Responses of Nestling Black-crowned Night Herons (*Nycticorax nycticorax*) to Aquatic and Terrestrial Recreational Activities: a Manipulative Study

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Abstract.—We assessed the effects of the presence and the frequency of canoe and pedestrian disturbance during two breeding seasons on multiple behavioral responses (scanning, freezing, grooming, sleeping, moving, wing-raising, and standing-up) of Black-crowned Night Heron (*Nycticorax nycticorax*) nestlings in a breeding colony in southeast Chicago. Short-term responses (min) of Black-crowned Night Heron nestlings showed that they were sensitive to the presence of aquatic and pedestrian disturbance by increasing vigilant (scanning) and anti-predator (freezing) behaviors and decreasing maintenance (grooming, sleeping) behaviors. Nestlings were also sensitive to recreationist behavior, with less time allocated to sleeping and more time to freezing and scanning in the presence of inquisitive pedestrians than pedestrians who passed by the colony without stopping. However, medium-term responses (days) were insensitive to the frequency of disturbance, but spatial proximity to the source of disturbance influenced time scanning, sleeping, and freezing). Our results have wide implications for the protection of the Black-crowned Night Heron in States in which it is considered a species of conservation concern. We recommend that boating activities should be precluded during the initial part of the breeding season and buffer zones of 50 m should be established around the colony to minimize human disturbance. However, under these conditions, restrictions on the number of visitors during the breeding period may not be necessary. *Received 23 October 2006 accepted 20 May 2007.*

Key words.—colonial waterbirds, frequency of disturbance, human disturbance, human-wildlife coexistence, recreational activities.

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Negative effects of human disturbance (e.g., recreationists) on wildlife have been studied at individual, population, and community levels (Gutzwiller and Anderson 1999; Miller *et al.* 2001; Fernández-Juricic 2002). Individual-based studies conducted at local scales provide insight into the mechanisms behind human-wildlife interactions (Taylor and Knight 2003). Assessing responses to varying levels of disturbance can allow managers to determine the probabilities of habitat use, patch use, or even breeding success of species of conservation concern (Beale and Monaghan 2005a; Blumstein *et al.* 2005). When such studies experimentally *manipulate* disturbance levels, rather than taking a correlational approach, more specific management recommendations can be developed because various threshold levels may trigger different types of responses (e.g., Rodríguez-Prieto and Fernández-Juricic 2005).

The effects of human disturbance on birds during the breeding season are particularly important, because they could negatively affect hatching success (Giese 1996), parental investment (Steidl and Anthony 2000), stress levels of juveniles (Müllner *et al.* 2004), chick survival (Müllner *et al.* 2004), nest predation (Miller *et al.* 1998), and eventually reproductive success (Safina and Burger 1983; Beale and Monagham 2004; Bijlsma 2006). Assessment of individual responses to determine tolerance to recreational activities, such as flight initiation distances, within colonies can be difficult because the reaction of a few highly exposed individuals can be transmitted quickly across the colony (Rodgers, Jr. and Smith 1995). A potential solution is to study various behavioral responses to estimate tolerance levels more comprehensively (Blumstein *et al.* 2005).

The goal of this study was to assess the effects of the presence and frequency of canoe and pedestrian disturbance on multiple behavioral responses of Black-crowned Night Heron (*Nycticorax nycticorax*) nestlings in a breeding colony in southeast Chicago, Illinois. Black-crowned Night Heron nestlings can be affected negatively by researcher disturbance (Tremblay and Ellison 1979; Parsons and Burger 1982); however, little evidence exists pertaining to disturbance thresholds that would increase or reduce these effects. We conducted our study during two breeding seasons (2004, aquatic disturbance; 2005, pedestrian disturbance) assessing short-term responses to the presence and type of disturbance, and medium-term responses to variations in the frequency of disturbance in different sectors of the colony during the breeding season.

METHODS

Study Area

The study was conducted in wetlands near Lake Calumet which is located about 5.25 km southwest of Lake Michigan. The larger Calumet region, which includes communities in southeast Chicago and northwest Indiana, contains a remnant wetland system surrounded by industry, abandoned industrial facilities, and landfills (Westphal *et al.* 2005).

The study colony of Black-crowned night heron occurred in a complex of wetlands on Chicago's southeast side. The herons nested in Indian Ridge Marsh (39.9 ha of wetland, Fig. 1a) and in Heron Pond (12.16 ha of wetland, Fig. 1b) in 2004 and 2005, respectively, along with Snowy Egrets (*Ardea alba*) and Great Blue Herons (*Ardea Herodias*). Wetlands are dominated by invasive species, such as Common Reed (*Phragmites australis*), Narrow-leaved Cattail (*Typha angustifolia*), Reed Canary Grass (*Phalaris arundinacea*), and Purple Loosestrife (*Lythrum salicaria*). Native plants include Red-oiser Dogwood (*Cornus stolonifera*), Virginia Creeper (*Parthenocissus quinquefolia*), Jewelweed (*Impatiens capensis*), Blue Vervain (*Verbena hastate*), and Pale Sedge (*Carex grannularis*).

The short- and medium-term effects of aquatic and pedestrian disturbance on the behavior of nestling Black-crowned Night Herons were studied during the 2004 and 2005 breeding seasons, respectively. In both seasons, Black-crowned Night Herons nested in stands of common reed. Tremblay and Ellison (1979) determined young Black-crowned Night Heron fledge at 29 to 34 days of age. Sampling in this study was focused on individuals younger than 28 days by following nests since egg laying. In 2004 sampling took place from 23 June to 24 July; in 2005 sampling took place from 7 June to 5 July.

Effects of Aquatic Disturbance in 2004

The effects of aquatic recreation on nestlings were tested by canoeing around Indian Ridge Marsh near the Black-crowned Night Heron colony on pre-determined paths (Fig. 1a). The breeding colony was divided into three areas based on the frequency of visitation: high-disturbance (the area closest to the shore), low-disturbance (intermediate distance to the shore), and control area (farthest from the shore and not exposed to aquatic disturbance).

Behavioral responses of Black-crowned Night Heron nestlings were recorded with weatherproof, infrared, black-and-white Pelikancam bullet cameras (TC855) mounted on stakes that were installed about 0.5-1.0 m away from and 0.25-0.75 m above each nest. Cameras were connected with coaxial video cable to a centrally-located Pelikancam DPLEX16 multiplexer and a Pelikancam WJ2096 time-lapse VCR, which were both housed in plastic containers anchored to a wooden platform in the center of the marsh. The multiplexer allowed us to record 16 cameras concurrently. Cameras, the multiplexer, and the VCR were powered with twelve volt batteries.

Two paths were marked by stakes in the water that were placed five m, 25 m, and 45 m from the edge of vegetation at roughly the halfway points across the high- and low-disturbance areas (Fig. 1a). Disturbance treatments were applied by approaching the colony along these paths, which were monitored by two cameras, in a five-m fiberglass canoe containing two people. The remaining 14 cameras recorded the behavior of Black-crowned Night Herons during disturbance treatments and during periods of non-disturbance for comparisons. At any given moment during the season, five nests were monitored in the high-disturbance area, another five in the low-disturbance area, and four in the control area.

The aquatic disturbance was conducted two to four days per week for four to five h per day in the late mornings and early afternoons of the nesting season. For each disturbance event, two people paddled from shore to the high disturbance path (solid line in Fig. 1a), where they paused and played a noise tape (people talking) for three min at the 45 m, 25 m, and five m stakes. Afterwards, they returned to the 45 m stake on the high disturbance path and repeated the aforementioned approach. After completing two passes along the high-disturbance path, they paddled to the low-disturbance path (dotted line Fig. 1a), and repeated the canoe approach procedure including playing the tape for three min at each stake. They approached the high and low disturbance areas for the rest of the sampling day in the same way and order as described above such that the high-disturbance area was approached twice as frequently as the low-disturbance area. The control area was never approached with the canoe, and it was far enough from the disturbed areas that birds could not hear tape noises or see the canoe.

Cameras were moved to a new set of nests in each area every week to maximize sample size. Particular care was taken to minimize the amount of time spent moving, aiming, and troubleshooting cameras to reduce stress on nesting birds. Thirteen, 15, and 17 nests were recorded in the control, low disturbance, and high disturbance areas, respectively. The distance from each of the 45 nests to the five m stake located nearest to the colony was measured at the end of the breeding season

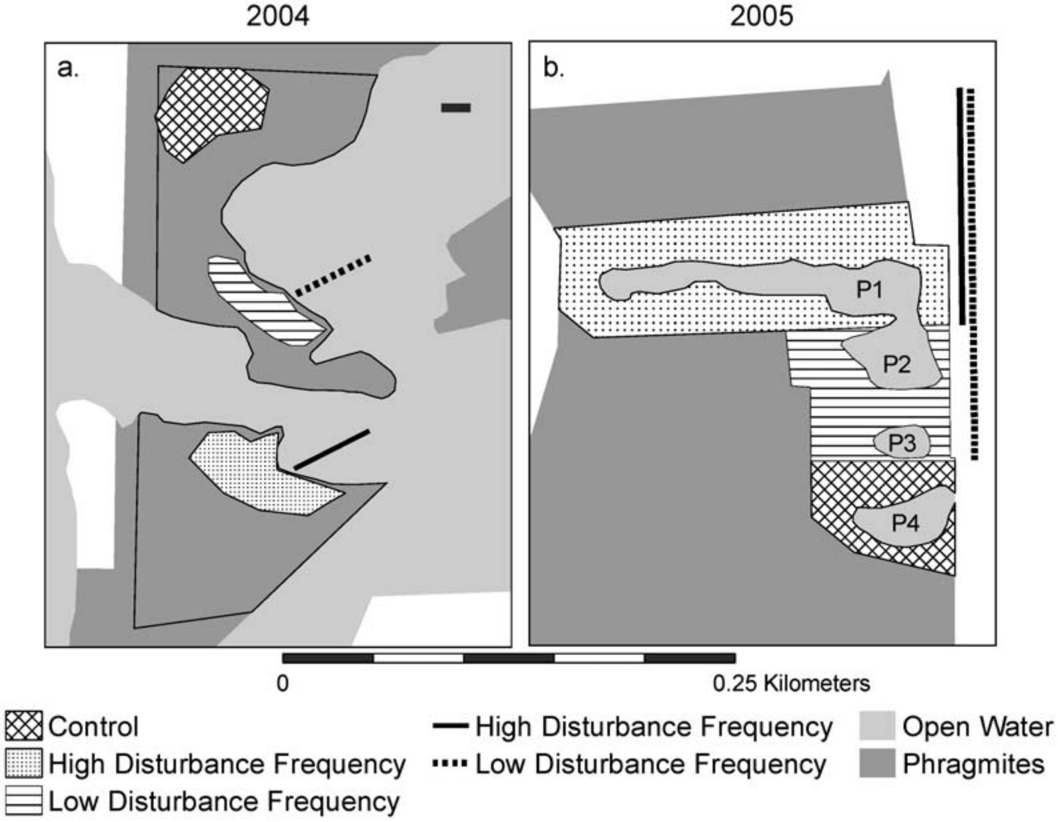

Figure 1. Panels (a) and (b) depict the study sites used during the summers of 2004 and 2005, respectively. The dotted polygons show the areas where the colony was disturbed with a high frequency during each year. The striped polygons depict the areas where the colony was disturbed with low frequency during each year. The crosshatched polygons depict control areas where the colony was not experimentally disturbed. The solid lines show the approach paths that were used for the high frequency of disturbance areas during aquatic disturbance in 2004 (panel a) and terrestrial disturbance in 2005 (panel b). The dotted lines show the approach paths that were used for low frequency of disturbance areas during aquatic disturbance in 2004 (panel a) and terrestrial disturbance in 2005 (panel b). P1, P2, P3, and P4 refer to ponds 1-4, as described in the text.

(post-fledging). This was considered the distance to the source of disturbance in the medium-term disturbance analyses (see below).

Effects of Pedestrian Disturbance in 2005

During the summer of 2005, the majority of the breeding colony moved to Heron Pond (Fig. 1). Changes in breeding location between years are not uncommon for this colony (Levengood *et al.* 2005). Birds nested on the edges and between four adjacent ponds within the marsh running roughly north-south along an abandoned road (Fig. 1b). The pond located farthest north (Pond 1) was designated as the high-disturbance area. Pond 4 was a control area that did not receive any pedestrian disturbance. The two middle ponds (2 and 3) were designated as low-disturbance, although most of the video-recording occurred in Pond 3 because of its higher concentration of nests. During the summer of 2004, the area experienced extreme drought effects, which, although consistent across ponds, resulted in non-unifrom consequences. For example, prior to the implementation of our treatments, we observed considerable variation in nest success across ponds. Following Erwin *et al.* (1996), if the nest had more than one individual after 14 days, we considered it successful. During the weeks prior to the experiment, a great number of nests in all four ponds lost chicks or eggs to presumed predation but the highest rates of loss were observed in ponds 2 (79% of nests lost all eggs or chicks) and 3 (70%), while lower rates were observed in ponds 1 (53%) and 4 (65%).

Cameras were mounted on stakes in the common reed located about 0.5-1.0 m away from and 0.25-0.75 m above each study nest. The same recording equipment as in 2004 was used, with 16 cameras connected to a central multiplexer and time lapse VCR that was located in a waterproof storage box on an elevated platform in the northeast corner of Pond 2. At any time, five nests were monitored in the high-disturbance area, four in the low-disturbance area, and four in the control area. The other three cameras monitored the walking path so that the video would have a temporally synchronized record of when disturbance occurred in ponds 1, 2, and 3. The behavior of nestlings was recorded during sessions with and without disturbance for comparisons.

In the 2005 season, two disturbance factors were manipulated: frequency of disturbance and type of pedestrian behavior. Frequency of disturbance involved three levels: control area, low disturbance, and high disturbance. Type of pedestrian behavior included three levels: normal walking (pedestrians walking along the path at 1.5 steps per s), inquisitive walking (pedestrians walking at less than one step per s and stopping frequently to peer through vegetation into the ponds), and fast walking (pedestrians walking along the path at more than three steps per s). These treatments mimicked levels of disturbance that could occur if the marsh were opened to recreational use.

The three types of pedestrian behavior were conducted in random order three times per week: Tuesday, Wednesday, and Thursday, weather permitting. Each type of pedestrian behavior was conducted for a whole day (late morning and early afternoon) each week (four to five hours per day). On a given day, disturbance events were conducted every 20 min and consisted of two to three people walking south down the path from north of Pond 1 to particular stopping points and back to the starting point. The first event each hour involved walking from the starting point on the path (north of Pond 1) to the stopping point at the southern edge of Pond 1, and then back to the starting point (solid line in Fig. 1a). Twenty minutes later, this pattern was repeated a second time. Twenty minutes later, the third event involved walking from the starting point on the walking path past ponds 1 and 2 to the southern edge of Pond 3 (along the dotted line in Fig. 1a), and back to the starting point. Thus, the high disturbance area experienced three times as many pedestrian disturbance events as the low disturbance area. Normal conversation occurred during the disturbance events, but no noise tape was played. Walking disturbance events did not occur near the control pond (Pond 4).

Each week, cameras were moved to a new set of nests on Monday minimizing stress on nesting birds as much as possible. However, the high proportion of unsuccessful nests during the 2005 season substantially constrained our sample size (see Results). Overall, nine nests were recorded in the control area, 15 nests in the low disturbance area, and seven nests in the high disturbance area throughout the season. The distance from each of the 31 nests to the nearest point on the walking path was measured late in the summer after nestlings had fledged,. This was considered the distance to the source of disturbance in the medium-term disturbance analyses (see below).

Behavioral Observations

Sampling units were individual nests. The behavior of nestlings, but not adults, was recorded because the latter were often absent from the nest during our diurnal focal observations. Sampled nests contained one to four nestlings. The focal individual was chosen randomly in nests with more than one individual.

JWatcher 1.0 (Blumstein *et al.* 2006) was used to record the duration and number of the following events that took place within the nest: scanning (individual monitored the surroundings visually by moving its head while in head-up position), freezing (individual suddenly stopped moving while in head-up position), grooming (preening), sleeping (individual retracted neck and closed eyes), moving (individual walked around the nest or nearby, but within camera view), wing-raising (individual outstretched wings), and standing-up. With this information we calculated proportion of time scanning, freezing, grooming, and walking, and wing-raising and standing-up rates. Other behaviors (e.g., interactions with adults, pecking, etc.) were recorded as well, so proportions do no add up to one. All rates were expressed as number of events per min. Scanning is an indicator of the level of vigilance. Grooming and sleeping are indicators of self-maintenance activities that could be disrupted by disturbance (Davis, Jr. 1993). Freezing, walking, wing-raising, and standing up are indicators of stress or agonistic behaviors that Black-crowned Night Herons use to respond to human disturbance (Parsons and Burger 1982).

In the 2004 season, the behavior of Black-crowned Night Heron nestlings was recorded in the presence and absence of the canoe with focal observations that lasted between six and 20 min. In the 2005 season, nestling behavior was recorded without pedestrians and with pedestrians walking around the pond using 21 min focal observations. Sampling was balanced by having at least one sample with and one sample without disturbance per nest per day, which depended on disturbance timing, availability of individuals in the nest, correct technical operation of the equipment, weather conditions, etc. In the 2004 season, between one and eight samples per nest per day were recorded. In the 2005 season, between one and six samples per nest per day were recorded.

Statistical Analysis

Some of the dependent variables describing Black-crowned Night Heron behavior are interdependent (for instance, an increase in freezing proportion will decrease movement proportion), so that the associated results cannot be combined for hypothesis testing. In spite of this, statistical analyses were conducted on them in order to characterize from a mechanistic perspective the effects of disturbance on several behavioral dimensions.

Two types of analyses were done: (a) short-term responses of nestlings to disturbance (over min), and (b) medium-term responses (over the days in which the nests were monitored). The goal of this two-tiered approach was to assess whether short-term changes in behavior could eventually generate sensitization or habituation responses in areas subject to different frequencies of human disturbance.

To assess short-term responses, focal observations were pooled from individual nests taken at different times during the breeding season. For the 2004 season, general linear models assessing the variation in different behaviors (scanning, freezing, grooming, sleeping, moving, wing-raising, and standing-up) were used in relation to the presence/absence of the canoe (fixed factor). Nest identification (nest ID) was incorporated as a random factor to reduce potential biases given by differences in responses between nests. Date was also included to control for temporal variations in responses of nestlings to human disturbance (Parsons and Burger 1982). For the 2005 season, general linear models were used to assess the effects of presence/absence of pedestrians (fixed factor) and type of pedestrian behavior (fixed factor: normal walking, inquisitive walking, fast walking) on scanning, freezing, grooming, sleeping, walking, wing-raising, and standing-up behaviors. Nest identification (random factor) and date were also included in the model. Within these short-term response models, a significant disturbance factor (presence/absence of canoe or pedestrians, or type of pedestrian behavior) would indicate that the effect was important in controlling for between-nest variation in behavioral responses to disturbance. Planned comparisons were used to assess differences between levels of significant factors or interaction effects.

To assess medium-term responses to different frequencies of disturbance in both seasons, behavioral responses (scanning, freezing, grooming, sleeping, moving, wing-raising, and standing-up) were averaged for each nest during the days in which the nests were video-taped. Thus, in these analyses, each data point corresponded to a different nest. Only samples under disturbance conditions were considered. General linear models were used including frequency of disturbance (categorical factor: control, low, high), distance to the source of disturbance (continuous factor), and the interaction between these two factors. For 2004, distance to the closest canoe path was used, whereas for 2005, the distance to the pedestrian pathway. Linear regressions were used to assess the significant interaction between frequency of disturbance and distance to the canoe path. To estimate thresholds where spatial proximity of human disturbance impacted specific behaviors, these regression relationships were used to estimate the distance at which the frequencies of behaviors by subject birds exceeded the values observed in the controls.

All proportion variables were arcsin transformed and rate variables were log-transformed to meet normality assumptions. Transformed means ± SE were presented throughout.

RESULTS

Short-term Responses to Aquatic Disturbance

In the sectors of the colony that were disturbed in the 2004 breeding season, the presence of the canoe increased significantly the proportion of time Black-crowned Night Heron nestlings allotted to scanning (canoe absent, 0.357 ± 0.022; canoe present, 0.655 ± 0.073; $F_{1, 362} = 16.41$, $P < 0.001$). The proportion of time freezing was not significantly affected by the canoe presence (canoe absent, 0.023 ± 0.005; canoe present, 0.020 ± 0.010; $F_{1, 362} = 0.09$, $P = 0.758$). Black-crowned Night Heron nestlings decreased significantly the proportion of time grooming (canoe absent, 0.257 ± 0.019; canoe present, 0.172 ± 0.036; $F_{1, 362} = 4.29$, $P = 0.039$) and sleeping (canoe absent, 0.629 ± 0.036; canoe present, 0.357 ± 0.078; $F_{1, 362} = 4.27$, $P = 0.040$) during the day with the presence of the canoe. Nestlings increased significantly the proportion of time moving around the nest when the canoe was present (canoe absent, 0.629 ± 0.036; canoe present, 0.357 ± 0.078; $F_{1, 362} = 5.52$, $P = 0.019$), but the proportion of time moving decreased as the season progressed (coefficient = -0.013, $F_{1, 362} = 10.61$, $P < 0.001$).

The presence of the canoe did not influence significantly wing-raising (canoe absent, 0.007 ± 0.001; canoe present, 0.005 ± 0.001; $F_{1, 362} = 0.71$, $P = 0.400$) and standing-up rates (canoe absent, 0.007 ± 0.001; canoe present, 0.006 ± 0.002; $F_{1, 362} = 0.01$, $P = 0.903$), although both rates decreased during the course of the breeding season (wing-raising coefficient = -0.002, $F_{1, 362} = 5.99$, $P = 0.015$; standing-up coefficient = -0.002, $F_{1, 362} = 6.70$, $P = 0.010$). In six of the seven variables studied, significant differences ($F_{32, 362} > 1.48$, $P < 0.05$) were found in nestling responses between nests (scanning proportion, grooming proportion, sleeping proportion, moving proportion, wing-raising rate, standing-up rate, but not freezing).

Short-term Responses to Terrestrial Disturbance

In the ponds that were exposed to disturbance in the 2005 breeding season, proportion of time nestlings spent scanning significantly increased with the presence of disturbance ($F_{1, 210} = 13.76$, $P < 0.001$), and varied with pedestrian behavior ($F_{2, 210} = 4.09$, $P = 0.018$; Fig. 2a). Both inquisitive walking ($F_{1,210} = 10.28$, $P = 0.002$) and normal walking ($F_{1,210} = 6.62$, $P = 0.011$) increased significantly scanning proportion in relation to fast walking, but there was no significant difference between inquisitive and normal walking ($F_{1,210} = 0.0004$, $P = 0.983$; Fig. 2a). Proportion of time freezing was significantly higher when pedestrians were present ($F_{1, 210} = 7.66$, $P = 0.006$), and it also changed with the type of pedestrian behavior ($F_{2, 210} = 14.29$, $P < 0.001$), leading to an almost significant interaction effect between these factors ($F_{2, 210} = 2.91$, $P = 0.057$, Fig. 2b). Inquisitive walking generated the highest significant increase in freezing proportion in relation to both normal walking ($F_{1,210} = 25.59$, $P < 0.001$; Fig. 2b) and fast walking ($F_{1,210} = 10.28$, $P = 0.002$; Fig.

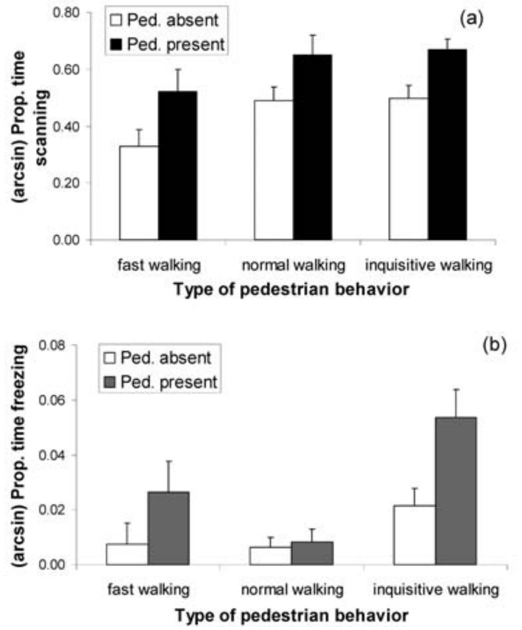

Figure 2. Combined effects of presence (Ped. present) and absence (Ped. absent) of pedestrians and type of pedestrian behavior (fast walking, normal walking, inquisitive walking) on (a) proportion of time scanning, and (b) proportion of time freezing of Black-crowned Night Heron nestlings in the 2005 breeding season.

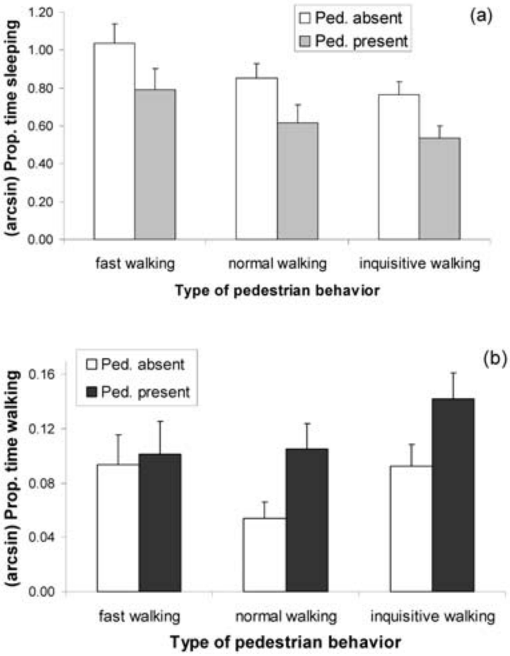

Figure 3. Combined effects of presence (Ped. present) and absence (Ped. absent) of pedestrians and type of pedestrian behavior (fast walking, normal walking, inquisitive walking) on (a) proportion of time sleeping, and (b) proportion of time walking of Black-crowned Night Heron nestlings in the 2005 breeding season.

2b). There was no significant difference in the proportion of time spent freezing between normal walking and fast walking ($F_{1,210}$ = 0.89, P = 0.347; Fig. 2b). Moreover, the proportion of time freezing decreased significantly as the season progressed (coefficient = -0.0001, $F_{1,\,210}$ = 4.36, P = 0.038).

Proportion of time nestlings spent grooming was not significantly influenced by the presence of disturbance (pedestrians absent, 0.217 ± 0.022; pedestrians present, 0.224 ± 0.022; $F_{1,\,210}$ = 0.12, P = 0.732) or the type of pedestrian behavior (normal walking, 0.189 ± 0.025; inquisitive walking, 0.247 ± 0.023; fast walking, 0.212 ± 0.037; $F_{2,\,210}$ = 1.37, P = 0.255). Proportion of time Black-crowned Night Heron nestlings spent sleeping decreased significantly with the presence of pedestrians ($F_{1,\,210}$ = 12.13, P = 0.001), and varied with type of pedestrian behavior ($F_{2,\,210}$ = 4.70, P = 0.010; Fig. 3a). There was no significant difference between inquisitive and normal walking ($F_{1,\,210}$ = 0.88, P = 0.349; Fig. 3a). However, proportion of time sleeping was significantly higher with fast walking than with inquisitive ($F_{1,210}$ = 9.36, P = 0.003) and normal walking ($F_{1,210}$ = 4.99, P = 0.026) (Fig. 3a). Proportion of time nestlings allocated to moving increased significantly with the presence of pedestrians ($F_{1,210}$ = 5.00, P = 0.026), and varied with pedestrian behavior ($F_{2,210}$ = 3.56, P = 0.030, Fig. 3b). There was no significant difference between fast walking and normal walking ($F_{1,210}$ = 0.04, P = 0.848, Fig. 3b), and between fast walking and inquisitive walking ($F_{1,210}$ = 3.29, P = 0.071, Fig. 3b). The proportion of time nestlings allocated to moving was higher when pedestrians walked inquisitively than when they walked normally ($F_{1,210}$ = 6.17, P = 0.014, Fig. 3b).

Wing-raising increased significantly only with the presence of pedestrians ($F_{1,210}$ = 5.54, P = 0.030; pedestrians absent, 0.058 ± 0.007; pedestrians present, 0.087 ± 0.011), but not with variations in their behaviors (normal walking, 0.060 ± 0.009; inquisitive walking, 0.079 ± 0.010; fast walking, 0.076 ± 0.017;

$F_{2,210}$ = 1.39, P = 0.252). Standing-up rates did not vary significantly with the presence/absence of disturbance (pedestrians absent, 0.057 ± 0.007; pedestrians present, 0.067 ± 0.007; $F_{1,210}$ = 1.28, P = 0.260), but they were influenced significantly by different types of pedestrian disturbance (normal walking, 0.048 ± 0.008; inquisitive walking, 0.075 ± 0.007; fast walking, 0.056 ± 0.011; $F_{2,210}$ = 6.70, P = 0.002). There were no significant differences between normal walking and fast walking ($F_{1,210}$ = 0.12, P = 0.729). However, nestlings increased significantly standing-up rates during inquisitive walking relative to both normal walking ($F_{1,210}$ = 11.83, P < 0.001) and fast walking ($F_{1,210}$ = 5.89, P = 0.016). Furthermore, standing-up rate decreased significantly as the season progressed (coefficient = -0.0271; $F_{1,210}$ = 7.54, P = 0.007).

Finally, significant differences ($F_{12,210}$ > 1.86, P < 0.05) in bird responses were found between nests in five of the seven variables studied (freezing proportion, grooming proportion, sleeping proportion, moving proportion, wing-raising rate, but not scanning proportion and standing-up rate).

Medium-term Responses to Aquatic Disturbance

For locations that consistently received different frequencies of disturbance, there were no significant differences in the proportion of time allocated to scanning (control, 0.336 ± 0.054; low disturbance, 0.358 ± 0.063; high disturbance, 0.445 ± 0.050; $F_{2,40}$ = 1.18, P = 0.318), freezing (control, 0.033 ± 0.019; low disturbance, 0.061 ± 0.026; high disturbance, 0.052 ± 0.016; $F_{2,40}$ = 1.69, P = 0.197), grooming (control, 0.367 ± 0.048; low disturbance, 0.263 ± 0.061; high disturbance, 0.329 ± 0.045; $F_{2,40}$ = 1.47, P = 0.241), sleeping (control, 0.604 ± 0.093; low disturbance, 0.659 ± 0.102; high disturbance, 0.670 ± 0.068; $F_{2,40}$ = 0.17, P = 0.682), and moving (control, 0.144 ± 0.051; low disturbance, 0.134 ± 0.026; high disturbance, 0.117 ± 0.019; $F_{2,40}$ = 0.25, P = 0.782) among the frequency of disturbance treatments accumulated over the days the nests were monitored. Similarly, wing-raising (control, 0.003 ± 0.001; low disturbance, 0.008 ± 0.003; high disturbance, 0.006 ± 0.002; $F_{2,40}$ = 0.61, P = 0.551) and standing-up (control, 0.012 ± 0.005; low disturbance, 0.007 ± 0.003; high disturbance, 0.011 ± 0.004; $F_{2,40}$ = 0.02, P = 0.982) rates did not vary significantly with the frequency of disturbance.

Distance to the source of disturbance did not affect the behavioral responses of Black-crowned Night Heron nestlings ($F_{1,40}$ < 3.06, P > 0.05). However, the interaction between distance to the source of disturbance and frequency of disturbance significantly affected the proportion of time sleeping ($F_{2,40}$ = 3.86, P = 0.029). Birds decreased significantly the proportion of time sleeping at distances closer than 40 m to the canoe path under high frequency of disturbance ($F_{1,16}$ = 4.51, P = 0.049, Fig. 4). However, the relationship between proportion of time sleeping and distance to the source of disturbance was not significant in low frequency of disturbance ($F_{1,11}$ = 0.78, P = 0.396) and control ($F_{1,13}$ = 3.26, P = 0.094) areas.

Medium-term Responses to Terrestrial Disturbance

No significant differences among control, low, and high frequency of disturbance treatments were found in the medium-term behavioral responses of Black-crowned Night Heron nestlings: scanning proportion (control, 0.641 ± 0.035; low disturbance,

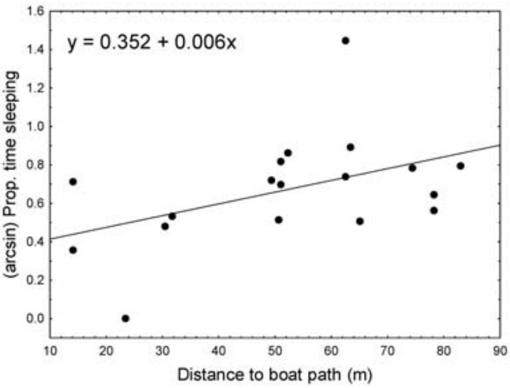

Figure 4. Effects of the distance from Black-crowned Night Heron nests to the canoe path on the proportion of time sleeping in the 2004 breeding season.

0.599 ± 0.050; high disturbance, 0.612 ± 0.057; $F_{2,17} = 2.26$, $P = 0.134$), freezing proportion (control, 0.022 ± 0.009; low disturbance, 0.038 ± 0.014; high disturbance, 0.024 ± 0.009; $F_{2,17} = 1.18$, $P = 0.331$), grooming proportion (control, 0.299 ± 0.033; low disturbance, 0.235 ± 0.045; high disturbance, 0.268 ± 0.057; $F_{2,17} = 0.11$, $P = 0.897$), sleeping proportion (control, 0.721 ± 0.048; low disturbance, 0.670 ± 0.156; high disturbance, 0.731 ± 0.107; $F_{2,17} = 0.94$, $P = 0.409$), walking proportion (control, 0.130 ± 0.024; low disturbance, 0.155 ± 0.031; high disturbance, 0.119 ± 0.020; $F_{2,17} = 2.04$, $P = 0.161$), wing-raising rate (control, 0.064 ± 0.016; low disturbance, 0.078 ± 0.014; high disturbance, 0.074 ± 0.010; $F_{2,17} = 0.01$, $P = 0.988$), and standing-up rate (control, 0.062 ± 0.012; low disturbance, 0.061 ± 0.006; high disturbance, 0.071 ± 0.009; $F_{2,17} = 0.09$, $P = 0.918$).

However, a significant distance-to-source-of-disturbance effect was found in three of the seven variables evaluated. The proportion of time spent scanning ($F_{1,17} = 28.45$, $P < 0.001$; Fig. 5a) and freezing decreased ($F_{1,17} = 5.56$, $P = 0.031$; Fig. 5b), whereas the proportion of time sleeping increased ($F_{1,17} = 6.17$, $P = 0.024$; Fig. 5c), as the nests were farther away from the pathway. Examination of the distance at which the regression relationships predicted rates of bird responses to exceed levels observed in the control treatment revealed that nestlings changed their proportion of time scanning when disturbance agents were within 35 m. Similarly, nestlings increased their time freezing over control treatments when human disturbance agents were within 22 m, and decreased their time sleeping over control treatments when human disturbance agents were within 47 m.

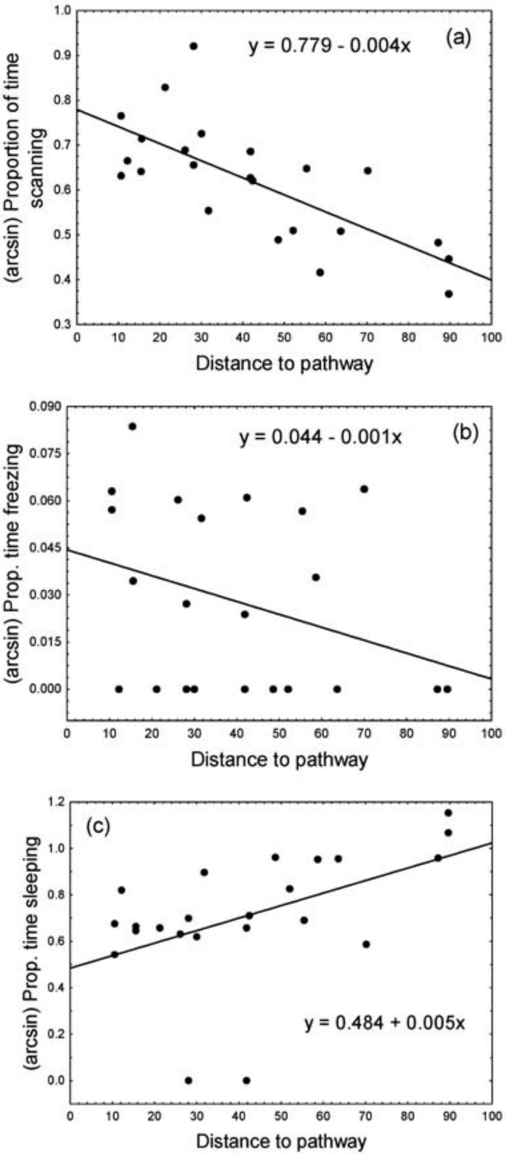

Figure 5. Effects of the distance from Black-crowned Night Heron nests to the pedestrian walking patch on the proportion of time (a) scanning, (b) freezing, and (c) sleeping in the 2005 breeding season.

DISCUSSION

Short-term responses of Black-crowned Night Heron nestlings to both aquatic and terrestrial human disturbance were often significant but varied depending upon the type of human behavior. We found little evidence supporting medium-term responses to variations in the frequency of disturbance over the breeding season, although some responses (scanning, sleeping, freezing) varied with the distance to the source of disturbance.

Canoeing activity around the nests during daylight hours increased the proportion of time Black-crowned Night Heron nestlings spent scanning and moving around the nest, and decreased the time allocated to grooming and sleeping, which could potentially disrupt resting time. Other avian species also have been found to be responsive to boating activities, although effects appear to be habitat-specific (Knight and Knight 1984; Vos *et al.* 1985). We also found that the presence of terrestrial disturbance around the nesting area increased wing-raising and the proportion of time scanning, freezing, and sleeping, while decreasing the proportion of time sleeping. Similar types of short-term behavioral responses have been documented in this (Parsons and Burger 1982) and other bird species (e.g., Henson and Grant. 1991; Klein 1993; Fernández-Juricic and Tellería 2000).

Nestlings were sensitive to the type of recreationist behavior during the pedestrian experiments. Inquisitive walking simulated novice birdwatchers looking for birds or people trying to access the nesting site. Inquisitive walking generated the most negative responses, whereas normal walking generally caused intermediate responses. Fast walking generated the least disturbing responses probably because of shorter time that pedestrians remained in the areas around the nests. Thus, Black-crowned Night Heron nestling tolerance to pedestrian activity depends on movement speed and probably on visual contact with humans.

Some behavioral responses of nestlings (e.g., proportion of time scanning, freezing, sleeping, and walking, Figs. 2-3) to different pedestrian behaviors differed even when recreationists were absent from the area surrounding the nests. Furthermore, we detected a significant effect of the type of pedestrian behavior in other responses (e.g., standing-up rates), when pedestrians were not immediately present in the nesting area. One potential explanation for both of these counterintuitive effects is that animals maintained the level of response even in the intervals between two consecutive disturbance events. These daily temporal lags may have the potential of influencing the baseline level of response.

The increase in short-term avoidance responses to humans by nestlings can lessen time available for self-maintaining activities, which could potentially trigger sensitization (heightening of the responses after repeated disturbance events) or habituation effects (decrease in the strength of the responses with time). However, we did not find evidence clearly supporting either effect with an increase in the frequency of disturbance. Riffel *et al.* (1996) failed to find detectable cumulative effects of recreationists in forest bird communities exposed to disturbance over a five-year period. These results do not account for other variables (e.g., stress-related hormones) that may be more indicative of cumulative responses. For instance, hoatzin (*Opisthocomus hoazin*) juveniles show a greater corticosterone response in areas exposed to recreationists despite their less intense behavioral reaction (Müllner *et al.* 2004), suggesting that their previous frequent interactions with recreationists were perceived as stressful. Similar hormonal results were reported for Magellanic Penguins (*Spheniscus magellanicus*; Fowler 1999).

Nevertheless, some of the short-term responses of Black-crowned Night Herons might indirectly suggest habituation effects. As the season progressed, we found a decrease in the proportion of time moving and freezing, and in wing-raising and standing-up rates in relation to canoeing activities, and in standing-up rates in relation to pedestrian disturbance. Differences in responses between types of disturbance could have been the result of vegetation structure or nest success variations between different locations of the colony. Vegetation type and height were similar, although we found low levels of nest success in two of the ponds, as noted in the Methods. Other colonial species, such as Great Blue Herons (*Ardea herodias*), have been found to habituate to boating activities (Vos *et al.* 1985). A decrease in the level of flight reactions in areas exposed to higher levels of human-wildlife interactions has been interpreted as evidence of habituation (Keller 1989; van Heezik and Seddon 1990), which could reduce the perception of disturbance. However, the rates of habituation seem to vary substantially among individuals even within the same population (Runyan and Blumstein 2004); thus, understanding habituation for management purposes requires knowing the identity of individuals. Another explanation for the decrease in response with time in Black-crowned Night Herons could be the reduction in perceived risk of predation with age. In some species, tolerance to disturbance decreases when the susceptibility to natural predation increases (Müllner *et al.* 2004).

The effects of behavioral responses on stress hormone and eventually breeding success and reproduction in species breeding in colonies are not consistent across studies. Responses of Wood Storks (*Mycteria americana*) to tourist disturbance showed minor immediate behavioral modifications to the presence of close disturbance, but substantial changes in breeding success with increasing frequency of disturbance (Bouton *et al.* 2005). Müllner *et al.* (2004) found that the hormonal, rather than behavioral, responses were better associated with how changes in the presence of tourists affected hoatzin fledging survival. Our results show that short-term behavioral responses of Black-crowned Night Heron nestlings may not be a good predictor of medium-term responses, but the effects of distance to the source of disturbance may. Behavioral responses to pedestrians over the season were heightened as the distance to the pathway decreased, which may have increased the chances of nestlings acoustically or visually detecting humans, possibly causing changes in breeding success. More comprehensive studies on different species are needed following the behavior, stress hormone concentrations, and different measures of breeding success of individually marked animals in relation to varying frequency of disturbance, visitor group size, and recreationist behavior since responses to human disturbance appear to be species-specific (Blumstein *et al.* 2003).

Management Implications

Species management plans based only on individual-based studies have been criticized for over- or underestimating the negative effects of disturbance because observed behavioral responses may be biased by the availability of alternative habitats (Gill *et al.* 2001), perceived predation risk (Yasué 2006), and body condition of the study subjects (Stillman and Goss-Custard 2002; Beale and Monaghan 2005b). Such errors can lead to situations in which a population may be greatly affected by disturbance behaviorally, but without population size or reproductive success effects at the regional level (Finney *et al.* 2005). Nevertheless, studies based upon behavioral responses to human disturbance are valuable when predicting the probabilities of breeding patch use by species of local concern relative to different levels of human visitation. This is particularly important when the goal of managers is to provide opportunities for people to watch wildlife and their natural behavior (e.g., breeding activities) without disruption and/or abandonment of the breeding area.

Despite its widespread distribution, the Black-crowned Night Heron is protected under the US Migratory Act, and it is a species of conservation concern in some continental States (e.g., Michigan, Illinois, New Jersey, Florida, Pennsylvania, etc.) due to recent local population declines caused by habitat destruction, disturbance to colonies, and water pollution (Davis 1993). The case study we present was conducted in Calumet, Illinois, where the species is considered endangered. Our results can provide guidelines for the development of an area for human recreation in a way that is compatible with the persistence and success of local colonies of Black-crowned Night Herons. We recommend restricting boating activities during the initial part of the season to minimize nest abandonment. Pedestrians should be managed in such a way as to increase the distance between pathways and nests, particularly due to the responses of nestlings to inquisitive pedestrians. We also recommend a 50 m buffer zone around the colony based on the responses obtained in the Calumet colony. Frequency of disturbance does not appear to influence substantially the medium-term behavioral responses of nestlings, so restrictions on the number of visitors during the breeding period may not be necessary.

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