

A MULTI-LEVEL STUDY OF HUMAN RECREATIONAL ACTIVITY AND LEAST
TERN (*STERNA ANTILLARUM*) RESPONSES: HATCHING SUCCESS,
BEHAVIORAL RESPONSES, AND STRESS HORMONE LEVELS

by

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ABSTRACT OF THE THESIS

A multi-level study of human recreational activity and Least Tern (*Sterna antillarum*)

responses: hatching success, behavioral responses, and stress hormone levels

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In New Jersey, Least Terns (*Sterna antillarum*) nest primarily on sandy ocean beaches, where they must often share their breeding space with beach recreationists. The goal of this study was to determine whether hatching success, behavioral responses, or stress hormone levels in nesting Least Terns vary with exposure to human recreational activity. In particular, I was interested in knowing if birds exposed to more frequent activity exhibit elevated responses or if they habituate to human activity, and whether any such changes have consequences for hatching success. I quantified human activity at multiple sections of beach at a single site where human activity varied with distance from public entrances. Birds were observed for several behavioral responses and were subjected to a capture-stress protocol to measure adrenocortical stress responses. There was no clear relationship between human activity and hatching success. Although a significant negative relationship was found for birds laying early in the season, it was heavily dependent on a single nest. Hatching success was influenced mainly by lay date, due to gull predation on late-nesting birds. Behavioral responses were related to human activity levels. Nests in areas of high human activity had a significantly higher probability of flushing in response to human approaches and were left exposed more frequently than

nests in low activity areas. Neither nest failure (all causes combined), nor nest predation specifically, was related to flush probability or frequency of nest departures. Thus the increased flushing did not appear to be sufficient to decrease hatching success. Whether flush rates experienced at beaches with higher traffic would reduce hatching, and whether chick survival is affected differently by such exposure, remain open questions.

Successful nests were more aggressively defended than nests that failed. No relationships were found between human activity levels and stress hormone levels, but few birds were trapped ($N = 12$) and power to detect patterns was likely low. Given that behavioral responses were elevated over the relatively low levels of traffic observed at this beach, and that the consequences of such increases are not fully understood, there should be some sites where recreation is prohibited.

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Introduction

Human activity has the potential to cause negative effects on breeding birds. Colonially breeding birds are particularly vulnerable because they congregate in large numbers, allowing many birds to be affected by a single event. Beach-nesting birds, such as Least Terns (*Sterna antillarum*), face the added problem of nesting in a habitat that is favored for human recreational activities and is often readily accessible. The goal of this study was to determine whether hatching success, behavioral responses, or stress hormone levels in Least Terns vary with the level of recreational activity near the nest.

Negative impacts of human activity on colonial birds most often occur in situations where people can enter colonies, causing direct destruction of eggs or nests, or via facilitation of intraspecific aggression or predation by nearby avian predators (Kury and Gochfeld 1975, Anderson and Keith 1980, Quinn 1984, Burger et al. 1995, Yorio et al. 2001 and references cited therein). In some cases, reduced hatching or fledging success is associated with human recreational activity (e.g., Hunt 1972, Anderson and Keith 1980, Burger et al. 1995, Giese 1996). There is also evidence, however, for tolerance of human activity where it is frequent or predictable. This is perhaps most convincingly demonstrated by the fact that many species tolerate intensive scientific study without effects on reproductive success (e.g., Nisbet 1981, Hill and Talent 1990, Nisbet et al. 1999, Nisbet 2000, Shealer and Haverland 2000). Studies of ecotourism suggest that some species can also habituate to such activity (Burger and Gochfeld 1999, Fowler 1999, Walker et al. 2006).

Several species that have historically nested on beaches on the Atlantic coast (e.g., Common Terns (*Sterna hirundo*), Black Skimmers (*Rynchops niger*), American

Oystercatchers (*Haematopus palliatus*)) are increasingly using salt-marsh islands as nesting sites, and it has been suggested that this shift is a response to increased human activity on beaches (Erwin et al. 1981, Burger and Gochfeld 1990a, 1991, Toland 1992). Least Terns, which have a stronger preference for sparsely vegetated sites (Burger and Gochfeld 1990b), do not nest on salt marsh islands but have also used alternative nesting habitats when available, such as dredged material islands. Reduced maintenance of such islands in recent decades and subsequent vegetational succession has resulted in a majority of New Jersey's Least Tern population nesting on beaches in recent years (Erwin et al. 2003). As a result, many of the terns share breeding space with beach recreationists. The New Jersey Division of Fish and Wildlife's Endangered and Nongame Species Program staff marks Least Tern colonies using string and post fences and educational signs, which are largely effective in preventing direct destruction of nests by humans (Burger 1989). Large crowds of beachgoers often form nearby, however, and people can approach to within meters of the colony edges, sometimes eliciting flushing and defensive behavior from the terns. Knowing whether such exposure to recreational activity negatively impacts Least Terns would better inform their management.

Sensitivity to human activity is often assessed using behavioral measures such as flush distance. Altered behavioral responses are possible mechanisms by which human activities might impact reproductive success. Greater flush distances, for example, could conceivably lead to more time off the nest and reduced hatching. Such relationships are rarely tested, however, and more complex relationships between behavior and reproductive success have been found (e.g., Keller 1989). Increased use of physiological measures might prove useful in assessing impacts, as disturbance can have physiological

effects that are not obvious from behavioral observation. In several bird species, increased heart rate occurs at approach distances greater than those necessary to elicit overt behavioral responses (Jungius and Hirsch 1979, Giese 1998). Similarly, Fowler (1999) found that Magellanic Penguins (*Spheniscus magellanicus*) exposed to moderate levels of human activity appeared habituated with respect to a behavioral measure of alarm, yet still showed a physiological stress response to nest site visitation. Thus behavioral habituation might mask physiological effects. From a conservation perspective, assuming that apparently habituated birds are *not* experiencing any negative effects could be counterproductive.

A more comprehensive approach to assessing the impact of human activities might involve examining behavioral and physiological responses as well as reproductive success. Biologists are increasingly using glucocorticoid hormones to assess the impact of both natural and anthropogenic forms of disturbance (Fowler et al. 1995, Wingfield et al. 1997, Fowler 1999, Romero and Wikelski 2001, 2002). These hormones are released from the adrenal cortex as a part of a cascade of hormone release in the hypothalamic-pituitary-adrenal (HPA) axis in response to unpredictable events such as predator attacks and severe weather. The general result of this stress response is a temporary suppression of activities associated with long-term processes such as growth and reproduction, and a stimulation of processes necessary for an immediate response, such as increased cardiac activity and the breakdown of fat and muscle protein into more readily-available energy sources (Sapolsky 1992, Wingfield et al. 1997). Short-term elevations of corticosterone (the major glucocorticoid in birds) have been suggested as a mechanism underlying nest abandonment. Elevated corticosterone levels have been observed in bird populations

exhibiting high abandonment rates coincident with reduced food availability (Astheimer et al. 1995, Wingfield et al. 1999). Further, experimentally increasing corticosterone levels with implants can result in altered parental behavior, such as reduced nest attendance (Kitaysky et al. 2001), and decreased feeding of nestlings or nest abandonment (Silverin 1986). Stress hormone levels therefore have potential as predictors of reproductive success. Chronic exposure to stressors (i.e., long term or repeated exposure), resulting in repeated activation of the stress response, can have multiple deleterious effects. Prolonged stress responses have been shown to result in reproductive failure, immune system suppression, impaired growth, cardiovascular and gastrointestinal disease, and neuron death (Wingfield 1985, Sapolsky 1987, Wingfield et al. 1997). Corticosterone can in fact be a predictor of survival under conditions of extreme environmental stress (Romero and Wikelski 2001).

In using a more integrated approach, I hoped to determine at which levels human activity influences Least Terns and to gain some insight into how these levels interact. Human activity could influence behavior or physiology. Depending on how these responses relate to hatching success, however, such changes may or may not have reproductive consequences. I was particularly interested in whether behavioral and hormonal responses were elevated at higher activity areas or whether they were reduced (suggesting possible habituation), and how any such changes related to hatching success. Human activity could also affect hatching success independently of behavior or physiology, for example by attracting predators to an area. To explore these relationships, I examined whether hatching success, behavioral responses, or stress hormone levels of Least Terns varied with the level of recreational activity near the nest,

and whether any of the behavioral or hormonal responses measured were related to hatching success.

Methods

Study site

The study was conducted in 2004 at a single colony, within which human activity levels varied. A single-colony design was chosen because a pilot study conducted in 2003 indicated that a multi-colony design (comparing low-, medium-, and high-recreation colonies) involved several logistical difficulties. Comparing nests within the same colony also avoids much of the difficulty associated with such factors as weather and food availability that can vary among colonies and affect reproductive success.

The site was a public beach in Monmouth Beach, New Jersey (40°19'N, 73°58'W), located on the southern end of the Sandy Hook spit (Figure 1). This beach is separated from the road by a concrete and boulder sea wall; beach access is therefore limited to stairways built over the sea wall. Public access stairways are located roughly half a kilometer apart. The distribution of people along the beach is somewhat “clumped” near these entrances, while that of the terns is more widely dispersed. As a consequence, those birds nesting near public entrances are exposed to larger crowds and more frequent approaches than those nesting farther from entrances. Before Least Terns begin nesting (generally in May), portions of the beach are pre-fenced by the Endangered and Nongame Species Program staff using string and post fencing, with paths left between fences at entrances. Fences are expanded and added as nests are established.

Nest monitoring

Nests were marked with numbered tongue-depressors placed approximately 1 meter from the nest and at random directions to avoid learned responses from predators. At the end of the breeding season, the percent vegetation cover within a 1 meter radius was recorded

for each nest. Tern nests in the vicinity of Piping Plovers (*Charadrius melodus*) could not be studied, as disturbance to the federally endangered plovers had to be minimized. As a result, not all parts of the colony could be used. The study focused on two groups of nests, separated by approximately 320 m, which I refer to as subcolonies. Subcolony A began approximately 30 m south of a public entrance and was spread over two fenced areas with a narrow corridor in between. The total length (north to south) of the combined fenced areas was approximately 325 m long including the corridor. Subcolony B was contained in a single fenced area that began approximately 80 m south of a different public entrance. This subcolony was approximately 180 m long and was about 40 m from a beach club on its southern end. Both subcolonies were fairly linear in shape. They were bordered on their western side by dunes, followed by the sea wall, followed by a sidewalk and street.

Least Tern chicks can leave the nest as early as two days after hatching (Thompson et al. 1997). Therefore, nests were checked every other day, weather permitting, for hatching or for evidence of flooding, human activity, predation (broken, punctured or missing eggs, tracks) or abandonment (eggs cold to the touch, displaced from the nest scrape, or with sand building up around the edges). Once nests began hatching, nest checks were done using binoculars when possible to reduce disturbance to chicks.

Quantification of Human Activity and Behavioral Observations

To quantify human activity levels, fenced areas were divided into 10-m long sections. Observations were conducted on four 10-m sections at a time, during which all incidents of people approaching any 10-m section were noted. Any movement directly toward or

tangential to the colony was recorded and is referred to here as an “approach”. The time of the approach and the closest distance the person or people came to the fence edge were recorded. While data on human approaches were collected by an assistant, I performed behavioral observations on incubating birds. These were all-occurrence observations in which each incidence of a bird leaving its nest was recorded. I recorded the time the bird left, any apparent cause, the bird’s behavior when leaving (e.g., whether it engaged in defensive behavior, walked a short distance from the nest, flew out of view), and the time it returned to the nest. Least Tern defensive behavior includes alarm calling, diving at, and defecating on intruders (Burger 1989). A tern was considered to have flushed in response to an approaching human if it either a) engaged in defensive behavior against the person(s), or b) left the nest as the person(s) approached, returned to the nest only after they moved away, and did not engage in behavior directed at another animal in the intervening time. For example, if a tern skirmished with another Least Tern or mobbed a passing gull while a person was passing, the tern was not considered to have flushed in response to the approaching person.

To balance observations of different areas of each subcolony with respect to time of day and type of day (weekend vs. weekday), sections of beach were observed in random order within each of several time categories (weekday mornings, afternoons and evenings, weekend mornings, afternoons and evenings). For example, if a subcolony was divided into 5 sections, each of 5 sequential weekday morning observations was made from a different section, and the order was randomly determined for each 5-day period. Within sections, behavioral observations on nests were similarly randomized. Morning sessions were those before 12:00 p.m., afternoon sessions were those between 12:00 p.m.

and 5:00 p.m., and evening sessions were those after 5:00 p.m. An average rate of human activity was determined for each 10 meter section based on its set of observation sessions.

Trapping

Under appropriate state and federal permits, birds were trapped at the nest using wire treadle traps (26 cm x 25 ½ cm x 23 ½ cm high). These traps are placed over the eggs and close when the bird (returning to incubate) enters the trap. Trapping was limited to birds that had been incubating for at least 10 days and was not done in inclement weather (i.e., rain or temperatures below 21 °C or above 31 °C, following Hill and Talent 1990) to minimize adverse effects. Trapping was also limited to periods when there were relatively few people on the beach. Once trapped, a bird was removed immediately from the trap, placed in a mesh bag and brought to a tent for a stress-series protocol. This protocol uses a series of blood samples to measure both baseline and stress-induced levels of corticosterone, using capture as a standardized stressor to suggest how individuals respond to other stressful stimuli (Wingfield et al. 1997). Blood samples were taken immediately and at 15 and 30 minutes following capture. Blood was taken from the wing vein using a 25 gauge needle and was collected into heparinized capillary tubes. During handling, a small drawstring bag was used that covered the eyes but allowed exposure of the beak, following Hill and Talent (1990), who noted that masking calmed Least Terns. All protocols were approved by the Institutional Review Board for Use and Care of Animals of Rutgers University.

Laboratory Analyses

Blood samples were kept on ice (or if held overnight, refrigerated) until they were brought to the lab and centrifuged. Samples were centrifuged at 1800 rpm for 10 minutes at 4°C. The plasma and blood cells were then stored separately at -20°C. Plasma corticosterone levels were measured using radioimmunoassay after extraction with ether following published procedures (Wingfield and Farner 1975, Smith and John-Alder 1999). Samples of up to 25 µl were extracted twice in diethyl ether and dried under a stream of ultrafiltered air. Dried samples were reconstituted in assay buffer and allowed to equilibrate overnight prior to radioimmunoassay. Recovery of corticosterone was measured for each sample. All samples were assayed in a single assay, with each sample assayed in duplicate. Previous corticosterone assays using these procedures have had intra-assay variations of 8% (Smith and John-Alder 1999, Tsipoura et al. 1999).

Blood cells were used to sex the birds using PCR to amplify CHD1 introns, following Fridolfsson and Ellegren (1999). This method uses a single pair of primers to amplify introns which differ in size between the Z and W chromosomes, resulting in PCR products of a single length for males (ZZ) and products of two different lengths for females (ZW). This method was first confirmed using museum tissue samples from Least Terns of known sex. DNA was extracted from these samples using a Qiagen DNeasy Tissue Kit, which isolates DNA via lysis of tissue with proteinase K, selective binding of DNA to a silica-gel membrane, removal of contaminants, and elution of purified DNA in buffer. For blood samples, direct PCR of blood (i.e., without DNA extraction) was performed, using a modified version of the protocol used by Tomasulo et al. (2002). In a total reaction volume of 25 µl, 1 µl of extracted DNA or 5 µl of diluted blood cells, 1 µl each of primers 2550F and 2718R (50 pmol) and 18-22 µl of Qiagen *Taq*

PCR Master Mix were used. The PCR cycle used included an initial denaturing step of 94°C for 3 minutes, 45 cycles of 94°C for 30 seconds, 50°C for 40 seconds, and 72°C for 40 seconds, followed by an extension step of 72°C for 10 minutes. Products were visualized on agarose gel stained with ethidium bromide.

Statistical Analyses

Statistical analyses were performed with SAS 9.1 (SAS Institute Inc. 2004). Data that were not normally distributed were log-transformed, or in the case of percentages, arcsine or square-root transformed to improve normality (Sokal and Rohlf 1981). Untransformed data are shown in figures.

Human Activity Patterns

Changes in human activity with time of day and type of day were examined with repeated measures MANOVA using 10-m sections as observations. Changes over season could not be examined using repeated measures without large numbers of sections being excluded from the analysis; this is because most sections had periods when no nests were active and counts were generally not done at these times. An ANOVA was run using sessions as observations and including time in season (early vs. late half), time of day, type of day, and subcolony as factors, with distance from the public entrance of the section observed as a covariate. Plausible two-way interactions (subcolony x time in season, time of day and type of day, time in season x time of day and type of day) were tested but none were significant; these were removed to simplify the model.

Activity and hatching success

Logistic regression was used to relate hatching success to human activity level (where success was defined as hatching at least 1 chick). Though human activity was the main

factor of interest, several potential confounders were also considered: nest density, nearest neighbor distance, lay date, percent vegetation cover, and distance to the fence. Nest density was defined as the number of nests within a 5-meter radius of a nest. For this measure and for nearest neighbor distance, the last week of each nest's incubation period was used. For lay date, the period over which laying occurred was divided into three roughly equal lay periods (early: before 6/1, middle: 6/1 through 6/19, late: after 6/19). As logistic regression is sensitive to collinearity among the independent variables, these variables were first examined for intercorrelation (Hosmer and Lemeshow 2000). Nearest neighbor and density were correlated ($r = -0.37$, $P = 0.002$); since these variables provide similar information, only one (density) was included in the model. Distance to fence and percent vegetation cover were also correlated ($r = 0.46$, $P < 0.0001$). Because these two variables measure qualitatively different things, both measures were included in the analysis. Following the recommendation of Hosmer and Lemeshow (2000), a limited number of biologically plausible interactions were included, rather than including all possible pairwise interactions. The activity x fence distance interaction was included, since effects of recreation might be more likely to occur closer to the fence, as was the activity x lay period interaction, because of high nest losses observed late in the season (see results). The 3-way activity x lay period x fence distance interaction was also included. A backward elimination procedure was used, and variables not significant at $P < 0.15$ were excluded, as using lower P values can exclude important variables in stepwise logistic regression (Hosmer and Lemeshow 2000).

Behavioral analyses

Because males and females cannot be distinguished visually, behavioral data are for nests rather than individual birds. For each nest, several behavioral measures were calculated for each observation session and were then averaged over each nest's sessions. Three of the measures focused on responsiveness to human approaches: 1) percentage of approaches eliciting a flush response (% flush), 2) the mean time it took to resume incubation after flushing (return time), and 3) the percentage of responses that were aggressive (i.e., those in which the bird circled or dove at the approacher, % aggressive). The frequency or overall time of nest exposure might be more important in influencing reproductive success, however. I therefore also calculated nest departures per hour and percent attendance, the percentage of observation minutes a nest was attended.

MANOVAs were used to examine whether nests in high activity vs. low activity areas (above or below the median activity level) or successful vs. failed nests differed in behavioral responses. Because some nests were missing data (for return time and % aggressive), combining all responses in a single MANOVA resulted in removal of observations. Graphical analyses suggested that this removal resulted in exaggeration of some differences and the loss of others. To avoid such artifacts of missing data, two separate MANOVAs were run for each comparison, with return time and % aggressive in one analysis and % flush, departures per hour, and % attendance in another.

Multiple regressions were run to determine whether distance from the fence, density, lay date, or vegetation cover influenced behavioral responses.

Corticosterone analyses

Because there was some variation in the time of day birds were trapped, the relationship between time of capture and initial corticosterone levels was examined using linear

regression. The relationships of corticosterone with sex and body mass were also examined, using repeated measures MANOVA and correlation, respectively.

To examine the relationship between human activity and corticosterone levels, repeated measures MANOVA was used to compare stress responses of nests from high activity areas ($>$ median activity level) vs. low activity areas ($<$ median activity level). I was primarily interested in whether high and low activity nests differed in either baseline corticosterone levels or the stress response (the activity level \times time interaction). Similarly repeated measures MANOVA was used to compare the baseline corticosterone levels and stress responses of successful vs. failed nests. Some nests were missing data for some sample times, but graphical analyses indicated that the patterns were the same in the complete and partial data sets. Graphs show the data for all available nests at each sample time.

Results

Human Activity Patterns

Human traffic near colonies varied significantly with both time of day ($F = 20.11$, $P < 0.0001$) and type of day ($F = 19.42$, $P < 0.0001$) (repeated measures MANOVAs, Figure 2). Activity was lowest in the mornings and peaked during afternoons, and was greater on weekends than on weekdays. There were no differences in these patterns between the two subcolonies (time of day x subcolony interaction: $F = 0.00$, $P = 0.996$, type of day x subcolony interaction: $F = 0.03$, $P = 0.855$). As in the repeated measures analyses, in the analysis using sessions as observations, effects of time of day and type of day were significant (ANOVA: $F = 8.97$, $P = 0.0003$, $F = 12.06$, $P = 0.0008$, respectively). Activity did not differ significantly in the early vs. late half of the season ($F = 0.05$, $P = 0.820$). There was a significant effect of subcolony (with subcolony A having higher activity than subcolony B), but this disappeared when distance from public entrance was controlled for ($F = 0.00$, $P = 0.972$). This suggests that the overall activity in subcolony A was higher because it began closer to a public entrance, but at a given distance, the subcolonies did not differ significantly.

Human activity generally declined with distance from public entrances, eventually leveling off in each subcolony (Figure 3). Activity was slightly elevated at the sections farthest from the entrances relative to the adjacent sections. This is likely due to the beach club south of subcolony B, and a private beach access at the southern end of subcolony A.

Causes of nest failure

Eighty (80) nests were marked and followed for hatching success. Of these, 67.5% (54) were successful (hatched at least 1 chick) and 32.5% (26) failed. The major causes of nest failure were predation and abandonment, which together accounted for 22 of the losses (Table 1). Much of the predation occurred in mid- through late July, when Great Black-backed Gulls (*Larus marinus*) walked through the colony regularly. They were observed eating eggs at several nests. For other nests, evidence of gull predation included tracks at the nest or eggs missing at nest checks < 24 hours after gulls were observed near the nest. Gulls may have eaten chicks as well. Though chicks were not marked, many seemed to stay in the general vicinity of the nest in the days after hatching, and in some cases were noticeably absent after gulls were in the area. It is also possible that adults moved the chicks elsewhere on the beach in the wake of the gull activity. In two cases of eggs disappearing, mammalian tracks were seen near the nest. These were somewhat faint but suggested a cat, though cats generally prey on chicks or adults (Burger 1989, Kress and Hall 2004).

Of the 26 nests that failed to hatch, there was evidence of possible human activity at 2 nests; each had shoeprints near the nest on the day the nest was found to be empty. In neither case was any human activity witnessed, however, and one of these nests failed during the period of high gull predation, so predation is an equally plausible cause of failure.

Human activity levels and hatching success

The final logistic regression model was statistically significant (Likelihood ratio $X^2 = 15.70$, $P = 0.001$, $N = 68$, Table 2) and there was no evidence of a lack of fit in the model (Hosmer and Lemeshow goodness-of-fit test, $X^2 = 11.70$, $P = 0.111$). The model

suggests an interaction between human activity and lay period, with a negative relationship between human activity and the probability of hatching in the early and middle lay periods and a positive relationship in the late lay period (significant only in the early period, Table 2, Figure 4). Visual inspection of the data suggests that the regression depends heavily on a small number of nests, however (Figure 4). It appears likely that the single nest in the highest-activity section in the early period is heavily impacting the regression. Similarly, the nest in the highest-activity section in the late lay period is likely causing the positive (though non-significant) relationship in this period. When the data are broken up by lay period, nests in higher activity sections become particularly sparse, and observations rare in predictor space can have a large influence on logistic regressions (Hosmer and Lemeshow 2000). The data were therefore examined using influence statistics. Examination of dfbetas (the standardized change in the coefficient due to deleting an observation) indicated that the two nests in the highest-activity section were the most influential on the interaction and on the main effect of activity in their respective lay periods. Running the regression without the early lay period nest results in a negative, but nonsignificant, relationship between activity and success in this lay period (logistic coefficient = -0.24, $P = 0.747$) and loss of the significant activity x lay interaction. If the late lay period nest is removed, the activity-success relationship in this lay period is no longer positive (logistic coefficient = -0.31, $P = 0.690$) and the activity x lay period interaction is not significant. Because of the influence of individual nests, the logistic regression model is regarded with caution.

More evident is the generally low success rate in the late lay period compared to the early and middle periods (**Early**: 80% successful (24/30), **Middle**: 83.3% successful

(25/30), **Late**: 28.6% successful (4/14), Fisher's exact test, $P = 0.0008$). This shift coincides with the onset of gull predation. While the early and middle periods include only nests that hatched or failed prior to the gull predation events, the late lay period is comprised almost entirely (13/14) of nests that were still in the incubation period when the gull predation began. Prior to these events, there were several causes of nest failure, with abandonment being the most common (Table 3). Once the gull predation began, however, it became the major cause of failure among nests still active at this time. It accounts for 8 of the 10 nest failures, and cannot be ruled out for the remaining 2. Another nest that was still attended at this time was overdue to hatch, and so technically failed prior to the gull activity (possibly due to infertility or thermal stress to the eggs). This nest was only abandoned, however, after gulls were seen in the vicinity; a day after gulls were observed near the nest being dive-bombed by terns, the eggs were scattered and the nest was unattended.

Depending on how human activity influences Least Terns, it might increase the likelihood of a particular cause of failure, such as abandonment or predation, rather than the likelihood of failure generally. I therefore compared the relative frequency of the different causes of failure at high and low activity areas. High and low activity areas did not differ significantly in the relative frequency of predation, abandonment, and other combined causes of nest failure (**High**: 30% predation, 30% abandonment, 40% other causes, **Low**: 50% predation, 43% abandonment, 7% other causes, Fisher's exact test, $P = 0.206$). Gull predation did not appear to be temporally associated with human activity either; observations of gull activity in the colony did not suggest any overlap with human-caused disturbances. Causes of abandonment were unclear. Five abandoned

nests were never observed to be active, making a date of abandonment, and the circumstances surrounding it, impossible to determine. The remaining five nests abandoned after the colony had thinned out to some extent, so social stimulation may have diminished at this point. It is also possible that abandonment was due to predation on adult terns followed by subsequent abandonment by the mate. Mammalian tracks were observed near one nest that was subsequently abandoned. Cat predation in particular is likely given the proximity of the colony to a residential area. Given the nocturnal hunting habits of cats, their prevalence was unknown.

Behavioral responses

Human activity and behavioral responses

Thirty-nine (39) nests were analyzed for behavioral responses, 19 in areas categorized as high-activity and 20 in low-activity areas. Nests from high activity areas were more likely to flush and left the nest more frequently than did nests in low activity areas, while percent attendance did not differ with activity level (MANOVA: Wilks' $\lambda = 0.611$, $F = 6.58$, $P = 0.001$, univariate ANOVAs: % flush: $F = 5.66$, $P = 0.023$, departures per hour: $F = 18.20$, $P = 0.0002$, % attendance: $F = 1.05$, $P = 0.314$, Figure 5). Aggressiveness and return time did not differ with activity level (MANOVA: Wilks' $\lambda = 0.898$, $F = 1.08$, $P = 0.359$, Figure 5). Departures per hour also had a negative relationship with nest density (linear regression, $r^2 = 0.25$, $P = 0.001$). Among the nests included in the behavioral analyses, nests from high activity areas had significantly lower densities than nests from low activity areas (**high**: mean = 0.32 nests / 5 m radius, **low**: mean = 1.05 nests / 5 m radius, Mann-Whitney U test: $U = 296.5$, $P = 0.001$). The MANOVA was therefore also run with density as a covariate to separate the effects of

activity level and density on departures per hour. The effect of activity level on departures per hour remains significant when controlling for the effect of density (activity level: $F = 9.20$, $P = 0.005$, density: $F = 2.32$, $P = 0.138$). Regression analyses also indicated that aggression increased with distance from the fence ($r^2 = 0.32$, $P = 0.006$). Distance to the fence was similar, however, for nests in high and low activity areas (**high**: mean = 11.0 m, **low**: mean = 10.6 m, Mann-Whitney U test: $U = 206.5$, $P = 0.653$); therefore it was not considered further.

Behavioral responses and hatching success

Of the nests observed for behavioral responses, 25 successfully hatched a chick and 14 failed. Probability of flushing, departures per hour, and percent attendance did not differ between successful and failed nests (MANOVA: Wilks' $\lambda = 0.923$, $F = 0.87$, 0.469, Figure 6). Birds at successful nests were more aggressive than those at failed nests, but did not differ in return times (MANOVA: Wilks' $\lambda = 0.692$, $F = 4.22$, $P = 0.030$, univariate ANOVAs: % aggressive: $F = 8.70$, $P = 0.008$, return time: $F = 0.00$, $P = 0.996$, Figure 6). As mentioned, aggressiveness and departures per hour showed relationships with fence distance and density, respectively, but neither of these variables differed between successful and failed nests (**successful**: mean fence distance = 10.3 m, **failed**: mean fence distance = 11.7 m, Mann-Whitney U test : $U = 191$, $P = 0.650$, **successful**: mean density = 0.64 nests / 5 m radius, **failed**: mean density = 0.79 nests / 5 m radius, Mann-Whitney U test: $U = 191.5$, $P = 0.610$).

It might be expected that an increased flush rate would be related to predation risk in particular, rather than all causes of failure combined, because flushing exposes the nest. Percent flush and departures per hour (those responses that were elevated at high

activity levels) were therefore compared for depredated and successful nests. Depredated nests did not have a higher probability of flushing or more departures per hour than nests that successfully hatched (Wilks' $\lambda = 0.976$, $F = 0.33$, $P = 0.725$).

Corticosterone levels

Twelve terns (8 males and 4 females) were trapped and bled, from sections with human activity levels ranging from 0.1 to 5.4 approaches per hour. Of the twelve nests where birds were trapped, 7 successfully hatched chicks and 5 failed. Two nests failed due to abandonment, but the rate of abandonment among trapped nests (16.67%) was not significantly different than the rate among non-trapped nests (11.76%) (Fisher's exact test, $P = 0.641$). The times of the initial blood samples ranged between 3 and 4 minutes after capture. Corticosterone levels from these samples probably cannot be considered "basal" as blood corticosterone levels can increase as soon as 2 to 3 minutes after capture (Hood et al. 1998, Müller et al. 2006). I therefore refer to these as initial (rather than baseline) corticosterone levels.

Initial corticosterone did not vary significantly with time of day (linear regression, $r^2 = 0.03$, $P = 0.597$). Body mass had a near-significant relationship with initial corticosterone levels ($r = 0.61$, $P = 0.060$, Pearson correlation), but was not significantly related to 15-minute levels ($r = -0.04$, $P = 0.934$, Pearson correlation), or 30-minute levels ($r = 0.09$, $P = 0.815$, Spearman rank correlation). Although body mass and initial corticosterone had a moderate correlation that neared significance, body mass did not differ significantly in birds from high vs. low activity areas nor in birds from successful vs. failed nests, (**high**: mean = 48.6 g, **low**: mean = 49.3 g, $t = -0.40$, $P = 0.702$, **successful**: mean = 50.0 g, **failed**: mean = 47.8 g, Mann-Whitney U test: $U = 21.5$, $P =$

0.268), and was not considered further. There was some variation in the amount of time birds took to enter the traps after they were set (mean \pm SD = 18 \pm 5 minutes), but corticosterone levels did not vary significantly with time to enter the trap (linear regression, initial levels: $r^2 = 0.03$, $P = 0.611$, 15-minute levels: $r^2 = 0.005$, $P = 0.870$, 30-minute levels: $r^2 = 0.15$, $P = 0.270$). Further, neither high vs. low activity nests nor successful vs. failed nests differed significantly in the time to enter (**high**: mean = 17.8 min, **low**: mean = 19.8 min, $t = -0.64$, $P = 0.534$, **successful**: mean = 20.4 min, **failed**: mean = 16.6 min, $t = 1.28$, $P = 0.228$).

Sex did not appear to contribute much to variation in secretion patterns (Repeated measures MANOVA: main effect of sex: $F = 0.00$, $P = 0.967$, main effect of time since capture: Wilks' $\lambda = 0.537$, $F = 1.73$, $P = 0.288$, sex x time interaction: Wilks' $\lambda = 0.789$, $F = 0.54$, $P = 0.622$, Figure 7a). The data are suggestive of a slower initial increase but a longer overall response in birds in high activity areas compared to those in low activity areas (Figure 7b). Similar secretion patterns are suggested when birds are broken up into successful and failed nests, with failed nests having a longer response (Figure 7c). Neither of these differences was significant, however, perhaps due to small sample size (Repeated measures MANOVAs: **Human activity**: main effect of activity: $F = 0.21$, $P = 0.665$, main effect of time since capture: Wilks' $\lambda = 0.459$, $F = 2.35$, $P = 0.211$, human activity x time interaction: Wilks' $\lambda = 0.415$, $F = 2.82$, $P = 0.173$, **Success**: main effect of success: $F = 0.20$, $P = 0.673$, main effect of time since capture: Wilks' $\lambda = 0.357$, $F = 3.60$, $P = 0.128$, success x time interaction: Wilks' $\lambda = 0.438$, $F = 2.57$, $P = 0.192$). The similarity in patterns between high activity and failed nests and between low activity and successful nests could result if these pairs of groups contained the same nests. While the

groups did not overlap completely (the high activity nests included 3 successes and 3 failures, the low activity nests included 4 successes and 2 failures), sharing even a few nests could result in similar patterns when sample sizes are this small. The independence of these two patterns is thus somewhat unclear, and a larger sample would be needed to include both factors in a single analysis.

Discussion

Hatching success

There was no clear relationship between human activity and hatching success; the negative relationship between human activity and hatching found for the early lay period depended heavily on a single failed nest. While it is interesting that the nest in the busiest section failed during a period when a majority of nests hatched a chick, the relatively small number of nests in high activity areas makes it impossible to know whether this is a typical outcome. The main factor influencing hatching success was lay period, due primarily to gull predation late in the season. Gulls did not appear to take advantage of human-caused disturbance as has been noted in other studies (Kury and Gochfeld 1975, Anderson and Keith 1980, Quinn 1984) and nest failure due to predation was no more frequent in high activity areas than in low activity areas. Although there did not appear to be a within-site relationship between human activity and gull predation, it is possible that the overall number of gulls on the beach, and the resulting predation, is greater than it would be without human recreation. Despite being ubiquitous on the beach throughout the breeding season, however, gulls did not have an impact until fairly late in the season. Gull predation in tern colonies is often the work of a small number of specialists (Guillemette and Brousseau 2001, Kress and Hall 2004); it is possible that a few such individuals began foraging at this site late in the season. The tern colony was also larger early in the season and exhibited more impressive antipredator defense which may have deterred the gulls. Few gulls were observed walking into the fenced area during this time; when they did, they were generally met with aggression on the part of the terns and walked out. As the season wore on, however, the colony thinned out and the defense of

the colony appeared diminished. This is consistent with findings that individual and group defensive aggression decreases at lower nest densities in several species of terns, including Least Terns (Burger and Gochfeld 1988, 1991). Further, Brunton (1997, 1999) found that gulls and crows were less effective at depredating large Least Tern colonies and suggested that this was due to more effective defense of large colonies. Mammalian predation was not a major cause of egg predation, but cannot be ruled out as an indirect cause of abandonment.

Behavioral responses

Birds at nests in high activity areas were more likely than birds in low activity areas to flush in response to human approaches. In contrast, several other studies have shown birds exposed to more frequent human activity to have reduced behavioral responses compared to birds exposed to less activity (Burger and Gochfeld 1999 (Laysan Albatrosses, *Diomedea immutabilis*), Fowler 1999 (Magellanic Penguins, *Spheniscus magellanicus*), Müllner et al. 2004 (Hoatzins, *Opisthocomus hoazin*), Walker et al. 2006 (Magellanic Penguins)). Beach recreation may be more variable in nature compared to the types of activity birds were exposed to in these studies (ecotourism in the Hoatzin and Magellanic Penguin studies, pedestrian and vehicle traffic in the Laysan Albatross study). In busier sections of beach, people settled in front of the colony for variable periods of time, walked to and from the ocean, and occasionally played sports, whereas in quieter areas people were more likely to be walking the beach. Perhaps the activity at busy sections, though frequent, was less predictable in nature and thus difficult to habituate to.

Birds in high activity areas, being more likely to flush and being approached more often, also left nests more frequently than did birds in low activity areas (i.e., more per

hour as well as per approach). Resulting exposure of eggs could reduce hatching via thermal stress, as has been suggested for some species (e.g., Teal 1965, Hunt 1972, Safina and Burger 1983), or increase susceptibility to predators (e.g., Kury and Gochfeld 1975, Anderson and Keith 1980, Quinn 1984). There is little to suggest that either of these mechanisms was operating here, however. Unhatched eggs were rare (assuming that depredated and abandoned nests would have otherwise hatched), suggesting thermal stress did not reach lethal levels. Predation was no more likely where human approaches were more frequent, nor did depredated nests differ from successful nests in the likelihood or frequency of flushing. This may be because gulls at this beach did not appear to associate human approaches with access to prey. Approach rates might need to be greater than those observed at this beach, or result in longer return times, to result in exposure levels that have consequences for hatching; despite being left more frequently, nests in high activity areas maintained overall attendance levels similar to nests in low activity areas.

The human traffic at this site, however, is moderate compared to other beaches where Least Terns nest in New Jersey (personal observation). At more heavily recreated sites, birds might be flushed with much greater frequency and with potentially damaging results. Frequent departures by adults might also have different consequences for chicks than for eggs. Fledging success was not examined here, in part because relating human activity to fledging success within a colony would be complicated by the fact that Least Tern chicks are highly mobile; they can wander up to several hundred meters from the nest within days of hatching (Thompson et al. 1997, Kress and Hall 2004). As a result, the level of human activity to which chicks and adults are exposed can become more

variable after the chicks leave the nest. Goodrich (1982), examining disturbances at the colony level, found that the duration (but not the frequency) of colony disturbances caused by humans was related to Least Tern colony fledging success, although the effects on eggs and chicks were not examined separately. Hunt (1972) found that chick losses were higher at a Herring Gull (*Larus argentatus*) colony where nest attendance was lower.

The results of this study illustrate that elevated rates of disruptive behaviors may not have the consequences for reproductive success that we might expect; whether or not reproductive success is affected might depend on the magnitude of human activity levels and the behavior of predators at the site. It is perhaps even more important to examine such relationships when the reverse pattern (habituation) is suggested, as reduced behavioral responses might not compensate for effects of frequent human activity. Keller (1989), for example, found that Great Crested Grebes (*Podiceps cristatus*) flush at lower distances on lakes with recreation than on a lake without recreation. Birds with low flush distances are also less likely to show species-typical egg-covering behavior upon leaving their nests, leaving them more visible. Despite their increased tolerance of human approaches, birds at disturbed lakes suffer greater losses, a result attributed to the high frequency of close approaches in combination with reduced egg-covering at such sites. Similarly, adult Hoatzins exposed to ecotourism have lower flush distances than birds in undisturbed areas, but fledging success is reduced in ecotourist areas, likely due to physiological effects of ecotourism on juveniles (discussed below) (Müllner et al. 2004). In such a situation, if ecotourism guidelines were determined primarily on the basis of the

flushing behavior of adults, the impacts on juveniles would be missed and serious consequences could result.

Successful Least Tern nests were defended more aggressively against human approaches than were failed nests. It seems unlikely that aggression against people *per se* had much effect on hatching success, as people rarely entered the fenced areas. It is possible that terns that responded more aggressively toward people may have been more aggressive toward predators as well, thereby improving their chances of success. Alternatively, successful birds could have been in better condition, thus better able to mount energetically demanding aggressive responses. There is some evidence that defensive behavior is positively related to physical condition (Alvarez and Sanchez 2003, Hogstad 2005).

Aggressiveness toward humans also increased with distance from the fence. This is somewhat surprising, as defense is generally expected to decrease with detectability of a nest (Montgomerie and Weatherhead 1988). Sites farther from the fence may be preferred, as both people and gulls tended to approach from the direction of the fence. If so, this relationship could also reflect a common link with body condition, as birds in better condition might be better able to obtain preferred nesting sites. A preference for sites far from the fence might not be expected where mammalian predators are prevalent, however, as mammals can enter Least Tern colonies from the dune side (Burger and Gochfeld 1990b).

Corticosterone levels

Neither initial corticosterone levels nor stress responses differed significantly between Least Terns from high and low activity areas, nor did they differ between birds

from successful and failed nests. The data suggest the possibility that shorter stress responses are associated with nesting in low activity areas and/ or with successful hatching, while a more moderate, but longer response may be typical in busy areas and/or birds that subsequently failed. It would be interesting to see if either of these patterns persists in a study with a larger sample size.

Stress hormones have similarly been used to examine effects of other forms of recreation. Wintering grouse living in areas with high levels of ski recreation have higher levels of fecal corticosterone metabolites than birds in areas with lower levels of such recreation (Arlettaz et al. 2007, Thiel et al. 2008). Studies on the effects of ecotourism suggest that in some cases, habituation of the stress response can occur. For example, in Magellanic Penguins nesting in ecotourist sites and Galápagos Marine Iguanas (*Amblyrhynchus cristatus*) living near tourist trails, stress responses are reduced compared to animals exposed to few people (Fowler 1999, Romero and Wikelski 2002, Walker et al. 2006). Questions remain about the circumstances under which habituation occurs. While penguins at heavily-trafficked tourist sites have decreased responses, penguins exposed to intermediate levels of human activity (researchers only) show no such decrease compared to controls (Fowler 1999). As with behavioral responses, the nature of the human activity, as well as the frequency, may be important. Walker et al. (2006) suggest that short, intense and regular visits may be necessary to promote habituation of the stress response. While such patterns might occasionally occur in ecotourism, especially when it consists of guided tours, other forms of recreation may tend to be more sporadic and variable. The likelihood of habituation also appears to vary with life history stage. Unlike adults, Magellanic Penguin chicks of various ages exhibit

no decrease in the stress response at tourist sites compared to those at non-tourist sites; among newly hatched chicks, stress responses are actually elevated in tourist areas (Walker et al. 2005). Similarly, juvenile Hoatzins exposed to ecotourism have increased stress responses compared to controls, and experience lower survival rates despite similar predation levels (Müllner et al. 2004).

The consequences of decreased stress responses are also unclear. Romero and Wikelski (2002) point out that the reduction of the stress response seen in iguanas near tourist trails may or may not be beneficial. While elevated circulating levels of stress hormones can clearly have negative effects, a robust stress response is adaptive in the face of real threats to survival (Sapolsky 1992, Wingfield et al. 1997). Recently, biologists have also begun to consider the role of such factors as corticosterone-binding globulins (CBG) and corticosterone receptors (e.g., Love et al. 2004), which might be regulated to compensate for changes in corticosterone levels. These issues underscore the potential complexity of relationships between corticosterone and reproductive success. As with behavioral responses, it is important to examine the reproductive or survival consequences of any changes in stress physiology.

Methodological issues

A few methodological issues should be considered when interpreting the results of this study. As mentioned, I could not study terns nesting near Piping Plovers, which might bias the results if there were slight differences in habitat in areas preferred by plovers. Also, human activity can be measured in multiple ways. In this study, it was defined in terms of human approaches, because these can be quantified fairly easily and can elicit observable behavioral responses in the birds. It is possible that the time of

exposure to continuous human presence near the nest (e.g., the number of hours in a typical day that people are settled near a nest) is more important than approach rate. Spatial variation in such exposure may differ from spatial variation in approach rates, and both should be considered in future studies.

General conclusions and recommendations for future study and management

Human recreational activity was associated with increased flush rates – birds in high activity areas were more likely to flush when approached and left the nest more frequently than those in low activity areas. Although this increase did not appear to have consequences for hatching here, it is still cause for concern as Least Terns are exposed to higher levels of activity at other sites. Future studies on Least Terns should examine these responses over a wider range of activity levels. It is also important to determine whether increased frequency of flushing by adults has consequences for chick survival, and whether human activities affect chicks directly, as has been shown in other species (Müllner et al. 2004, Walker et al. 2005). Tracking Least Tern chicks beyond a few days after hatching is difficult due to their mobility, crypsis, and the open habitats in which they nest, but the use of radio transmitters shows some promise (Whittier and Leslie 2005).

Because the stress series protocol had not previously been used on Least Terns, a limited trapping schedule and a short blood sampling protocol were used in this study to be cautious. As the procedure seemed generally well-tolerated by the terns, a larger scale study with a longer protocol (45-60 minutes) is recommended to more closely examine the variation in the length of stress response suggested by this study. Any such study should include measures to minimize adverse effects (e.g., avoiding trapping before day

10 of incubation and during temperature extremes) and close monitoring of trapped nests for abandonment.

Given that flush rates can be elevated over the relatively low ranges of activity observed here, and that the consequences of frequent flushing are still largely unknown, it is advisable to maintain some Least Tern nesting sites that are closed to recreational activity. There are currently several such sites in New Jersey. Flush rates might also be reduced at beaches by increasing buffer zones between colonies and recreationists (Erwin 1989, Rodgers and Smith 1995, Rodgers and Schwikert 2002). Increased buffers should not be considered a substitute for recreation-free sites, however. Should physiological responses prove sensitive to activity levels, threshold distances for such effects might differ from those for flushing, as physiological responses do not always correspond to behavioral responses (Jungius and Hirsch 1979, Giese 1998, Fowler 1999). Further, on some beaches in New Jersey, there is a relatively narrow space to divide between terns and recreationists, limiting the potential for a substantial buffer zone.

Humans are only one threat facing Least Terns. Predation has long contributed to colony failures in New Jersey (Burger 1989). In this study, gulls were a significant cause of nest failure, but only late in the season, despite their presence throughout the nesting period. Because predatory gulls can exact heavy tolls on tern colonies, measures to control gulls are sometimes taken; selective culling of individual specialists can be an effective (and relatively cost-effective) method of reducing their impact (Guillemette and Brousseau 2001, Kress and Hall 2004). Therefore, where control of gulls is considered, careful consideration should be given to determining whether it is the work of a few individuals.

In general, research on the impacts of human activities could benefit from a more integrated approach. By simultaneously examining responses at multiple levels and considering the causes of failure, one can clarify the relationships between behavioral or physiological responses and reproductive effects. This is important for determining whether elevated responses are sufficient to reduce hatching or fledging, and perhaps more importantly, to determine whether apparent habituation is sufficient to counteract the effects of high activity levels.



Fig. 1. Location of study site (Monmouth Beach, New Jersey).

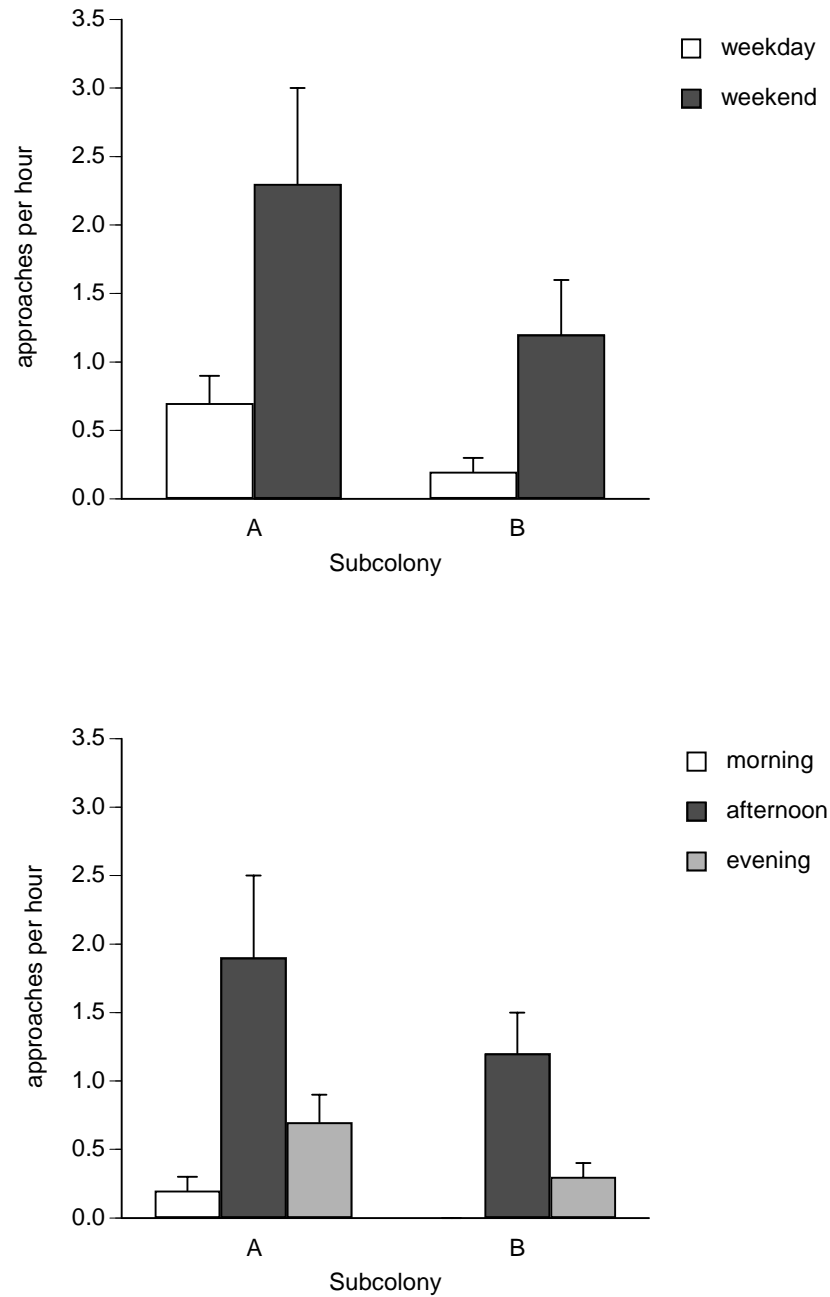


Fig. 2. Human activity broken down by type of day and time of day. Mean (+ se) number of approaches per hour within 15 meters of the fence is shown. Main effects of both time of day and type of day were significant at $P < 0.0001$.

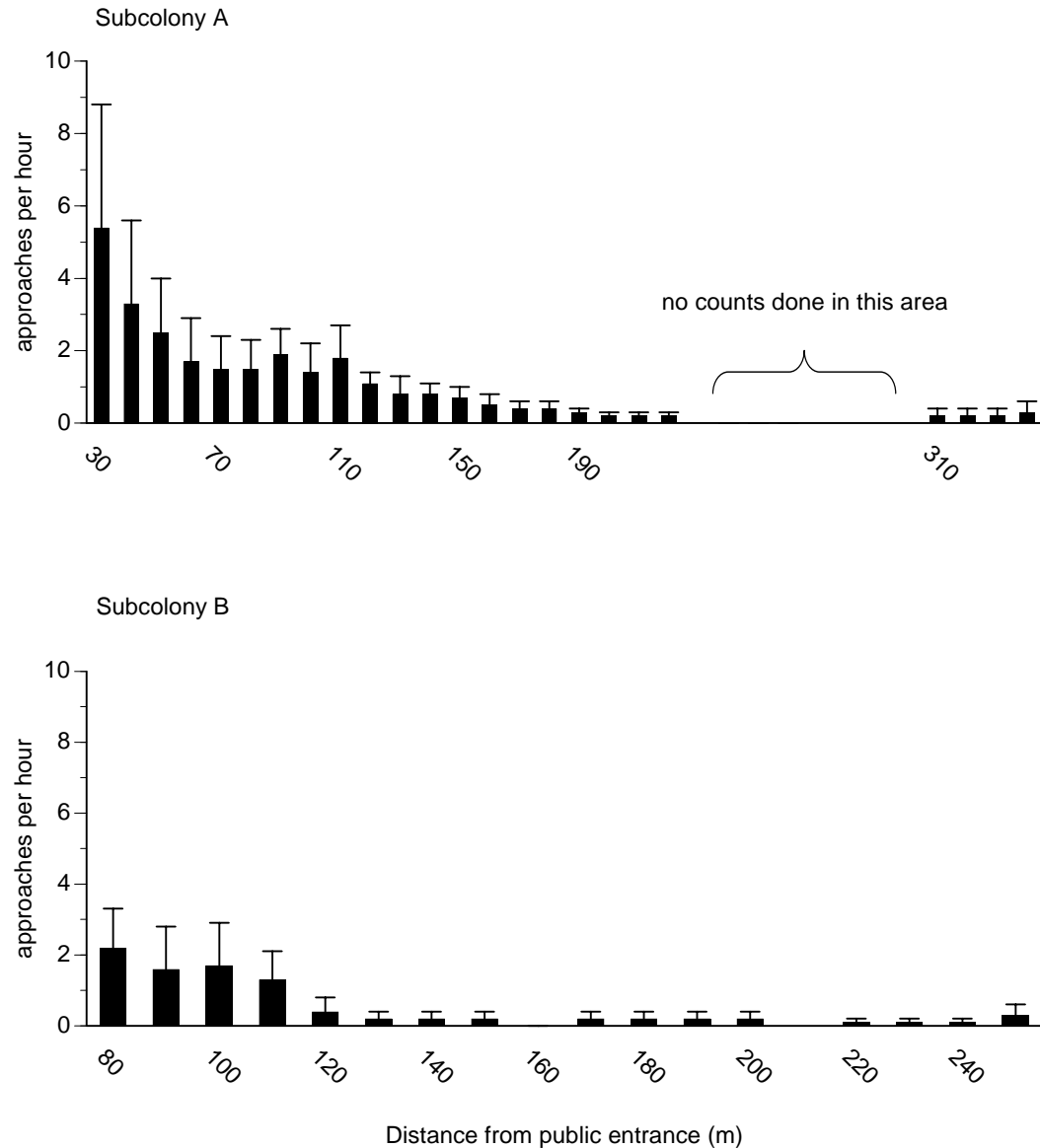


Fig. 3. Human activity rates at various distances from the nearest public entrance. Mean (+ se) number of approaches per hour within 15 meters of the fence is shown. Note that the x-axes start at different distances because subcolony A began 30 m from its nearest entrance and subcolony B began 80 m from its nearest entrance. The region from 230 m to 310 m in subcolony A contained sections where observations were stopped because of nesting Piping Plovers.

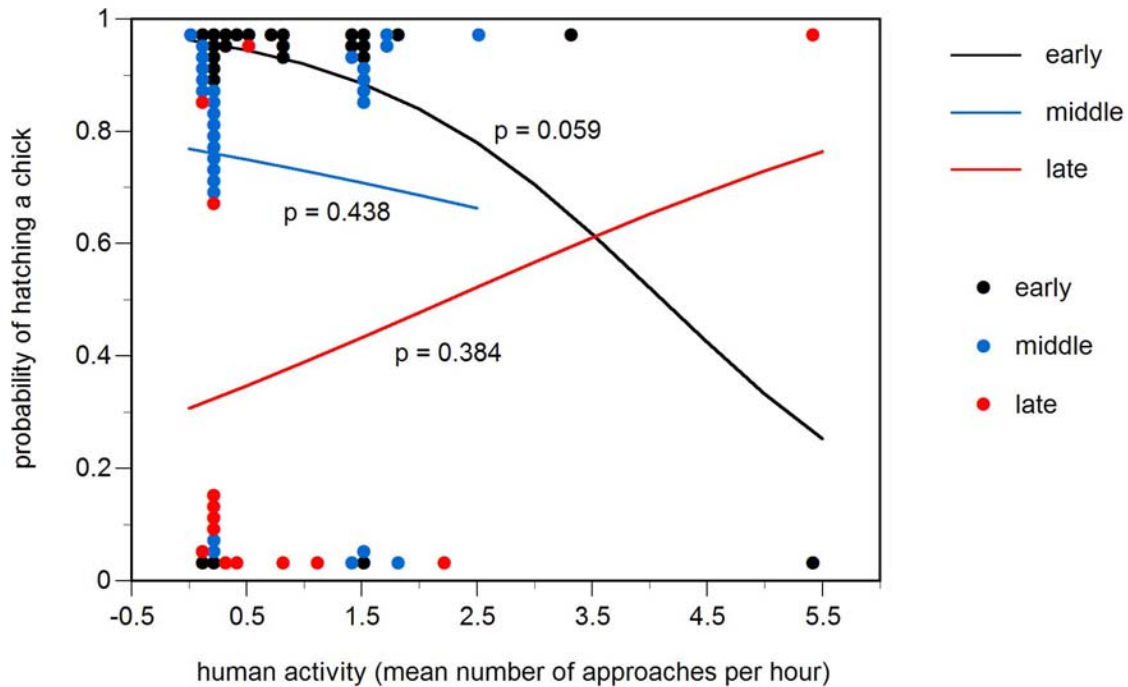


Fig. 4. Probability of hatching a chick as a function of human activity level as modeled by the logistic regression (solid lines), and fates of individual nests (dots), broken down by lay period. Successful nests are indicated at the top of the graph and failed nests at the bottom. $N = 68$ nests (excluded nests were either near Piping Plover nests and had no data on activity level, or were never observed active and could not be classified by lay date). The nests in the highest-activity section heavily influence the regressions (see notes in text).

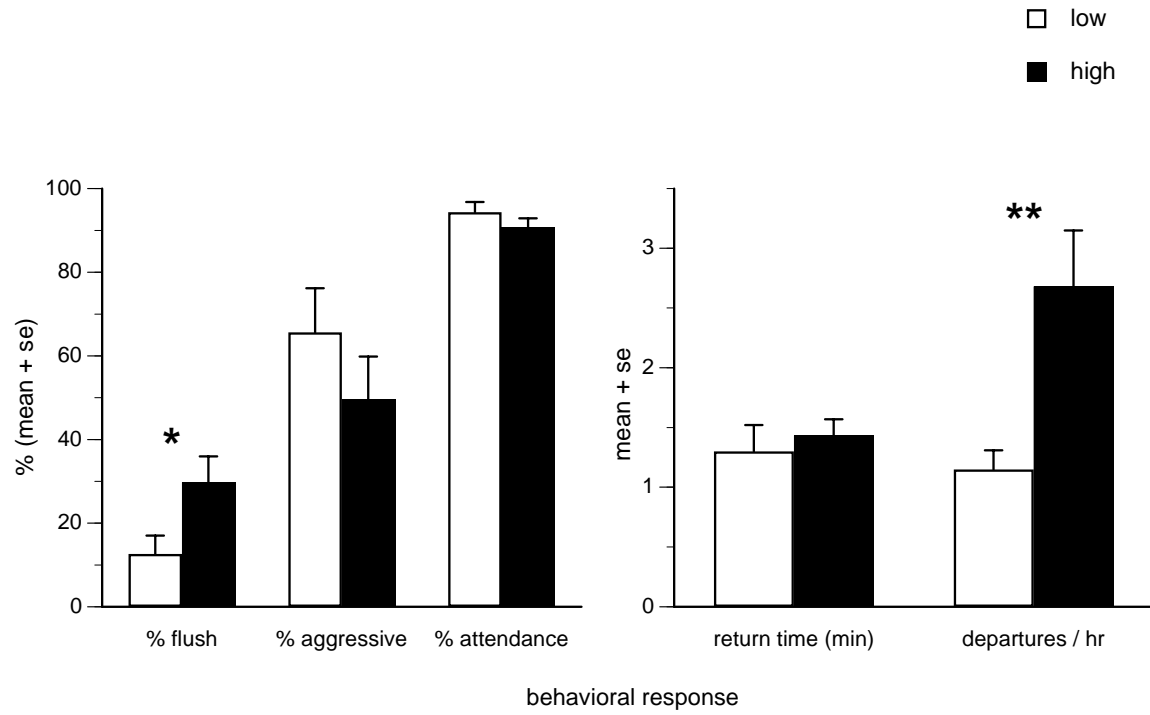


Fig. 5. Behavioral responses of birds at nests in areas of high (N = 19) and low (N = 20) human activity. Responses with similar scales are graphed together. * $P < 0.05$, ** $P < 0.01$

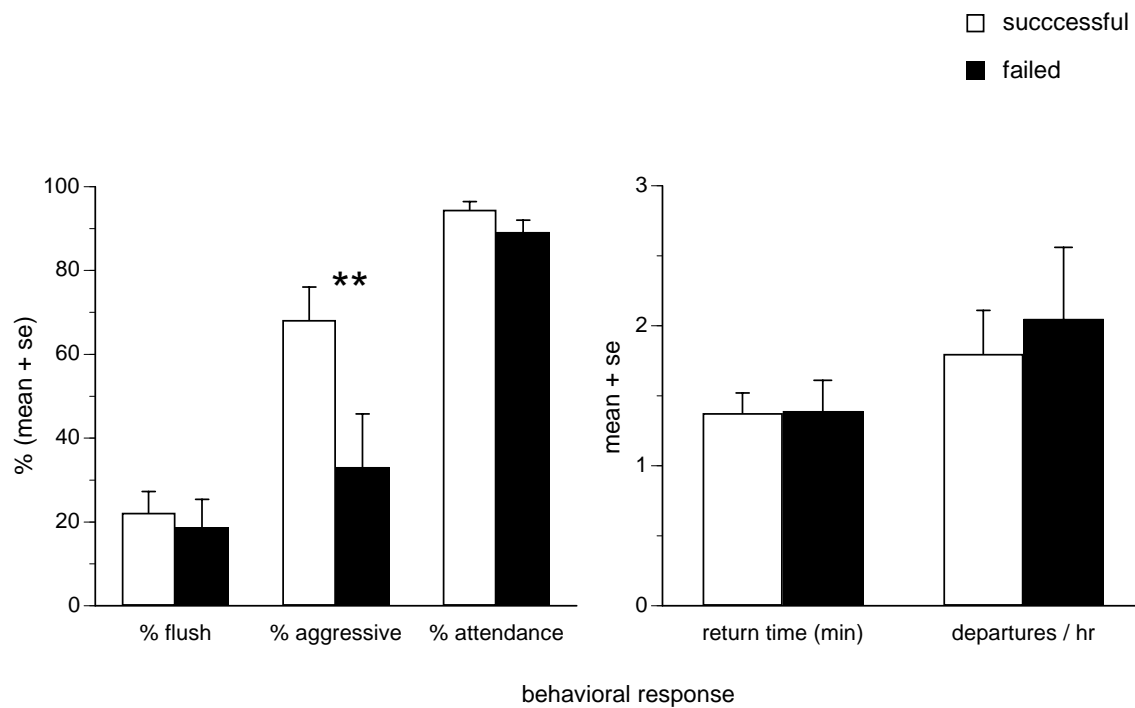


Fig. 6. Behavioral responses of birds at successful (N = 25) and failed (N = 14) nests. Responses with similar scales are graphed together. * $P < 0.05$, ** $P < 0.01$

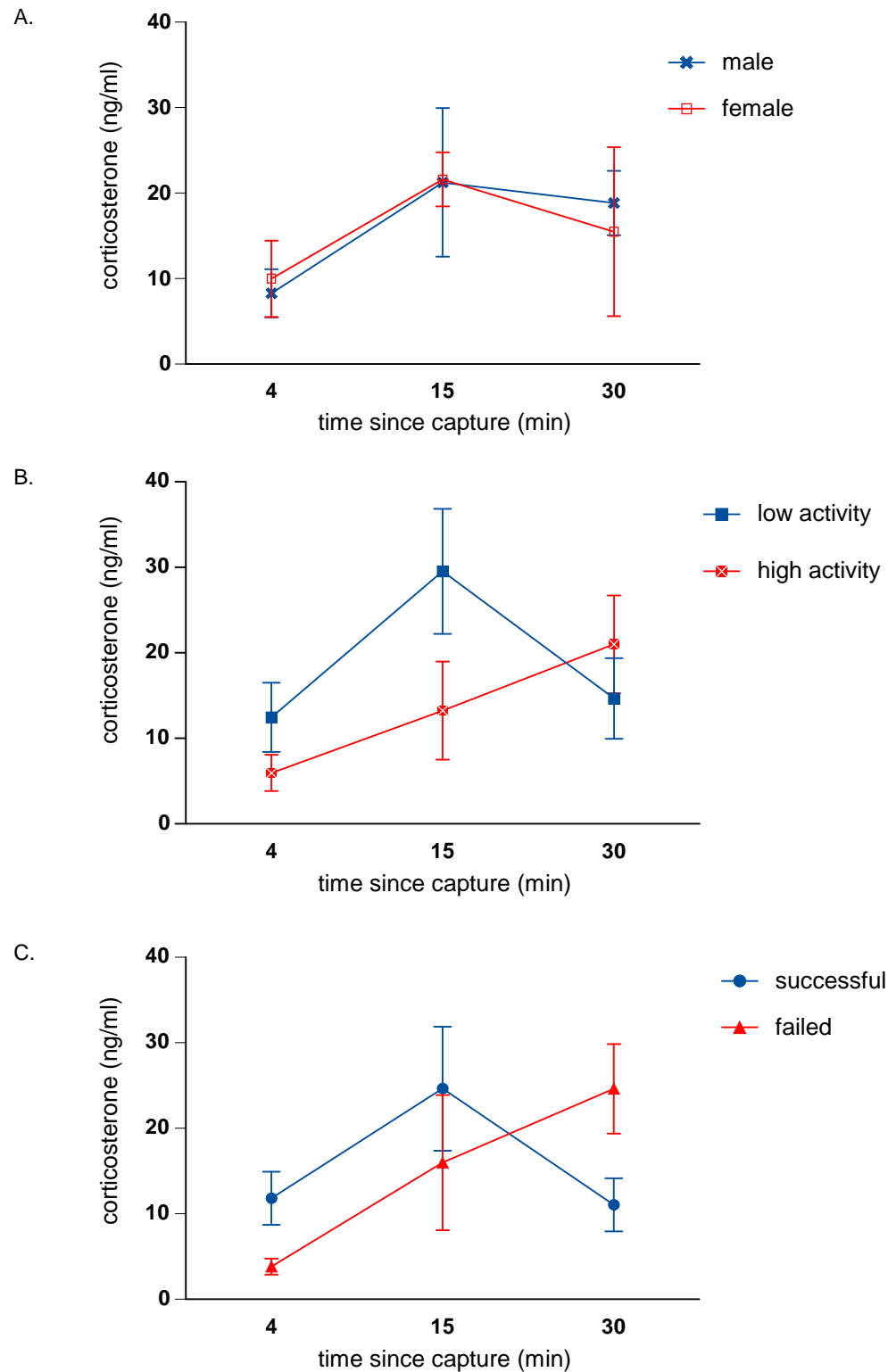


Fig. 7. Corticosterone secretion patterns (mean \pm se) when broken down by A) sex (N = 8 males, N = 4 females) B) human activity levels (N = 6 low, N = 6 high) and C) hatching success (N = 7 successful, N = 5 failed). Differences were not statistically significant.

Table 1. Causes of nest failure

Cause	Number of nests	% of failed nests	% of total
Predation - gull	8	30.8	10
Predation - mammal	2	7.7	2.5
Predation – unknown	1	3.8	1.3
Predation – total	11	42.3	13.8
Undetermined (human activity or predation)	2	7.7	2.5
Undetermined (predation or abandonment)	1	3.8	1.3
Abandonment	10	38.5	12.5
Infertility or embryo death	1	3.8	1.3
Flooding	1	3.8	1.3

Table. 2. Results of the logistic regression analysis on hatching success. Variables retained at $P < 0.15$.

Effect	Logistic coefficient	Wald X^2	P
Activity x lay period	0.57	3.35	0.067
Lay period	-2.02	11.52	0.0007
Activity (early lay period)	-0.78	3.58	0.059
Activity (middle lay period)	-0.21	0.60	0.438
Activity (late lay period)	0.36	0.76	0.384

Table 3. Causes of nest failure before and after the onset of gull predation

	Before	After
Cause of failure	# Losses (%)	# Losses (%)
Predation – gull	NA	8 (61.5%)
Predation – mammal	2 (3%)	
Predation – unknown		1 (7.7%)
Undetermined (human activity or predation)	1 (1.5%)	1 (7.7%)
Undetermined (predation or abandonment)	1 (1.5%)	
Abandonment	10 (15%)	
Infertility or embryo death	1 (1.5%)	
Flooding	1 (1.5%)	
Total failed (total nests)	16 (67)	10 (13)

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