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Effect of Investigator Disturbance on Nest Attendance and Egg Predation in Eurasian Oystercatchers

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ABSTRACT.—Eurasian Oystercatchers (*Haematopus ostralegus*) breeding on the salt marsh of Schiermonnikoog (Dutch Wadden Sea) lose many eggs to pred-

ators, mainly Herring (*Larus argentatus*) and Mew gulls (*L. canus*). We estimated that the probability for an egg to survive from laying until hatching was 69%. Daily egg mortality was higher during the laying period than during the incubation period. When researchers were present in the study area, oystercatchers spent more time at greater distances from the nest. We investigated whether human disturbance resulted in more eggs being lost to predators. Two experimental areas were in turn visited at high and at low frequency. From a preliminary analysis, we estimated higher daily egg mortality rates when nests were checked three times per day instead of once every oth-

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er day. However, high-frequency nest checks provided more information on newly laid and lost eggs, especially during the laying period. After correcting for that extra information (by simply deleting it), the egg mortality rates were no longer different. We conclude that human disturbance did not increase egg loss, rather egg mortality rates were underestimated when nests were checked only once per two days.

Because many life-history characters evolve under the influence of high predation pressure, it is important to know the level of nest predation in natural populations. Unfortunately, it is not always easy to obtain reliable estimates of predation rates. Predation events are seldom witnessed, and visiting nests to check the contents necessarily results in disturbance of the individuals being studied. Moreover, investigator disturbance may increase the probability of nest predation (Lenington 1979). Predators may be attracted by packed vegetation around the nest (Esler and Grand 1993), human scent (Whelan et al. 1994), or nest markers (Picozzi 1975, Yahner and Wright 1985). Human disturbance may also reduce nest attendance or enhance conspicuous behavior of the parents. Some studies have shown that predators learn to follow biologists in the field (e.g. MacInnes and Misra 1972, Götmark and Åhlund 1984). Other studies found no effect of human disturbance on nest predation (e.g. Sedingler 1990, Hannon et al. 1993). Obviously, it is of primary importance to find out if research activities influence nesting success of birds under study and if predation rates are affected by visiting nests.

We studied egg predation in a population of Eurasian Oystercatchers (*Haematopus ostralegus*). Oystercatchers typically experience high nest-predation rates (Harris 1967). That might be because they forage on intertidal areas, away from the breeding territory. Ens (1991) suggested that high predation rates during egg laying could be due to the first eggs being left unattended when the male escorts the female on feeding trips to prevent rival males from fertilizing subsequent eggs in the clutch. Thus, high egg-predation rates could be due to a trade-off between two conflicting activities: nest attendance and, for example, foraging or mate guarding.

The aim of this study was to find out if high levels of egg loss were due to limited nest attendance during the laying period or research activities in the study area, or both. We estimated the probability that oystercatcher eggs disappeared from the nest during different stages of the nesting cycle. In addition, we estimated egg-predation rates in artificial nests unattended by parents. If nest attendance reduces the probability of egg loss, we expect to find higher egg mortality rates in those nests as compared to natural nests, where parents are present. We further studied nest attendance in situations in which researchers were either present or absent in the direct vicinity of the nest. To find out if human

disturbance increased egg predation rates, we compared the rate at which eggs disappeared from two experimental areas that were in turn subjected to different levels of disturbance.

Study Area and Methods.—We studied Eurasian Oystercatchers breeding on the saltmarsh of Schiermonnikoog, an island in the Dutch Wadden Sea. Since 1985, we marked birds with color rings and measured their reproductive success as part of a long-term population study (Ens et al. 1992, Heg 1999). Occasional observations had indicated that oystercatchers in our study area lose many eggs to Mew (*Larus canus*) and Herring (*L. argentatus*) gulls. In 1990, we randomly selected 20 pairs to study nest attendance. Those pairs were observed from a blind every other day from laying until the first egg hatched, or until 6 July 1990 when all eggs and chicks were washed away by a catastrophic flood accompanied by bad weather. The observations lasted for one 1 h and started ~10 min after entering the blind when disturbed birds had settled down. With the aid of an electronic event recorder, we continuously monitored distance of the male and female from the nest. We analysed amount of time both parents spent within four distance classes: 0–1, 1–10, 10–50, >50 m. In addition, we recorded how long both parents spent incubating the eggs. The main cause of disturbance in the study area was the presence of colleagues checking nests or walking to or from a blind. We coded our observations as “disturbed” as long as people were present within a distance of 150 m from the nest and compared nest attendance during disturbed and undisturbed time intervals.

To estimate egg-predation rates, we searched the main study area (area A, Heg 1999) every other day to find new nests and to check the contents of nests already known to us. Some nests were found after the start of incubation. For those nests, the laying date was calculated using the date of hatching and assuming an incubation period of 27 days (Keighley and Buxton 1948). If the nest was found after laying and failed before hatching, or if the outcome was unknown, we assumed that we had discovered it one day after the last egg had been laid.

To estimate predation rates of eggs unattended by parents, we used oystercatcher eggs that became available after an egg removal experiment (Ens 1992). Those eggs were laid out on the salt marsh in locations that seemed suitable nest sites to human observers. We created four nests with three eggs each on five subsequent days (19 to 23 May) and recorded egg losses after 2 h of exposure.

The effect of human disturbance on egg predation was tested in two areas adjacent to the main study area (areas C and D, Heg 1999). In those areas, the birds were not ringed and no other research activities took place. Nests were checked by one observer who walked through the area in linear transects that were 5 to 10 m apart. The duration of one visit was

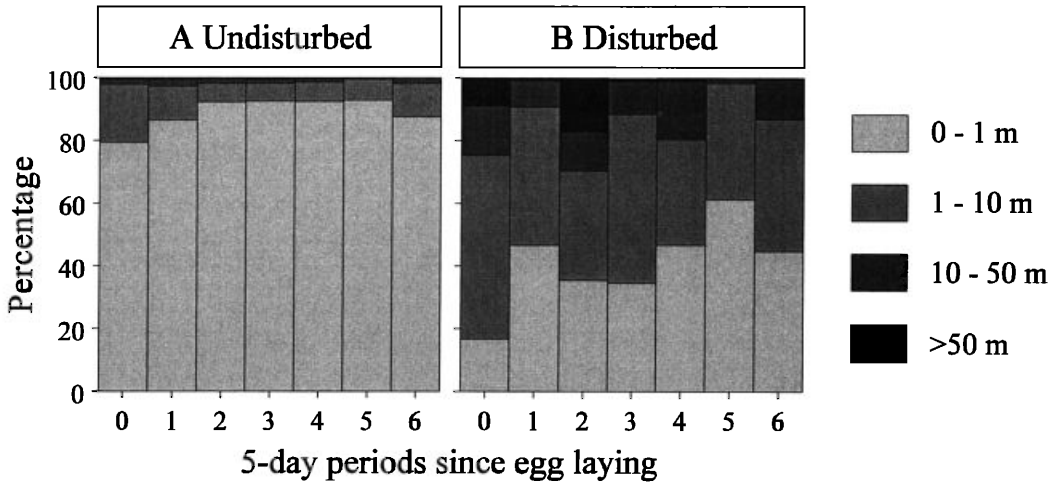


FIG. 1. The percentage of time the closest parent spent at different distances from the nest plotted for different stages of the nesting cycle. The stage of the nesting cycle is expressed as 5 day periods since egg laying (0 = egg laying). (A) undisturbed observations and (B) disturbed situations in which researchers were present within a distance of 150 m of the nest.

45 to 60 min. Each week, one area was subject to a high disturbance treatment whereas the other was subject to a low disturbance treatment. The pattern was reversed every other week until week eight when the experiment ended. The high disturbance treatment consisted of four days of intense nest inspection in which the nests were checked three times daily (morning, afternoon, and evening). After four days, one further nest check was made before the next week started. In the low-disturbance treatment, the nests were checked once every other day. Egg mortality rates were calculated over the interval of four days of thrice-daily nest checks and compared to egg mortality rates during periods of low visitation frequency.

Laying date and clutch size in the different areas were compared using generalised linear models with normal errors and "identity" link function (Crawley 1993), and P -values were calculated with F -tests. We analysed frequencies with the G -test for goodness-of-fit for single classification, and applied Williams' correction to reduce type I error (Sokal and Rohlf 1981). Daily egg mortality rates (m) were calculated by dividing number of eggs lost by total number of days eggs were exposed to predation (Mayfield 1961, 1975). Standard errors and significance levels were calculated according to Johnson (1979). We divided the incubation period into 5 day periods to analyse nest attendance and egg mortality in relation to the stage of the nesting cycle. Data were analysed using SAS (SAS Institute 1990), all tests are two-tailed, and means are reported ± 1 SE.

Results.—Nest attendance was high throughout the laying and incubation period. More than 95% of the time at least one parent was present within a dis-

tance of 50 m from the nest (Fig. 1A). The observations on incubation behavior showed that during egg laying the parents spent 78% of the time actually sitting on the eggs. The time spent close to the nest decreased dramatically when researchers were present in the study area (Fig. 1B).

In the main study area, a total of 38 clutches were laid between 4 April and 29 June 1990. The mean clutch size was 2.6 ± 0.2 eggs. In total, 21 eggs disappeared in 17 predation events. That means that usually one egg was taken at a time. We compared the daily egg mortality rates in nests with and without previous predation to find out if predators repeatedly visited the same nest. Those values were not significantly different ($m_{\text{previous predation}} = 0.031$, $m_{\text{no previous predation}} = 0.021$, $t = 0.4$, $df = 15$, $P = 0.7$) and the probability of committing type II error was low ($\beta = 0.10$). We conclude that nests preyed upon in the past were not more likely to be preyed upon in the future. Although that cannot firmly prove that eggs disappeared independently from each other, we use egg-predation rates rather than nest-predation rates. Both measures gave the same result unless otherwise stated.

The probability of an egg disappearing from the clutch decreased with the stage of the nesting cycle (Fig. 2). Daily egg mortality was significantly higher in the laying period than in the incubation period ($m_{\text{laying}} = 0.035 \pm 0.012$, $m_{\text{incubation}} = 0.007 \pm 0.002$, $t = 2.4$, $df = 19$, $P = 0.03$). The same was found for nest-predation rates, although the difference was not significant ($P = 0.14$). However, a decline in egg loss from laying to hatching could be confounded with calendar date, because younger nests tended to be found earlier in the breeding season. We split the data set into clutches laid before and after 1 May

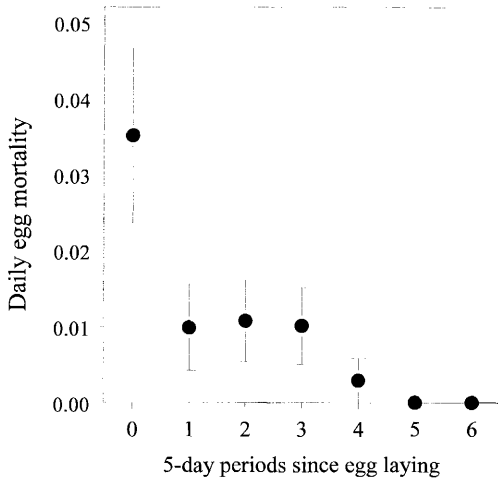


FIG. 2. Daily egg-mortality rates (\pm SE) in the non-experimental area plotted against the stage of the nesting cycle. The stage of the nestling cycle is expressed as 5 day periods since egg laying (0 = egg laying).

1990. We found no differences in daily egg mortality between the early and the late groups either during laying ($m_{\text{early}} = 0.034$, $m_{\text{late}} = 0.033$, $t = 0.04$, $df = 7$, $P = 0.1$) or during incubation ($m_{\text{early}} = 0.005$, $m_{\text{late}} = 0.008$, $t = 0.7$, $df = 10$, $P = 0.5$). The overall probability for an egg to survive a 5 day laying period together with the 27 day incubation period was $(1 - 0.035)^5 \times (1 - 0.007)^{27} = 69\%$.

Eggs in artificial nests were more likely to disappear than eggs from natural nests. Altogether 18 unattended eggs disappeared, which equals to a mortality rate of 0.15 ± 0.033 eggs per hour. Eggs in artificial clutches were thus approximately 60 times more likely to disappear than eggs in active nests, suggesting that nest attendance lowered the probability of egg predation.

The two experimental areas that were periodically subject to high visitation frequency had 48 and 50 clutches, which did not differ in mean laying date ($F = 0.02$, $df = 1$, $P = 0.89$) or clutch size ($F = 0.87$, $df = 1$, $P = 0.35$). Also, egg-predation rates in the two experimental areas were not significantly different from each other ($m = 0.032$ vs. $m = 0.022$, $t = 1.76$,

$df = 94$, $P = 0.08$). Clutch sizes of one tended to be more frequent in the two periodically disturbed areas as compared to the main study area (16% in the main study area vs. 31% in the experimental areas, $G_{\text{adj}} = 3.3$, $df = 1$, $P = 0.07$).

We found that daily egg mortality rates were higher when nests were checked three times daily compared to once every two days. That difference was significant for the laying period, but not for the incubation period (Table 1). That suggests that human disturbance increased the probability that eggs were taken by predators early in the nesting cycle. However, not only did visiting the study area cause disturbance, it also increased our knowledge about newly laid and lost eggs. During a disturbed block of four days, the area was checked as many as 12 times. We recalculated the daily egg mortality rates by taking into account only two of those visits to make the search effort, but not the actual disturbance, equal to that in control blocks, and the difference disappeared (Table 1). From freshly laid second, third, and fourth eggs during the high-frequency nest checks, we estimated that oystercatchers produced eggs at 30.5 ± 1.6 h intervals. Thus, inspecting the nests every other day was not enough to find all eggs that were laid. We conclude that human disturbance did not increase predation rates, rather we found more eggs before they were lost to predators when we visited the study area more frequently.

Discussion.—Our results show that many oystercatcher eggs at our study site were lost before hatching. That is in agreement with other studies in which egg predation by gulls was a major cause of low breeding success in this species (e.g. Heppleston 1972, Briggs 1984, Beineta and Müskens 1987). Harris and Wanless (1997) followed an oystercatcher population after the start of a large-scale gull control program. Although the breeding success remained low, number of breeding pairs increased markedly, suggesting that the absence of gulls made the nesting area more attractive for oystercatchers.

Predation rates were highest during the laying period, and eggs were lost despite the presence of at least one parent within 50 m of the nest most of the time. Nevertheless, nest attendance seemed to reduce

TABLE 1. Daily egg-mortality rates (\pm SE) on occasions when clutches were checked three times per day (high-level disturbance) and when clutches were checked once every two days (low-level disturbance). In the right-hand column, daily egg mortality rates are corrected for increased searching effort due to disturbance by ignoring the information on newly laid and lost eggs obtained during extra nest checks. P -values indicate significance levels for the comparison of high-level disturbance with low-level disturbance.

	Low	High	High (after correction)
Laying	0.0618 \pm 0.0128	0.2103 \pm 0.0483 ($P = 0.004$)	0.0708 \pm 0.0258 ($P = 0.8$)
Incubation	0.0160 \pm 0.0026	0.0275 \pm 0.0058 ($P = 0.08$)	0.0225 \pm 0.0052 ($P = 0.3$)

probability of an egg being lost because, assuming that clutches created by us mimicked real nests, we found higher predation rates in artificial nests than in nests where parents were present. Moreover, during laying, oystercatchers spent less time actually sitting on the eggs as opposed to being present in the territory. However, the fact that oystercatcher eggs were being incubated for no less than 78% of the time already before the clutch was complete could in itself be an adaptation to overcome high predation rates as suggested for pheasants (*Phasianus colchicus*) by Persson and Göransson (1999).

When people were present in the study area, parents spent more time at larger distances from the nest. However, when comparing egg predation for high and low levels of disturbance within the experimental areas, we found that the apparent difference in egg-mortality rates was due to extra information rather than to disturbance resulting from the extra nest checks. For the incubation period, that difference was less pronounced ($P = 0.08$, Table 1). That is not surprising, because at that time the clutches were complete and no additional information was gathered by checking the nests more frequently.

Several studies tested for an effect of human activity on nest predation by assigning nests to different visitation schedules, and the results are ambiguous. High visitation frequencies increased predation in some studies (e.g. Salathé 1987, Major 1990), but not in others (e.g. Willis 1973, Nichols et al. 1984, O'Grady et al. 1996). In some studies, artificial nests were used so that parental behavior was not taken into account (e.g. Esler and Grand 1993, Bayne and Hobson 1997). Other studies give the percentage of eggs or nests lost instead of Mayfield estimates (e.g. Robert and Ralph 1975). The latter will underestimate predation, unless the searching effort is high (Mayfield 1975) which, in this case, is equal to human disturbance.

After losing the first egg, oystercatchers often move to a new nest scrape to lay the remaining eggs of the clutch (Harris 1967). Also, if the complete clutch is lost early in the breeding season, they may switch to a new nest scrape and lay a replacement clutch (Ens et al. 1996). If those clutches are mistaken as first clutches, laying date and clutch size will be estimated incorrectly. Unfortunately, we can not be absolutely sure about birds moving to new nests in the experimental areas because here the birds were not ringed. However, single-egg clutches tended to be more frequent in the two periodically disturbed areas than in the main study area. Thus, searching effort may not only affect the estimation of egg-predation rates, but it may also have consequences for the determination of laying date and clutch size.

This study showed that searching effort influenced estimates of daily egg mortality. Because nest predation is a major determinant of avian reproductive success, we suggest that extra care should be taken

when interpreting the results of nesting studies with high egg-predation rates, especially during the laying period.

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Nocturnal Activities of Post-breeding Wood Storks

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ABSTRACT.—Postbreeding season activities of Wood Storks (*Mycteria americana*) were examined during 24 h long observation periods at inland impoundments and a coastal roost site. Storks were

present at inland impoundments and foraged more at night there than at other times of the day. Wood Stork attendance at the coastal roost site was significantly reduced during nocturnal low tides than during daytime low tides or at either period of higher tide levels. Presumably, storks were leaving the roost to forage on fish concentrated in tidal creeks by dropping tides. Nocturnal foraging in freshwater

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