly twice as many human stimuli within 25 m of nests in 2005 than in 2006 (Spiegel 2008). Our finding of variability by sex in response to disturbance between the two years illustrates the importance of considering factors that interact with disturbance for its influence on incubation to be adequately understood.

Although human stimuli were a small component of overall disturbance in our study area (Spiegel 2008), the reaction

of incubating birds to other forms of disturbance, such as potential predators, may predict the reaction of oystercatchers to greater levels of human disturbance in other nesting areas (Frid and Dill 2002). The addition of large amounts of human disturbance into an environment where incubation is already challenged by a high level of natural disturbance is unknown, however, and warrants further examination.

Despite the brevity of night at Harriman Fjord during the breeding season, nest failure was caused primarily by nocturnal or crepuscular mustelids. These predators, known to supplement their diet with eggs (Feldhamer et al. 2003), were not seen during daytime and would have been missed without monitoring 24 hr per day. Solely on the basis of nest remains, without video evidence, we may have falsely assigned nest loss to more visible diurnal predators.

Video revealed a change in the composition of mammalian egg predators active near nests at our field site after dark (Spiegel 2008), possibly explaining why the oystercatchers' incubation bouts were longer during nighttime. Skutch (1949) theorized that increased parental activity near nests leads to higher rates of failure and is selected against. Although empirical tests of this prediction have produced conflicting results (Roper and Goldstein 1997, Martin et al. 2000), experiments have confirmed that nest-activity levels can vary in response to perceived predation risk (Ghalambor and Martin 2002). The increase of numbers of mustelids hunting around Harriman Fjord at night likely raises the risk of nest loss. Thus selection may favor oystercatchers that take fewer recesses and incubate longer at night. Furthermore, the American mink, the nocturnal nest predator most frequently seen in video at Harriman Fjord, commonly preys on large adult waterbirds (Sullivan 1996). Therefore, nocturnal switches of incubation duty also could threaten adult oystercatchers that have trouble detecting the predators in darkness. Our findings contrast with those of Purdy and Miller (1988), who reported that the Black Oystercatcher's incubation bouts were of similar duration during daytime and nighttime in British Columbia (where nights are longer than in Alaska because of the lower latitude). However, Purdy and Miller (1988) did not use video to monitor nests and were limited by a small sample size and few nights of observation. While other studies have reported a prevalence of nocturnally active predators of oystercatcher nests (McGowan 2004, Sabine et al. 2006), particularly on mammal-accessible mainlands, to our knowledge, our study is unique in finding a link between nocturnal incubation patterns and predation risk.

Another explanation for longer nighttime incubation bouts could be a reduction in suitable nocturnal opportunities for foraging, resulting in fewer feeding-motivated recesses. This seems counterintuitive because oystercatchers' access to intertidal food resources is regulated primarily by the tide, not by time of day (Hulscher 1996). However, in 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, where high tides are higher during nighttime than during daytime (NOAA 2007). At Harriman Fjord, incubation-bout length was positively related to the height of the highest tide observed during a bout, indicating that the birds incubated more continuously when high tides prevented foraging. Thus the relationship between time of day and incubation patterns may be correlated with tide cycle and food availability. Subsequent studies of tidally regulated shorebirds should consider the influence of diurnal inequality if foraging patterns vary with the time of day.

At Harriman Fjord, ambient temperatures were lower at night than during the day ($P < 0.001$). Therefore, the longer incubation bouts at night could have been an artifact of bouts being longer when temperatures were lower. Low temperatures may impede embryo development and drain parental energy reserves during long incubation bouts, constraining incubation scheduling (Conway and Martin 2000). However, at Harriman Fjord temperatures were rarely cold enough to impede embryo development (Webb 1987), nests were left unattended for only short periods, and eggs of shorebirds breeding in high latitudes have unusually high tolerances of cooling (Norton 1972, Cantar and Montgomerie 1985). Thus we believe that the relationship between ambient temperature and incubation-bout length is more likely an artifact of the relationship between incubation-bout length and time of day than vice versa.

The samples of nests whose incubation patterns we analyzed were small when we separated the nests by stage of incubation, nest attempt, and year. Furthermore, analyses did not assess incubation patterns during the earliest stages of incubation (clutch initiation through day 6 of incubation). Despite these limitations, video monitoring provided a continuous and nearly complete record of incubation activity and behavior at each monitored nest. Future studies of oystercatcher incubation should use more recording units simultaneously to alleviate issues associated with small sample sizes. This is increasingly feasible as video technology becomes more efficient and cost-effective (e.g., Sabine et al. 2005). From research published after our field work (Sabine et al. 2008), it is evident that cameras could be placed at oystercatcher nests at clutch initiation without adverse effects, providing a complete picture of early incubation activity. Because limitations in the cameras' fields of view prevented certainty in our identifying the cause of 25% of departures, future video studies could use field observers to systematically verify that assumed disturbance recesses are motivated by disturbance stimuli, or they could employ newly developed high-resolution wide-angle cameras with digital zoom capabilities that could more clearly identify stimuli at wider fields of view.

Our study illustrates the complex and interactive ways that cyclical and stochastic processes can influence shorebirds' incubation patterns, highlighting the necessity for recording large and continuous behavioral datasets. Understanding how natural processes in the environment affect reproductive behavior is a crucial prerequisite for properly evaluating and contextualizing the effects of human disturbance on the reproductive success of poorly known species

and for implementing conservation measures appropriate for populations at risk. We identified disturbance and the threat of nest predation as factors influencing the Black Oystercatcher's incubation patterns, laying the groundwork for future assessment of threats to productivity. Further work is necessary to determine the degree to which behavioral responses to these factors influence nest survival and fecundity.

ACKNOWLEDGMENTS

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