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DOES INVESTIGATOR DISTURBANCE NEGATIVELY IMPACT PRODUCTIVITY?
AN EXPERIMENTAL STUDY IN BREEDING RING-BILLED GULLS
(*LARUS DELAWARENSIS*)

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Abstract

Understanding responses of waterbirds to investigator disturbance is essential for minimizing any adverse effects of research while maximizing data collection to inform management decisions. It has been suggested that while some behavioral effects may be observed, disturbance is only likely to be problematic if it alters survival or productivity, and habituation may minimize negative effects by increasing tolerance. In 2008, we undertook an experimental study of the effects of disturbance from monitoring activities on the survival of ring-billed gull (*Larus delawarensis*) chicks at a large, undisturbed colony in Lake Ontario. Throughout the chick-rearing period, we banded and recaptured chicks in six, approximately 40 m^2 fenced plots, each containing 21-25 nests. To separate potential disturbance effects from differences in data quality, plots were grouped into three areas that differed in intensity of investigator disturbance (visits near-daily, every six days, and once every two weeks) but not all plots were monitored on every visit. Survival was analyzed in a live-dead, multistate mark-recapture model that allowed us to focus only on prefledging survival and include dead recoveries. As plots differed in their monitoring frequency, we repeated the analyses three times using data subsampled from plots. Data quality (recapture probability) was much higher for nests checked near-daily but we found no evidence that this level of monitoring negatively impacted chick survival and nest productivity. We also found no difference in data quality between plots monitored every six days and those checked every two weeks. Our results indicate that ring-billed gulls at this site readily habituate to near-daily monitoring protocols with no adverse impacts on chick survival and that these protocols offer the best trade-off between investigator disturbance and data quality.

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Introduction

Understanding responses of waterbirds to investigator disturbance (disturbance caused by research activities) is essential to minimize any adverse effects of research while maximizing data collection and to inform management and conservation decisions. Studies of colonial waterbirds have made significant contributions to the general body of literature in ecology (Furness and Monaghan 1987, Hamer et al. 2002), however, research of the impacts of disturbance caused by researchers or other human factors on waterbirds have reported conflicting results (Anderson and Keith 1980, Brown and Morris 1994, 1995). Some studies suggest considerable negative effects of disturbance on breeding success (Carney and Sydeman 1999), such as nest abandonment, lowered hatching success, and lowered fledging success, while others have suggested little to no effect (Nisbet 2000).

The disparities between studies are often caused by whether the studies are measuring behavioral effects, such as flushing or attacking, or impacts on survival or reproductive success. It has been argued that disturbance is only a problem if it negatively affects survival or productivity (Nisbet 2000) as behavioral effects are temporary and thus ultimately unimportant evolutionarily. Research focusing on indirect effects of human disturbance has suggested that stress or reduced chick growth resulting from disturbance could negatively impact survival (Fowler 1999, Albores-Barajas et al. 2009), but has not measured differences in survival or reproductive output. Some research has found differences in behavior or physiology due to human disturbance, such as lowered nest attendance (Baudains and Lloyd 2007, Weston and Elgar 2007) and increased heart rate (Ellenberg et al. 2006), but it was not clear if these changes led to lowered productivity. Several studies have shown no effect of investigator disturbance on

breeding success (Davis and Parsons 1991, Blanco et al. 1999, Shealer and Haverland 2000), but many studies did not examine the behavioral or survival effects of investigator visits during the entire prefledging period (e.g., Brown and Morris 1994, Shealer and Haverland 2000, Ellenberg et al. 2006). Since disturbance rarely leads to mortality in adult waterbirds, breeding endpoints are the most important concern when making conservation or management decisions regarding investigator disturbance, and the focus should be on preventing fitness reductions, not behavioral responses (Yasue 2006).

The negative effects of disturbance have been shown to vary by species, with some species, such as brown pelicans (*Pelecanus occidentalis*), Atlantic puffins (*Fratercula arctica*) and Humboldt penguins (*Spheniscus humboldti*), suffering at low levels of human disturbance (Anderson and Keith 1980, Rodway et al. 1996, Ellenberg et al. 2006). Studies in other seabirds, such as terns and gulls, have reported that disturbance can have little impact (Brown and Morris 1994, Shealer and Haverland 2000, Nisbet 2000). However, adverse effects of disturbance have also been documented for these species (see Carney and Sydeman 1999) and there is currently disagreement over how much disturbance is tolerated (Carney and Sydeman 1999, Nisbet 2000). Such differences can be due to life history effects. For example, long-lived seabirds, such as albatrosses and petrels, are more likely to abandon nests when disturbance makes breeding conditions unfavorable since reproduction is costly and they have more breeding attempts in a lifetime (Blackmer et al. 2004).

The effects of disturbance can also depend on the type of activities performed by the researchers or other human intruders. More intrusive activities, such as radio-tagging, are likely to have a greater effect on survival than simply walking through nesting areas or banding chicks (Sharpe et al. 2009). The effects of disturbance on reproductive success can also vary depending

on whether birds are able to re-nest (Blackmer et al. 2004). Re-nesting can help increase the productivity of a colony after desertions, but at a cost of additional resources and during less than optimal environmental conditions (Arnold et al. 2004).

The timing of investigator visits can also influence the effects of disturbance. Waterbirds may exhibit more sensitivity to human disturbance and are more likely to abandon nests if disturbed earlier in the nesting period (Vennesland 2010) as the fitness value of the clutch increases with time (Shealer and Haverland 2000, Bolduc and Guillemette 2003). Alternatively, it is possible that familiarity with human intrusions when first nesting may mitigate these effects by increasing tolerance and leading to habituation (Blackmer et al. 2004). It is also possible that human disturbance can lead to lower nest site fidelity, for example in Leach's storm-petrels or ring-billed gulls (Conover and Miller 1979, Blackmer et al. 2004), which could negatively impact lifetime reproductive success if it results in lower mate fidelity (Blackmer et al. 2004).

Concern over potential impacts of disturbances to waterbirds may result in avoidance of important research that could guide management and conservation decisions (Nisbet and Paul 2004). However, several studies of waterbirds suggest that (with appropriately designed studies) birds can habituate to investigator disturbance so that impacts are minimized (Nisbet 2000). The objective of this study is to determine the impacts of disturbance caused by different intensities of monitoring for ring-billed gulls (*Larus delawarensis)* at a colony in Lake Ontario, Canada. Ring-billed gulls were chosen as a study species because they are of low conservation importance (Ryder 1993), but are expected to have responses similar to many other colonially nesting waterbirds, especially other gulls and terns, which may be of higher conservation concern. Gulls and terns are both thought to habituate to human disturbance (Nisbet 2000). Previous work has shown no effect of investigator disturbance during incubation and hatching

periods on hatching or fledging success of ring-billed gulls (Brown and Morris 1994, 1995).

However, the effects of investigator disturbance on survival of ring-billed gull chicks have been

mixed, with Fetterolf (1983) showing adverse effects but Brown and Morris (1994, 1995) finding

no effect. These differences could be due to different methodological approaches.

I developed a novel mark-recapture analysis using results from a field experiment that

exposed ring-billed gulls in study plots to different monitoring and disturbance frequencies

during the chick-rearing period. The model developed allowed separate estimates of survival

and recapture probabilities across study plots for chicks from hatching to fledging. I hypothesize

that chick survival (and therefore productivity) will be higher in study plots with high

disturbance intensity and that data quality (indexed by the probability of recapturing individual

chicks) will be greater in plots monitored most frequently.

Methods

Study Species

Ring-billed gulls are a species of colonially breeding waterbird that nest in the Great Lakes region, as well as Northern portions of the United States and much of Canada (Ryder 1993). In the lower Great Lakes, adults breed from mid-April until early-July. They nest on the ground, close to the water in low lying islands containing light or woody vegetation (Ryder 1993). Nests are constructed from nearby dead plant material. Hatching usually occurs from late May to early June (Ryder 1993). Clutch size varies from two to four eggs, with a mode of three (Ryder 1993). Young fledge around 36-37 days after hatching (Ryder 1993). The average productivity per breeding pair is 1.96 chicks fledged per nest (mode of clutch size (Ryder 1993) × mean % survival to fledging in the Great Lakes ; Blokpoel and Tessier (1986)).

Experimental Methods

The fieldwork was performed at Gull Island, Presqu'ile Provincial Park, Ontario, Canada (43°59'N, 77°45'W) from May to June 2008 (late-incubation through chick rearing). Six experimental plots, each containing 21-25 ring-billed gull nests (mean area ± SD: $37.5 ± 4.3$ m^2), were enclosed with 2 ft high, plastic, poultry fence prior to peak egg-hatching. Nests were marked with individually numbered wooden stakes on the first visit. This allowed us to note which chicks hatched from which nest and determine hatching order. The monitored area was divided into six plots that differed in intensity of investigator disturbance (visits ~ 1 day, every 6 days, and once every 2 weeks) and in monitoring frequency (not all plots were monitored on every visit; Fig. 1). For instance, the HH plot was visited near-daily and monitored every visit, while the HL plot was visited near-daily but only monitored every two weeks. Even though some plots were not monitored at every visit, the disturbance caused by monitoring activities was

mimicked on each visit. It was not always possible for monitoring frequencies to occur exactly every six days or every two weeks but efforts were made to remain close to this monitoring schedule. Each plot was named by its disturbance treatment (H, M, or L signifying high, medium and low) followed by its monitoring frequency (H, M, or L). Using this system, the six plots were designated HH, HM, HL, MM, ML, and LL.

All chicks were banded at hatching with standard hard metal bands and recaptured (or recovered, if dead) during every visit when monitoring was performed, until fledging. The study was conducted during the first year of research on the island to minimize effects of previous experience with humans since it has been suggested that the negative effects of disturbance are greater for birds that are naive to disturbance (Blackmer et al. 2004).
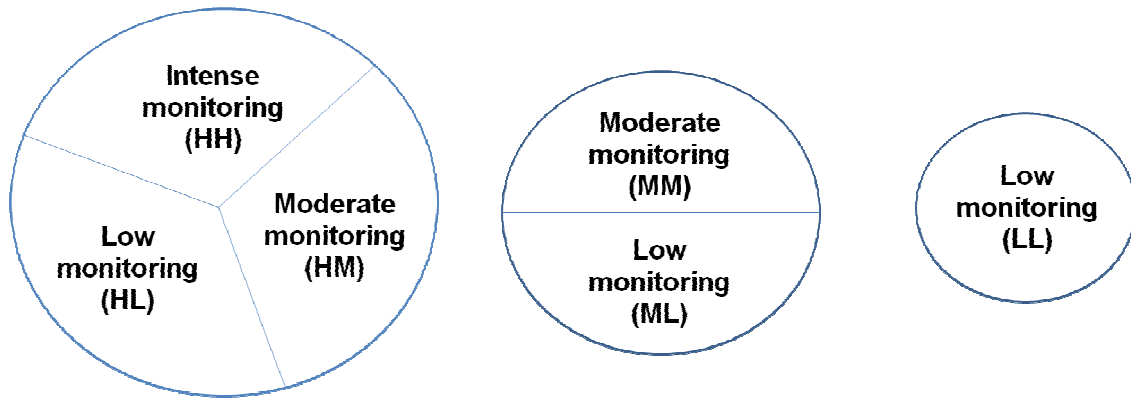

Figure 1. Schematic representation of the six experimental plots. Plots were separated into three areas of different visitation (disturbance) frequency: near daily, every 6 days, and every 12 days. These areas were separated by > 50m. Within the areas, not all plots were monitored on all visits, giving varying monitoring intensities: near daily, every 6 days, and every 12 days. Plots are labeled using two letters, the first indicating intensity of disturbance (high, medium, or low) and the second being frequency of monitoring. Our hypotheses (see text) were Survival: HH=HM=HL>MM=ML>LL and Recapture: HH>HM=MM>HL=ML=LL.

Analytical Methods

Multi-state live-dead models (Lebreton et al. 1999) were used to test two hypotheses. Our hypotheses were that highly-disturbed plots would have similar survival, which would be greater than medium or low disturbed plots, and the high monitored plot would have the best data quality, followed by medium monitored plots, with low monitored plots having the lowest data quality (Survival: HH=HM=HL>MM=ML>LL; Recapture: HH>HM=MM>HL=ML=LL). We predicted that chicks in plots that were disturbed more frequently would habituate to human presence and therefore have higher survival than those in less frequently disturbed plots. Similarly, we predicted that plots that were monitored more frequently would have better data quality since there would be more time intervals to analyze and investigators were able to anticipate where the chicks hide within each plot.

Due to unequal time intervals from different monitoring protocols for different plots (Fig. 1), three subsets of the data were used in separate analyses: HH plot only (29 recapture intervals); HH, HM, MM plots combined (10 intervals), and all plots combined (5 intervals). A total of 269 chicks were included in the All Plots analysis, with 143 chicks in the HH, HM, MM Plots analysis, and 49 chicks in the HH Plot only. All our multi-state, live-dead models used two states: pre-fledging and fledging, but we only investigated hypotheses for pre-fledged chicks. Thus, covariates were only used for the prefledged state. All models required chick age for probability of recovery and fledging since we fixed the transition probability from non-fledging to fledging state at age of 30 days, as a conservative estimate (Ryder 1993), since the date of fledging could not be reliably determined for the majority of chicks. Transition probability of moving from the fledging to pre-fledging state was fixed at 0 since it is impossible for a fledged chick to revert back to being pre-fledged. The individual covariates included for prefledged

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states were chick age, hatching order (A, B or C to represent first, second, and third hatched siblings, or unknown) and nest-specific hatch date (i.e. the hatching date of the A-chick from a nest; used as an index of parental quality; e.g. Arnold et al. 2004). For chicks that were in infrequently monitored plots, chick age was determined from their mass at banding using a regression equation based on masses of a subset of known age chicks (between 0-16 days old). The regression equation was: age (d)= -1.621 + 0.066 * mass (g); ($F_{1,96}$ = 1465, P<0.0001, R^2 = 0.94).

During modeling of each of the three data subsets, the most general model incorporated time-dependent plot effects for survival and recapture and plot effects for recoveries, for prefledged chicks (Table 1). For hypothesis testing, the general model was based on the hypothesis that survival would differ between plots of different disturbance frequency (see plot hypotheses above), especially during weather events (e.g. storms) and later in the season, and that survival would be higher for older chicks, A-chicks (first born of each nest), and chicks hatched from better quality parents. Recapture was hypothesized to show differences between plots caused by different monitoring over time, as well as to be lower for younger chicks and later in the season (due to small chicks being harder to find in the higher vegetation). Recovery was hypothesized to be lower for younger chicks in low disturbance plots.

Recapture and recovery GOF tests were performed for each of the three data subsets, using the most general model in each case, with the program U-CARE (Choquet et al. 2005). During GOF testing, data were stratified for groups based on both hatching order and plot. Since some of the groups contained few individuals (e.g. C chicks in the LL plot), tests were also run on each data set with no chick order or plot groupings (shown in results).

Table 1. Most general model used as a start for model selection. Notation is t = time period, order = hatching order, hatch = nest hatch date, M = state (prefledged or fledged). State transition from fledging to prefledging is fixed to 0. Covariates were not modeled for fledged chicks.

Parameter	Model Components	Underlying Hypothesis
Survival	t*plot + t*age + t*order+ t*hatch	Differs between plots, especially during weather events and late in the season, higher for older chicks, A-chicks and chicks from better quality parents (indexed by hatching date: hatch)
Recapture	t*plot*age +M*t + M*age	Plots with different monitoring frequencies are different, lower for younger chicks and late in the season, higher for older prefledged chicks
State Transition (Prefledging to Fledging)	age	Only dependent on reaching 30 d of age.
Recovery	plot +age + M	Lower for young chicks in low disturbance plots

Model selection used Akaike Information Criterion for small sample sizes (AIC$_c$) (Burham and Anderson 2002) to determine the minimum applicable model for the HH Plot (the plot with the most recapture intervals). This model then was used to inform model reduction for the other data subsets. Covariates for the HH, HM, MM Plots and All Plots analysis were fixed based on those in the best model for the HH Plot. This was done since the HH Plot data had the most intervals and therefore gave the best discrimination. Thus, only plot-dependency of recapture, recovery, and survival were determined through model selection in the other two datasets. AIC$_c$ was used for this model selection within the All Plots and HH, HM, MM Plots data subsets. Competing models with different time periods for survival were developed using *a priori* knowledge of potentially important weather events, such as extreme temperatures (Ryder 1993) or intense rain storms (J.M. Arnold pers. comm.), and by combining intervals where

survival estimates were similar. For the HH Plot analysis, the first five and last six time intervals were fixed at 0.975 (the mean estimate across all time periods) since there were not enough individuals present to accurately estimate the parameters. In the HH, HM, MM Plot analysis, the first and last time intervals were similarly fixed at 0.977, and in the All Plots analysis, the last time interval was fixed at 0.981. For recapture, competing models with different time intervals for recapture were generated based on *a priori* estimation of the effect of adverse weather on recapture effort. These intervals were different than those used for survival as adverse weather impacts survival and reproduction in different ways.

Results

Recapture and recovery GOF tests for the three datasets indicated that our data fitted the assumptions of multi-state live-dead models, but there were significant deviations for 3G.SM test for the HH, HM, MM and All Plots data subsets (Table 2). The 3G.SM test is a composite test that examines three different hypotheses on the effects of marking and state. Differences in the probability of moving to fledged state between previously-marked and newly-marked birds were not significant when there were many recapture periods (HH only) because few birds fledged between each time period. By retaining covariates and time periods from the HH only model, we avoid GOF problems for the datasets with fewer intervals. All the other assumptions were upheld, and therefore the model suited our analytical needs.

Table 2. Separate goodness of fit (GOF) results from U-CARE for the three datasets (HH; HH, HM, MM; ALL), each run separately as live recaptures (Recaptures) and dead recoveries (Recoveries). Results are shown from models without chick order or plot groupings. 3G.SM is a composite test for effect of marking and state; 3G.SR is a test of transience; M.ITEC tests for immediate effect of banding; M.LTEC tests for differences caused by absenteeism; Fit for AS indicates whether data are suitable for multi-state (Arnason-Schwarz) model. In all cases significance (*<0.05, ***<0.001) indicates a violation of the underlying assumptions of the test.

		HH Only	HH, HM, MM	All Plots
Model Component	Test Component			
Recaptures	3G.SM	10.42 (16)	**15.92 (6)***	**46.12 (2)***
	3G.SR	5.61 (6)	8.17 (7)	2.50 (3)
	M ITEC	6.68 (7)	0.35 (2)	N/A (-)
	M LTEC	2.00 (1)	<0.01 (1)	N/A (-)
	Fit for AS	24.71 (30)	24.44 (16)	**48.62 (5)***
Recoveries	M ITEC	<0.01 (3)	1.66 (1)	0.47 (2)
	M LTEC	5.78 (3)	1.88 (1)	<0.01 (1)
	Fit for AS	5.78 (6)	3.53 (2)	0.47 (3)

Mean recapture probability varied between 0.895 (SE: 0.059) and 0.971 (SE: 0.001), and mean survival probability varied between 0.939 (SE: 0.031) and 0.973 (SE: 0.015) in the

different plots. Recapture probability was highest for chicks in the HH plot (Fig 2b), but survival was not significantly different for chicks since plot was absent from the best models (Fig 2a) when using data from every other week (Table 3) or weekly (Table 4).

In the final HH only models, survival probabilities were different for two different time periods, as well as the fixed parameter for the first 5 and last 6 intervals. The one time period included 5/ 26-27, 30-31, 6/ 1-5, 11-12, and 6/ 29 to 7/ 1 (time intervals 7, 10-12, 14, and 22), which experienced lower survival probabilities than the other time period.

Survival decreased with hatching date and hatching order (Table 5). The best models for the All Plots and HH, HM, MM data sets, however, did not include hatching order since it was not possible to determine hatching order for many of the chicks during 6-day or two-week visits, and so it was dropped from the most general model in those datasets. Nest hatching date was still retained.
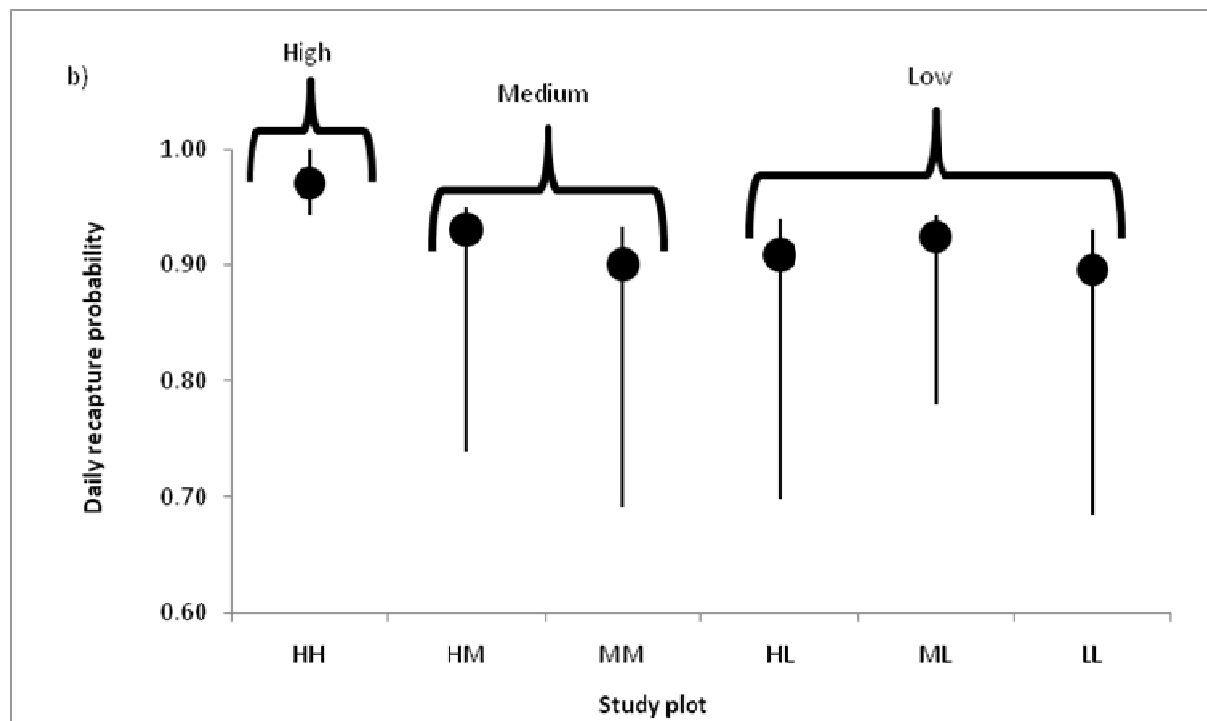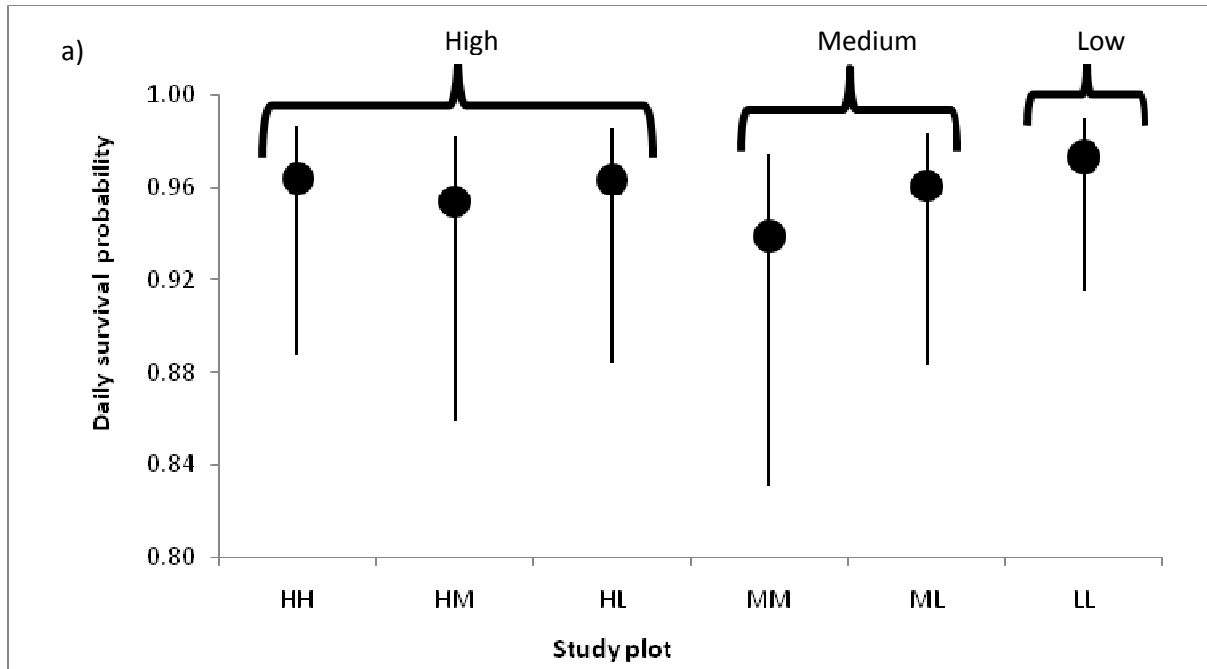
Figure 2. Differences in (a) survival and (b) recapture between the six study plots. Plots are arranged according to our hypotheses, and data are estimates and 95% CI from best live-dead multistate models for the All Plots dataset. The best model indicated no difference in survival but a higher recapture probability for the HH plot. For x-axis label definitions see text.

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Table 3. Best 5 models for All Plots dataset. There were no differences in survival between plots, but recapture was higher in the HH plot. Best model AICc = 896. HYPOTHESIS = the 6 plots grouped in to 3 groups, as per our hypotheses (see text) OTHERS = all other plots have same parameter.

Survival Parameters	Recapture Parameters	Number of Parameters	AIC weight	ΔAIC	Model Likelihood
S(time(5), hatch date)	P(plot [HH, OTHERS])	13	0.38	0.0	1.00
S(time(5), hatch date)	P(plot [HYPOTHESIS])	14	0.16	1.8	0.41
S(time(5), hatch date, plot [HH, OTHERS])	P(plot [HH, OTHERS])	14	0.14	2.0	0.37
S(time(5), hatch date, plot [HYPOTHESIS])	P(plot [HYPOTHESIS])	16	0.101	2.7	0.26
S(time(5), hatch date, plot [HYPOTHESIS])		14	0.04	4.3	0.12

Table 4. Ranked top 5 models for the HH, HM, MM Plots data set. There were no plot differences in survival, with recapture being higher in the HH plot compared to the HM and MM plots. Best model AICc = 978. ALL = all plots have different estimates; HYPOTHESIS = plots differ in parameter according to hypotheses (see text).

Survival Parameters	Recapture Parameters	Number of Parameters	AIC weight	ΔAIC	Model Likelihood
S(time(5), hatch date)	P(plot [HYPOTHESIS])	13	0.18	0.0	1.00
S(time(5), hatch date, plot [ALL])	P(plot [HYPOTHESIS])	15	0.14	0.5	0.79
S(time(5), hatch date)	P(plot [ALL])	14	0.08	1.7	0.44
S(time(5), hatch date, plot [HH, OTHERS])	P(plot [HYPOTHESIS])	14	0.07	1.8	0.42
S(time(5), hatch date, plot [HYPOTHESIS])	P(plot [HYPOTHESIS])	14	0.07	1.8	0.41

Table 5. Best 4 models for HH Plot data set. There were only three time periods that differed in survival and four for recapture. Time(#) indicates the number of time intervals in the model. Covariates entered were chick age, hatching order, and hatch date of the oldest sibling (nest hatch date). Best model AICc = 702.

Survival Parameters	Recapture Parameters	Number of Parameters	AIC weight	ΔAIC	Model Likelihood
time(3), hatch date, hatching order	time(4)	12	0.42	0.0	1.00
time(3), hatch date	time(4)	11	0.28	0.9	0.65
time(3), hatch date, hatching order, age	time(4)	13	0.16	1.9	0.39
time(3), hatch date, hatching order, age	time(5)	14	0.06	4.0	0.13

Discussion

We found no impact of investigator disturbance on survival of pre-fledged ring-billed gull chicks. Survival probabilities ranged from 0.939 (SE: 0.031) to 0.973 (SE: 0.015), with none of the best models showing differences in survival between plots. These results agree with previous studies that have shown no significant effect of disturbance on gulls during other parts of the breeding season and terns (Brown and Morris 1994, Shealer and Haverland 2000). They expand on the studies conducted by Brown and Morris (1994, 1995) as we monitored and disturbed chicks through fledging, instead of just through the hatching period, with no adverse productivity effects. This may be because chicks had already habituated to human presence by the time they became mobile. Our results contrast with the study conducted by Fetterolf (1983), which found that fledging success of ring-billed gull chicks decreased with increased disturbance. This difference may have been due to methodological differences (e.g. use of fences which limited chicks running far enough away to get lost or adopted).

Using a mark-recapture analysis to estimate survival potentially allowed for more accurate estimates of survival in plots visited less frequently (Cooch and White 2011). In addition, this analysis was able to account for differences in data quality that result from different frequencies of monitoring. These previous studies had different disturbance regimes but did not control for differential data quality caused by less frequent monitoring, which could also cause underestimation of chick survival.

The GOF testing initially showed some deviations in the 3G.SM test. This is a composite test that looks at three hypotheses relating to marking and state. The first assumption is that there is no difference in time or state of first reencounter between newly marked and previously marked animals seen again at least once. The second assumption is that there is no difference in

reencounter probabilities between individuals seen on an occasion in a particular state that has previously been encountered, based on state of most recent encounter. Finally, the third assumption is that there are no differences in timing of first reencounter between individuals in a certain state at occasion that have been previously encountered and will be encountered next in a different state. If these hypotheses are rejected, then the data does not fit the assumptions of multi-state live-dead models (Choquet et al. 2005). As we designated 30 days as fledging age, birds caught previously were more likely to enter the fledging state in the next time period than those that were newly marked. This was an issue in the All Plots and HH, HM, MM data sets but was resolved in the HH Plot data set, which had more time intervals and only a few birds fledged between each time period. Since covariates and time periods were retained from the HH Plot analysis, we avoided GOF problems for the datasets with fewer intervals.

Our results indicated that prefledged chick survival was reduced during certain time intervals (intervals 7, 10-12, 14 and 22). This may have been due to a major storm event that occurred on 5/31 (during interval 10) that likely lowered chick survival. Additional precipitation occurred on 6/3 and 6/5, which may have contributed to the lower survival during intervals 11 and 12. On 5/26 and 6/28-29 (intervals 7 and 22) precipitation also occurred. The amount of precipitation was large at the end of June, but less so on 5/26. However, since the end of May is the early part of the hatching season, the chicks would have been younger and more likely to become hypothermic once soaked during these moderate rain events thereby suffering survival effects. No weather events directly correlate with interval 14 (6/11-12), therefore it could be related to a predation event.

It had been suggested that vegetative cover could affect the survival of chicks during a disturbance, as chicks are able to hide in response to disturbance, rather than running into the

territory of other adults that will kill chicks that are not their own (Brown and Morris 1994, 1995). To reduce the effects of this confounding factor, we attempted to choose sites with similar vegetative properties at initial laying. Since the transition from prefledging to fledging state was fixed as occurring at 30 days, it is possible that survival may have been overestimated. Ring-billed gull chicks normally fledge at approximately 36-37 days (Ryder 1993), and some chicks that we considered fledged may have died between 30 days and actual fledging age. However, highest mortality and disappearance rates of chicks occur during their first week (Ryder 1993), and we expect mortality rates after 30 days to be low. Additionally, by conservatively estimating fledging age, we avoid underestimating survival in lower monitored plots where it is more likely that fledged chicks could be mistakenly categorized as dead.

Survival of ring-billed gull chicks also decreased with both hatching date and hatching order. Seasonal declines in productivity have been widely observed (Moreno 1998, Arnold et al. 2004) and more experienced ring-billed gulls normally lay their eggs earlier than younger birds (Ryder 1993), which may explain the correlation between hatching date and survival of chicks. In the HH plot, where hatching order could be sufficiently determined, A and B chicks from the same nest had similar survival, but C chicks had lower survival. This agrees with previous studies of three-chick brood colonial waterbirds (Hamer et al. 2002).

Ring-billed gulls may abandon an area to move away from disturbance, either by deserting nests or avoiding an area that was disturbed in subsequent years (Conover and Miller 1978), however, this effect is not seen in other similar species (Wendeln and Becker 1999). We also did not have nest desertions during the course of our study. It is possible the disturbance could lead to abandonment of the nesting area in the next breeding year, but previous work has indicated that nest site tenacity and breeding success may be unrelated in ring-billed gulls

(Kovacs and Ryder 1981), and it is unlikely that the disturbance would affect breeding success in subsequent years.

It has been suggested that habituation may reduce negative effects by increasing tolerance levels (Nisbet 2000). Some studies have asserted that habituation may have occurred (Baudains and Lloyd 2007, Martinez-Abrain 2008), but the terminology is often misused in the literature, with studies usually describing differences in tolerance levels, not habituation (Bejder et al. 2009).   Tolerance has been defined as "the intensity of disturbance that an individual tolerates without responding in a defined way" (Nisbet 2000 p. 315). Habituation refers to a reduced response resulting from repeated stimulation which is not followed by reinforcement or caused by fatigue or sensory adaption (Nisbet 2000, Ellenberg et al. 2009). To effectively demonstrate that habituation has occurred, the same animals must be followed over a period of time and other explanatory scenarios should be excluded. For instance, less tolerant members of a population leaving the disturbed area or exhibiting a dampened physiological response could both appear as reduced responses to disturbance, yet neither are accomplished through learning (Bejder et al. 2009). Both of those scenarios produce detrimental effects even though they may outwardly appear to be beneficial due to reduced responses. Outcomes that are truly neutral or beneficial for the animals from a fitness perspective would be seen only with actual habituation and not through other mechanisms (Bejder et al. 2009).

Our results suggest that in our study ring-billed gulls may have habituated to investigator disturbance. Monitoring began on the same date in all the plots, and the birds were naive to investigator disturbance prior to this study. In all plots, the chicks hatched during the disturbance regimes and so had no differential prior tolerances to the disturbance. Within each plot, the same individuals were followed from hatching to fledging, and no differences in

survival were found between disturbance treatments, suggesting that the chicks in the more frequently monitored plot became more tolerant of human presence over time and true habituation occurred (Bejder et al. 2009). Alternatively, it is possible that naive ring-billed gulls and their chicks may be naturally tolerant of this type of human disturbance, but this is unlikely as changes in behavior were observed during the experiment, and previous studies have shown that the gulls react behaviorally to disturbance (Fetterolf 1983, Brown and Morris 1995). Future work analyzing the behavioral and physiological responses of adults in this study is planned to corroborate that habituation, not just tolerance, is occurring (Nisbet 2000, Bejder et al. 2009).

In our study, near daily monitoring allowed a greater probability of recapture, thus increasing data quality by reducing the chance of mis-categorizing fledged chicks as dead. Although mark-recapture analyses are designed for recapture rates less than 100%, problems occur if recapture rates are particularly low (Lebreton et al. 1992). The HH plot had highest recapture rates because we knew where to find individual chicks and could always associate them with their nest. Thus, even though mark-recapture can use recapture rates of less than 100%, the error around estimates will generally be larger for plots visited less frequently. No differences in recapture were found between datasets from weekly monitoring visits and visits made every other week, suggesting that if daily monitoring is not feasible then the extra effort needed for weekly visits provides little return.

Our results suggest that ground-nesting gulls and possibly other colonial nesting waterbirds (particularly terns) can readily habituate to near-daily monitoring protocols with no adverse impacts on chick survival as suggested by Nisbet (2000). They also indicate that near-daily monitoring protocols offer the best trade-off between investigator disturbance and data quality. Even so, other species of waterbirds may have different levels of tolerance, e.g., brown

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pelicans (Anderson and Keith 1980), depending on their life-histories or proximity to humans throughout time. Effects of disturbance can also vary by site (Anderson and Keith 1980, Sachs and Jodice 2009) due to complex environmental factors, such as prey availability or quality of habitat that influences fitness decisions or previous experience with humans (Blackmer et al. 2004). Therefore, even though our results indicate that investigator disturbance resulting from monitoring has no adverse effect on ring-billed gulls, conservation and management decisions regarding monitoring and research should be made on an individual basis according to both species and location (e.g. Nisbet and Paul 2004).

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