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INVESTIGATOR DISTURBANCE, CHICK MOVEMENT, AND AGGRESSIVE BEHAVIOR IN RING-BILLED GULLS

KEVIN M. BROWN[1,2] AND RALPH D. MORRIS[1]

ABSTRACT.—Infanticidal attacks on conspecific young can be a major cause of chick mortality in ground nesting colonial seabirds, and past studies have shown that investigator disturbance scatters chicks, subjecting them to attacks by neighbors. In 1991, we studied the effects of investigator disturbance on aggressive behavior and chick movement at a Ring-billed Gull (*Larus delawarensis*) colony near Port Colborne, Ontario. The frequency of charges, jabs, and wingpulls increased during the period of investigator activity in the colony, while the duration of wingpulls and beakpulls decreased. Few chicks (<5%) less than seven days of age strayed from their natal territories during disturbances; most chicks (≥85%) remained crouched on the natal territory. However, chick mobility increased with age, and older (>7days) chicks strayed off their natal territories and were attacked more frequently during disturbances than before disturbance. In contrast to Fetterolf (1983; Wilson Bull. 95:23–41) who found that investigator disturbance increased chick mortality and decreased fledging success, in our study, no chicks were fatally attacked during investigator disturbance and stray chicks returned to their natal territories quickly after disturbance. Furthermore, the mean (± 1 SD) fledging success of pairs disturbed during this study (1.5 ± 0.8 chicks per pair) was not different from that recorded for undisturbed pairs (1.6 ± 0.8). As our results vary somewhat from Fetterolf's, we contrast the two sets of data in the context of experimental procedures that yielded them. In this study, suitable hiding places and termination of investigator visits into the colony after the hatching period were attributed to preventing human-induced chick mortality. We show that awareness of and attention to the potential impacts of investigator activity can reduce and even eliminate the negative consequences associated with such activity. *Received 14 March 1994, accepted 22 Aug. 1994.*

Infanticide and non-fatal attacks on conspecific young are commonly reported in ground nesting seabirds, especially gulls (Hunt and Hunt 1975, Davis and Dunn 1976, Fetterolf 1983a, Pierotti and Murphy 1987, Pierotti 1991). Infanticide can be an important cause of chick mortality. Pierotti (1982) observed that 92 percent of Herring Gull (*Larus argentatus*) chick mortality at one site on Great Island, Newfoundland, was attributable to attacks by neighbors. This high level of infanticide was attributed to small territory size, and a few deaths were a result of investigator disturbance (Pierotti, pers. comm.). Similarly, Hunt and Hunt (1976) found that attacks by Glaucous-winged Gulls (*L. glaucescens*) accounted for at least 49 percent of the observed chick mortality. However, at other colonies, and other sites within colonies, infanticide is less frequent. At an adjacent

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[1] Dept. of Biological Sciences, Brock Univ., St. Catharines, Ontario, Canada L2S 3A1.
[2] Present address: Dept. of Biology, York Univ., North York, Ontario, Canada M3J 1P3.

site on Great Island, Pierotti (1982) observed that 92 of 95 dead Herring Gull chicks were killed by predatory Great Black-backed Gulls (*L. marinus*), while Graves and Whiten (1980) observed that only three of 27 attacks on trespassing Herring Gull chicks were fatal. Butler and Butler (1982), and Fetterolf (1984) found that chick survival was negatively correlated with aggression in Great Black-backed and Ring-billed gulls (*L. delawarensis*), respectively.

Although colonial seabirds are ideal for studies related to breeding success and behavior, chicks scatter into territories of neighboring pairs in response to human (investigator or other) disturbance and are frequently attacked (Robert and Ralph 1975, Anderson and Keith 1980, Safina and Burger 1983, Schoen and Morris 1984). Fetterolf (1983b) observed that infanticide in Ring-billed Gulls was rare under natural conditions; three of 1100 chicks (<0.3%) were killed by conspecific attacks at undisturbed colony sites. He suggested that human-induced chick mortality in past studies may have confounded theoretical interpretations of reproductive strategies involving terrestrial nesting colonial seabirds.

However, numerous other factors have also been shown to influence chick movement and aggression by adjacent adults, including the extent of nest cover, nesting density (Hunt and Hunt 1976, Fetterolf 1984, Pierotti and Bellrose 1986, Pierotti 1987, Watanuki 1988), and nesting synchrony (Fetterolf 1984, Reville 1988). Watanuki (1988) also found that the rate of cannibalism varied among three colonies of Slaty-backed Gulls (*L. schistisagus*) and may reflect differences in food supply and predatory habits. Furthermore, investigators usually design their experimental protocols and visitation schedules in order to minimize disturbance effects by terminating visits into seabird colonies once chicks become mobile (Parsons 1972, Fetterolf 1984, Hébert and Barclay 1986, Morris and Siderius 1990). The purpose of this paper is to report the influence of disturbance caused by our activities in a Ring-billed Gull colony on (1) the frequency and duration of aggressive behaviors by adults towards neighboring adults and chicks and (2) chick movement and behavior. Our results are contrasted with those reported by Fetterolf (1983b).

STUDY AREA AND METHODS

The study site was an artificial breakwall located 1 km off the north shore of Lake Erie and 1 km west of the Welland Ship Canal near Port Colborne, Ont (42°53′N, 79°16′W). Approximately 2500 pairs of Ring-billed Gulls and 150 pairs of Herring Gulls nested on a limestone rockpile adjacent to the west arm of the breakwall. On 2 April 1991, prior to egg laying, a study area (7 × 7 m) was marked and an observation blind erected 2–3 m from one edge of the study plot which allowed for maximum visibility of study area. Nest density was subsequently 1.2 nests/m^2.

The study area was visited daily during the egg-laying, incubation and hatching periods.

The colony was not entered during mid-day or rainy periods. Activities performed by an assistant on each visit included (1) marking new nests, (2) numbering, measuring, and weighing eggs, and (3) individually marking chicks. All chicks from peak clutches were dyed with Rhomadine B with respect to hatch order: a-chicks (first hatched) on the head, b-chicks (second hatched) on the breast, and c-chicks (third hatched) on the rump. In addition, chicks from twelve 3-chick broods were uniquely color-banded. In these twelve broods, a- and b-chicks hatched on the same day and c-chicks hatched up to 48 h later. Visits to the colony lasted 30–60 min and were terminated 31 May following the hatching of all eggs from peak 3-egg clutches. Every attempt was made to minimize disturbance effects. For example, we restrained chicks that attempted to run by covering them with a hand until they crouched, or we placed them in nearby cover while working in the immediate vicinity (see Rodgers and Burger 1981).

Data regarding the influence of investigator disturbance on adult and chick interactions were recorded from a blind by continuous scan sampling 30 min prior to, 30 min during, and for two consecutive 30-min periods after investigator disturbance by an assistant (hereafter referred to as before, during, after and after(2) disturbance, respectively). As peak feeding and other activities in Ring-billed Gull colonies usually occurs two to four hours following sunrise and prior to sunset (Haymes and Blokpoel 1978, Kirkham and Morris 1979), most observation periods began between 06:00 and 08:00 (N = 18), three prior to 10:00, and four prior to 12:00 EST.

Adult–adult interactions.—The frequencies of adult–adult aggressive interactions were recorded from 23 April to 29 May (N = 23 days) including charges, jabs, wing pulling, beak pulling, and fighting (two or more jabs exchanged by two adults). In addition, the duration of beakpulls and wingpulls during each time period was timed using a stop watch and recorded (secs).

On 2, 3, and 4 May, two investigators simultaneously recorded the frequency of aggressive acts in order to standardize the recording of behavior categories. On 10 May, the two observers independently and simultaneously recorded the frequencies of aggressive interactions at five-min intervals for 2 h to determine reliability of category recording.

Chick movement and adult–chick interactions.—Chick movement and adult–chick interactions were recorded daily throughout the hatching period (15–31 May 1991). Chick movement data included whether a chick was straying from or returning to its natal territory and age and brood rank of the mobile chick. Adult–chick interactions included the number and identity of chicks attacked, the number of adults attacking each chick, the number of pecks delivered per attack, the number of 'chick-shakes' (adult grasps and shakes chick), and location of chick attacks (on or off their natal territories). The physical condition (e.g., head lacerations, damaged limbs) of chicks was also recorded.

Chick behavior.—The behavior of 36 leg-banded chicks was recorded by point-sampling at two 15-min intervals before, during, and after disturbance on six days between 25–31 May. Chick behaviors were grouped into four categories: active on territory, inactive on territory, active off territory, and inactive off territory. Active chicks were standing, wandering, begging, or being fed. Inactive chicks were hiding, crouching, or being brooded. Chicks not observed at the time of point sampling were not included.

Frequency data were analyzed using several non-parametric statistical tests including Freidman rank tests, Wilcoxon sign-rank tests, Kruskal Wallace ANOVAs, and Mann-Whitney *U*-tests.

RESULTS

Reliability.—Nest density in the study area was high (1.2 nests/m^2), and aggressive interactions relatively frequent. Accordingly, to control for

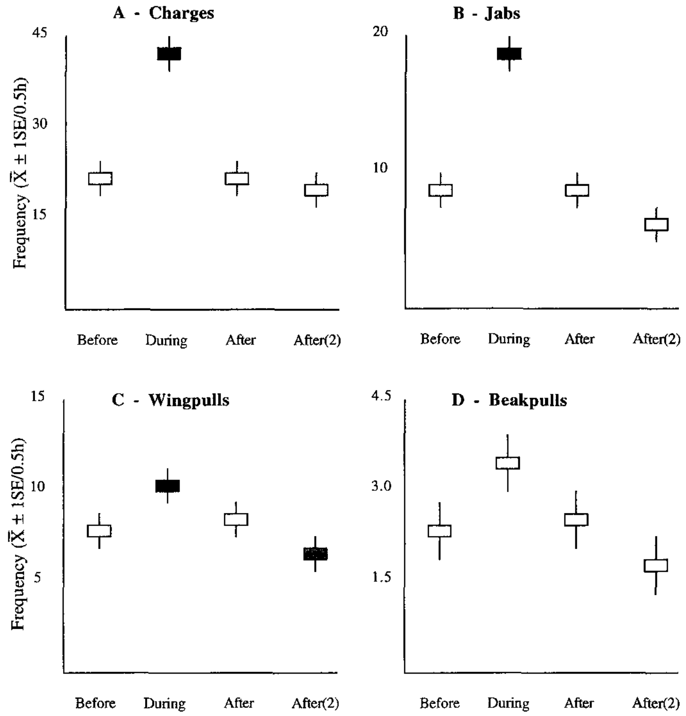

FIG. 1. The frequencies ($\bar{x}$ ± 1 SE/0.5 h, N = 23 per sampling category) of Ring-billed Gull aggressive interactions before, during, and two consecutive 0.5 h periods after (After and After2) investigator disturbance. A. Charges. B. Jabs. C. Wingpulls. D. Beakpulls. Different shades denote significance ($P < 0.05$) except wingpulls before vs after(2) ($P = 0.08$).

potential recorder error, adult behavior data were simultaneously collected by two independent observers at 5-min intervals over a 2 h period 10 May 1991. The Pearson correlation coefficient between observer one and observer two was 0.97, and $r^2 = 0.94$. Reliability was high; only 6% of the variation in the observed frequency of total aggressive interactions was due to error.

Adult–adult aggressive interactions.—The frequencies ($\bar{x} = 1$ SD) of charges, jabs, wingpulls, and beakpulls before, during and after investigator disturbance are shown in Fig. 1. There were significant differences in the frequencies of charges (Freidman rank test: $\chi^2 = 30.3$, df = 3, $P = 0.01$), jabs ($\chi^2 = 43.0$, df = 3, $P = 0.01$) and wingpulls ($\chi^2 = 15.8$, df = 3, $P = 0.01$) among the four sampling periods. Pairwise comparisons revealed that the frequencies of charges, jabs, and wingpulls were all significantly higher during disturbance than before disturbance and for

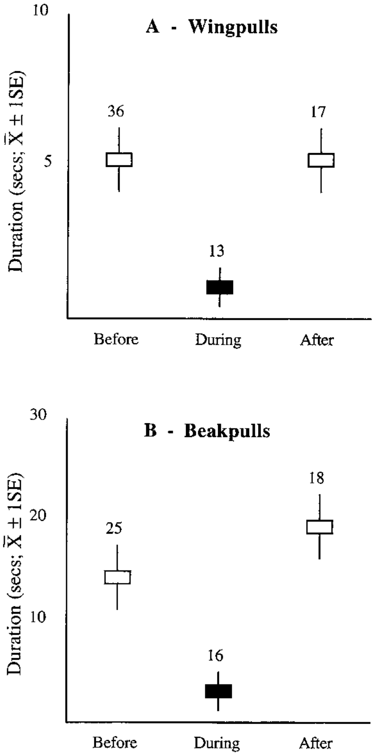

FIG. 2. The mean duration (secs; ± 1 SE) of wingpulls (A) and beakpulls (B) before, during and after investigator disturbance. Sample sizes are shown above bars. Different shades denote significance ($P < 0.05$).

both periods after disturbance (Wilcoxon sign rank tests; $P < 0.05$). Wingpulls were also more frequent during the first 30 min after disturbance than during the after(2) period ($Z = -2.3$, $P = 0.02$). Other pairwise comparisons were not significantly different ($P > 0.1$). The differences in the frequencies of beakpulls ($\chi^2 = 6.1$, df = 3, $P = 0.11$) and fights ($\chi^2 = 7.1$, df = 3, $P = 0.07$) among the four sampling periods approached significance. Fighting occurred infrequently in all time periods ($\bar{x} \pm 1$ SE frequency/0.5 h: before 0.2 ± 0.1, during 0.9 ± 0.2, after 0.5 ± 0.2, after[2] 0.3 ± 0.1).

There were also significant differences in the duration of wingpulls (H = 10.0, df = 2, $P < 0.01$) and beakpulls (Kruskal-Wallace ANOVA; H = 15.2, df = 2, $P < 0.01$) before, during, and after (after and after[2] pooled) disturbance (Fig. 2). Wingpulls were shorter during disturbance than before (Mann-Whitney: $Z = -3.1$, $N_1 = 36$, $N_2 = 13$, $P = 0.002$)

or after disturbance ($Z = -2.5$, $N_1 = 17$, $N_2 = 13$, $P = 0.0128$). The duration of beakpulls was also shorter during disturbance than before (Mann-Whitney *U*-test: $Z = -3.1$, $N_1 = 25$, $N_2 = 16$, $P = 0.0019$) or after ($Z = -3.5$, $N_1 = 18$, $N_2 = 16$, $P = 0.0004$). There were no differences in the duration of beakpulls ($P > 0.05$) or wingpulls ($P > 0.05$) before and after disturbance.

Chick movement and behavior.—Chick movement data and adult attacks on chicks were recorded from the onset of hatching (15 May) until all eggs from peak clutches had hatched (31 May). The first chick to stray from its natal territory was recorded on 21 May, and chick movement increased steadily thereafter until visits into the colony were terminated 31 May. Therefore, analysis of chick movement was restricted to data collected 21–31 May ($N = 10$ days); the number of chicks in the study plot ranged from 50 to 95.

There were significant differences in the numbers of chicks departing from their natal territories (Fig. 3A) among the four time periods (Freidman: $\chi^2 = 9.6$, $df = 3$, $P = 0.0219$). Pairwise comparisons revealed that significantly more chicks departed from their territories during disturbance than before (Wilcoxon sign-rank: $Z = -2.4$, $P = 0.0168$), after ($Z = -2.2$, $P = 0.0278$), and after(2) ($Z = -2.1$, $P = 0.0325$) disturbance. Other pairwise comparisons were not statistically different ($P > 0.05$). There were also significant differences in the numbers of chicks returning to their natal territories (Fig. 3B) among the four time periods (Friedman: $\chi^2 = 16.2$, $df = 3$, $P = 0.001$). More chicks returned after disturbance (usually within five min after the investigator returned to the blind) than before ($Z = -2.5$, $P = 0.0112$), during ($Z = -2.4$, $P = 0.0169$), and after(2) disturbance ($Z = -2.0$, $P = 0.0418$). In addition, more chicks returned during disturbance than before disturbance ($Z = -2.0$, $P = 0.0422$). Other pairwise comparisons were not statistically different ($P > 0.05$).

Although investigator disturbance increased chick movement, the proportion of chicks straying during disturbance was relatively low; range 2% (1 of 50 chicks, 21 May) to 17% (15 of 89 chicks, 29 May) per day (i.e., 30 min). Relatively few chicks (<5% per day) aged one to six days strayed from their territories during disturbance (Fig. 4). However, there was a steady increase in the percentage of chicks straying off their natal territories from age 7–13 days. In total, over the 10-day period, 53 chicks strayed from their natal territories during investigator disturbance and all but one returned within 24 h. This chick was missing and presumed dead.

Point sampling also revealed that more chicks were off their natal territories during investigator disturbance (3 × 2 contingency table: $\chi^2 = 13.69$, $df = 2$, $P < 0.005$) even though the number of stray chicks was

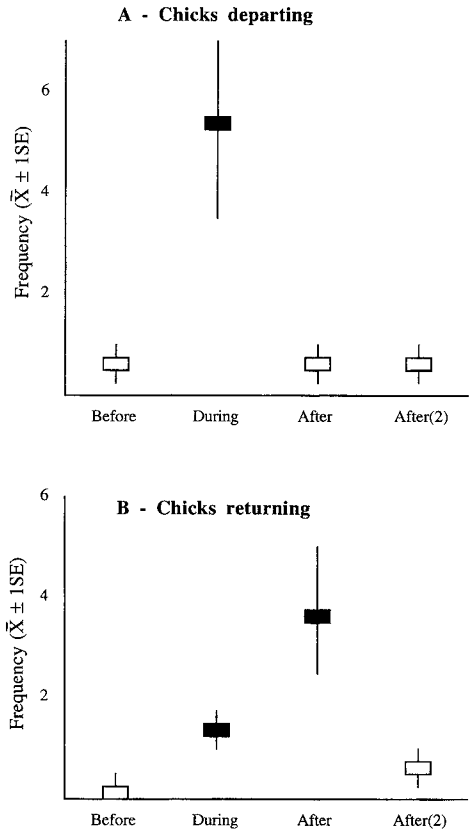

FIG. 3. The mean number (± 1 SE/0.5 h, N = 10 per sampling category) of Ring-billed Gull chicks departing from (A) and returning to (B) their natal territories before, during and two consecutive 0.5 h periods after investigator disturbance. Different shades denote significance ($P < 0.05$) except chicks returning during vs after(2) ($P > 0.1$).

low; overall, 91% of the chicks observed during disturbance were on their natal territory (Table 1). Chicks were also less active during disturbance (13%) than before (42%) and after (50%) disturbance ($\chi^2 = 110.66$, df = 2, $P < 0.01$).

Adult–chick interactions.—There were significant differences in the number of chicks attacked among the four time periods (Fig. 5: Freidman rank test; $\chi^2 = 9.2$, df = 3, $P < 0.05$). Data represent the number of individual chicks attacked (i.e., a chick attacked more than once in a sampling period was scored once). Significantly more chicks were attacked during disturbance than before (Wilcoxon sign rank test: $Z = -2.2$, $P < 0.05$) and after(2) disturbance ($Z = -2.1$, $P < 0.05$). The difference

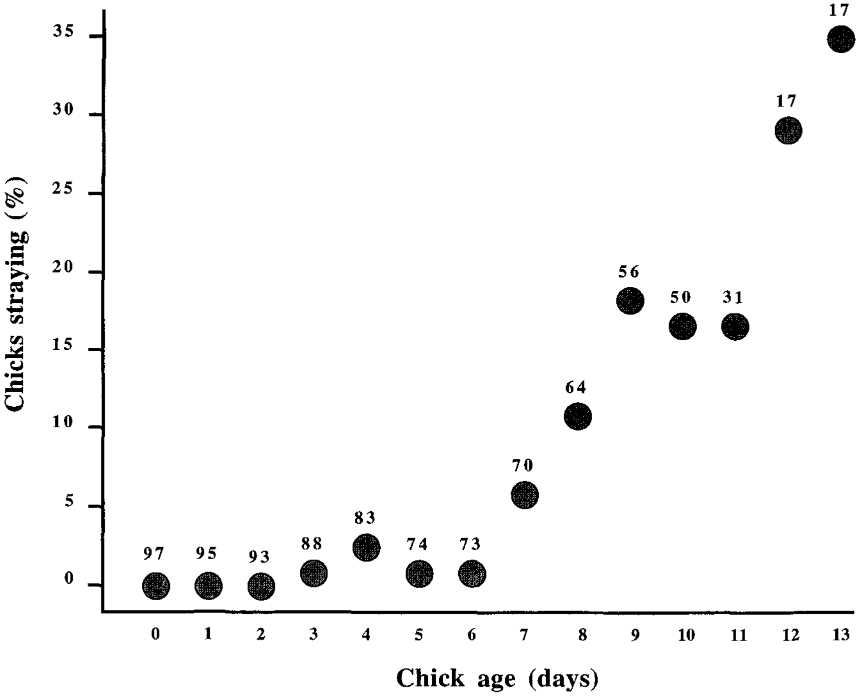

FIG. 4. The proportion of each age class of Ring-billed Gull chicks straying off their natal territories during investigator disturbance. The number above the circle represents the number of chicks in each age class.

between the number of chicks attacked during disturbance and the first 30 min after disturbance approached significance ($Z = -1.8$, $P = 0.07$). Other pairwise comparisons were not significant (before vs after $P = 0.1$, after vs after(2) $P = 0.1$, before vs after(2) $P > 0.1$). Although investigator disturbance increased the number of chicks attacks, the relative number attacked was low and none of the attacks observed during or after disturbance was fatal.

DISCUSSION

Many of our results can be compared with an earlier study by Fetterolf (1983b) that led to his claim that investigator disturbance confounded data from studies in which disturbance was not controlled. As our results vary somewhat from his, we contrast the two sets of data in the context of experimental procedures that yielded them.

As the investigator moved from nest to nest, adults scurried across

TABLE 1

THE NUMBER OF ACTIVE AND INACTIVE RING-BILLED GULL CHICKS ON OR OFF THEIR NATAL TERRITORIES BEFORE, DURING AND AFTER INVESTIGATOR DISTURBANCE

	Chicks on territory		Chicks off territory	
Disturbance period	Active[a] N (%)	Inactive[b] N (%)	Active[a] N (%)	Inactive[b] N (%)
Before	92 (41)[c]	131 (58)	3 (1)	0 (0)
During	15 (6)	203 (85)	17 (7)	3 (1)
After	115 (49)	113 (48)	3 (1)	6 (3)

[a] Active chicks were standing, wandering, begging, or being fed.

[b] Inactive chicks were hiding, crouching, or being brooded.

[c] The percent of the total is shown in parentheses.

territorial boundaries, facilitating aggression from the resident pairs towards intruding adults. Not surprisingly, we found that investigator disturbance increased the number of aggressive interactions among adults; charging and jabbing the beak at intruders increased two-fold during disturbance. Fetterolf (1983b) found that investigator disturbance increased the level of adult aggression approximately 10–15 times that observed prior to disturbance. We observed that slow movement by the investigator through the colony decreased the number of displaced adults, and localized disturbance effects into the immediate vicinity (1 or 2 m) of the investigator. Our assistant visited each nest once in a systematic fashion, usually checking several nests before moving, and returned to the blind when the nest check was complete (usually 30–60 min). This procedure

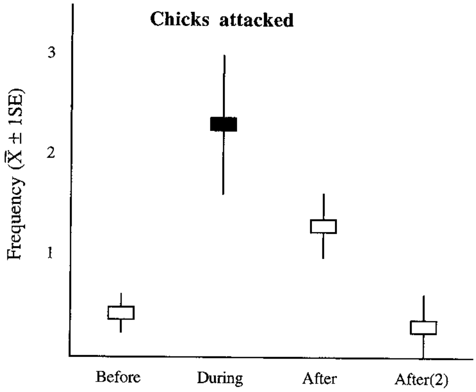

FIG. 5. The mean number (1 SE/0.5 h, N = 10 per sampling category) of Ring-billed Gull chicks attacked by adults before, during and two consecutive 0.5 h periods after investigator disturbance. Different shades denote significance ($P < 0.05$).

localized and minimized disturbance effects to the area within the study plot in which the investigator was working, usually displacing adults from their nests once per visit. In contrast, Fetterolf's assistant walked the perimeter of his 'moderately' disturbed plot spraying chicks with a weak picric acid solution from a plant mister which likely caused considerable disturbance in the adjacent, 'most' disturbed study area as well. We found that the duration of wingpulls and beakpulls decreased during investigator disturbance and that physical contests rarely escalated into a prolonged fight. This may have been because displaced gulls were not motivated to fight, behaved submissively and returned quickly to their own territories.

When an intruder enters a colony, chicks have two behavior options; they can hide or they can run. Like Fetterolf (1983b), we found that investigator disturbance increased chick movement. However, in contrast to Fetterolf, we found that relatively few chicks strayed off their natal territories during disturbance and that all but one returned after disturbance. Most chicks were inactive during disturbance and hid in the natal territory; chicks were frequently observed crouching in the same crevice as they did during non-disturbance times. The difference in the magnitude of chick displacement between our study and Fetterolf's (400–600 fold increase) may reflect differences in 1) the availability of nest cover between the two colonies, 2) the disturbance protocol, 3) nest density, and 4) the sampling method (also see Brown and Morris 1994). We consider these in turn.

First, the Mugg's Island Lake Ontario colony studied by Fetterolf was a sand bar with little vegetation or cover, whereas our colony was located on a rockpile that provided an abundance of rocky crevices in which chicks could hide. Graves et al. (1984) also noted that chicks ran more frequently when cover was sparse. Therefore, the abundance of suitable hiding places in close proximity to their natal territory may influence whether a chick runs or hides during disturbances. Second, we found that chick movement increased with age, so we stopped entering the study area once hatching was complete (31 May) and chicks were marked. This eliminated disturbance effects when chicks were older and more mobile. Although some chicks (N = 5) in the study area were 14 days old and fully mobile (Fig. 4), the procedures used in this study reduced problems associated with disturbance. Conversely, Fetterolf continued to disturb his gulls until the youngest chick was seven days old while chicks hatching earlier would have been 28–38 days old. Third, nest density has been found to increase the frequency of aggressive interactions among conspecifics (Hunt and Hunt 1976, Fetterolf 1984, Pierotti and Bellrose 1986). In 1991, nest density in our study plot (1.2 nests/m^2) was greater than that recorded in Fetterolf's plots (range: 0.5–0.7 nests/m^2) and so cannot account for the lower levels of aggression recorded during this study.

Finally, sampling methodologies differed between the two studies. We recorded the movements of individual chicks and were able to determine whether chicks were departing from or returning to their natal territories. In contrast, Fetterolf recorded chick runs where a new run was scored if the chick paused for five or more seconds. The latter method is somewhat misleading and overestimates chick movement because five chick runs may be five different chicks running once each or one chick running five times. In our study, chicks that strayed were usually older than one week, ran less than 1 m off their territory, and crouched in nearby cover. Parsons (1982) also observed Herring Gull chicks from "open" nests hiding in nearby vegetation during nest checks. Graves et al. (1984) observed that older chicks would run, rather than hide, during disturbances. Similarly, Burger (1981) found that Herring Gull chicks that were frequently handled responded to investigators by straying farther from their nests, and ran at a younger age, than chicks not previously handled. We also noticed that picking chicks up to check leg bands and dye spots increased the likelihood that these chicks would run after being returned to the nest. Therefore, we reduced chick movement by avoiding unnecessary handling of chicks and by placing handled chicks head first into a rock crevice near the nest scrape (see Rodgers and Burger 1981).

Although the differences in chick movement between our study and Fetterolf's are of interest, the fate of mobile chicks after departure by the investigator has more important consequences for their welfare. In both studies, investigator disturbance increased the number of individual chicks attacked (this study) and the frequency of attacks on chicks (Fetterolf 1983b). In this study, chicks that remained on territory and those that strayed short distances were rarely attacked because their immediate neighbors were also displaced from their territories. However, chicks that strayed greater distances were frequently attacked, occasionally by numerous adults. In contrast to Fetterolf who reported that his activities within the colony led to human-induced chick mortality, we found that, even though our activities increased chick movement and adult aggression towards wandering chicks, none of the attacks on chicks during or after disturbance was fatal. We observed that the chicks attacked were usually older than one week and more resilient to attacks, and that they were able to return to the safety of their own territory or find cover until attacks subsided. Finally, we found that the fledging success of pairs disturbed during this study ($\bar{x}$ ± 1 SD: 1.5 ± 0.8 chicks per pair) was not different from that recorded for undisturbed pairs (1.6 ± 0.8) at this colony during 1991 (see Brown and Morris 1994).

There are many types of human disturbances in seabird colonies (Rodgers and Burger 1981) and the responses by the birds are varied (Burger 1981, Brown and Morris 1994). We have shown here that awareness of and attention to the potential impacts can reduce and even eliminate the negative consequences associated with investigator disturbance. Since many variables influence the degree to which colonial waterbirds are impacted by human disturbances including species, colony type, and location (Rodgers and Burger, 1981), we suggest that it is the ethical responsibility of every field biologist to investigate the potential consequences of experimental protocols on the individual animals and to use procedures that minimize disturbance effects.

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