NESTING DENSITY IS AN IMPORTANT FACTOR AFFECTING CHICK GROWTH AND SURVIVAL IN THE HERRING GULL

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Abstract. The causes and consequences of coloniality in seabirds, and larids in particular, have received extensive study. Here, we use the Herring Gull (*Larus argentatus*) as a model organism to investigate the effect of nest density on chicks' growth rate and survival. On Appledore Island, Maine, Herring Gulls nest both in dense subcolonies and in more isolated situations, affording a unique opportunity for comparison of reproductive success of pairs nesting in both contexts on the same island. Chicks reared in dense subcolonies grew at a rate significantly higher than that of those reared in more isolated settings. Using mark–recapture analysis, we found that a chick's expected survival is dependent on hatch weight, hatch date, hatch order, and context (nest in dense or loose subcolony). The first chick to hatch in each nest had a significantly greater probability of surviving to fledging than the last-hatched chick. Last-hatched chicks had a significantly greater chance of survival from hatching to fledging if they were hatched and reared in the dense subcolony than in the loose subcolony. Further research is required to distinguish among the effects of parents' quality and age (and thus their ability to defend young and provide food), agonistic behavioral interactions, and proximity to nesting Great Black-backed Gulls (*L. marinus*, the main predator of Herring Gull chicks), on these differences. Our results suggest that pairs nesting in dense subcolonies benefit through chicks' greater growth rate and survival, possibly due to increased vigilance or greater access to food.

Key words: *breeding biology, chick survival, Herring Gull, mark–recapture analysis, nesting density, colonial breeding.*

La Densidad de Anidación es un Factor Importante que Afecta el Crecimiento de los Pichones y la Supervivencia en *Larus argentatus*

Resumen. Las causas y consecuencias de la vida colonial en las aves marinas, y en los laridos en particular, han sido estudiadas en profundidad. Aquí, usamos a *Larus argentatus* como un organismo modelo para investigar los efectos de la densidad de nidos en la tasa de crecimiento y supervivencia de los pichones. En la Isla Appledore, Maine, *L. argentatus* anida en sub-colonias densas y en situaciones más aisladas, proveyendo una oportunidad única para comparar el éxito reproductivo de parejas que anidan en ambos contextos en la misma isla. Los pichones criados en las sub-colonias densas crecieron a una tasa significativamente más alta que los criados en contextos más aislados. Usando análisis de marcado y recaptura, encontramos que la supervivencia esperada de un pichón depende del peso al momento de la eclosión, de la fecha de eclosión, del orden de eclosión y del contexto (nido en sub-colonias densas o esparcidas). El primer pichón en eclosionar en cada nido tuvo una probabilidad significativamente mayor de supervivencia hasta volantón que el último pichón eclosionado. Los últimos pichones eclosionados tuvieron una oportunidad significativamente mayor de supervivencia desde la eclosión hasta volantón si eclosionaron y fueron criados en la sub-colonia densa que en la sub-colonia esparcida. Se requieren investigaciones adicionales para distinguir entre los efectos de la calidad y edad de los padres (y por ende de su habilidad para defender a los jóvenes y brindar alimento), las interacciones agonísticas de comportamiento y la proximidad a los sitios de anidación de *L. marinus* (el depredador principal de los pichones de *L. argentatus*), en estas diferencias. Nuestros resultados sugieren que las parejas que anidan en sub-colonias densas se benefician de mayores tasas de crecimiento y supervivencia de los pichones, posiblemente debido a una mayor vigilancia o a un mayor acceso al alimento.

INTRODUCTION

Colonial breeding of gulls and other seabirds has been well studied from the perspectives of cost–benefit and net reproductive fitness (Ellis and Good 2006, Ashbrook et al. 2008).

Two of the main benefits of colonial nesting are thought to be group predator defense and increased foraging success through sharing of information, in which colonies act as information centers from which less successful birds follow others to feeding sites (Götmark 1990, Hernandez-Matias et al.

2003). Numerous hypotheses have been put forth to explain why colonial nesting might also be disadvantageous, including misdirected parental care (Beecher 1988), increased disease transmission due to the close proximity of other nesting conspecifics (Clancy et al. 2006), and intraspecific predation by other individuals in the colony (Hunt and Hunt 1976, Watanuki 1988). In these cases, however, the benefits of nesting colonially are thought to outweigh the costs, thereby allowing coloniality in seabirds to evolve and be conserved (Ashbrook et al. 2008).

In larids, it has been demonstrated that higher-quality individuals initiate laying earlier, produce larger eggs, have larger clutches, and have greater hatching success (Pierotti 1982, Kilpi 1995, Wendeln 1997). Clutch and egg size can be viewed as measures of reproductive effort or investment in reproduction (Bolton 1991, Borboroglu and Yorio 2004). The Herring Gull (*Larus argentatus*) is an asynchronously hatching species that lays two or three eggs per clutch, three more commonly than two (Pierotti and Good 1994). Hatch order has been shown to influence survival in *Larus* chicks, survival of the third chick (C) being much less than that of the first two chicks (A and B; Graves et al. 1984, Hario and Rudbaeck 1999, Lif et al. 2005).

Gulls generally nest colonially in single-species colonies or in mixed colonies of other seabirds, primarily on offshore islands devoid of terrestrial predators (Götmark 1982, Pierotti and Good 1994). In the Herring Gull, coloniality appears to be facultative, as birds nest in either dense subcolonies or in more isolated contexts (Pierotti and Good 1994). This variation allows for comparison of the fitness costs and benefits associated with different degrees of coloniality within a single species.

Appledore Island, Maine, supports hundreds of nesting Herring and Great Black-backed Gulls (*L. marinus*). Within the large colony of Appledore Island, there is a gradation of nesting habitats and nest densities (McGill-Harelstad 1985, Ellis and Good 2006). There are very dense aggregations of nests ("dense subcolony" context) as well as individuals that nest in relative isolation from other conspecifics and congeners ("loose subcolony" context).

Within colonies, habitat selection and distance to nearest conspecific neighbor are important factors predicting the growth rate and fledging success of Herring Gull chicks (Pierotti 1982). Chicks in denser colonies generally have higher growth rates and fledging success (Pierotti 1982), but the rate of chick growth rate has never been quantified in a colony with as stark a difference in nest densities as we see on Appledore Island, and chick survival has never been examined in relation to nest density in a mark–recapture framework.

The objective of this study was to quantify the advantages of coloniality in a bird whose nesting colonially is facultative, the Herring Gull. To test for differences in the species' reproductive output in different contexts, we first compared egg and clutch size of birds nesting in dense and loose subcolonies. Second, we compared the growth rate and estimated survival of chicks hatched in the two contexts.

We predicted that gulls nesting in the dense subcolony should have higher-quality (larger) eggs, larger clutches, greater hatching success, chicks hatching heavier, and first chicks hatching earlier than birds nesting in the loose subcolony. Furthermore, we predicted greater growth rates for chicks hatched and reared in dense subcolonies than for those hatched and reared in the loose subcolony and a positive correlation between survival of chicks and nest density. Finally, we predicted that survival of third chicks, from hatching to fledging, in the dense subcolony should be significantly greater than that of chicks in the loose subcolony because the third chick's survival is inherently more variable than that of the first two chicks.

METHODS

STUDY SITE

Appledore Island, Maine (42° 58′ N, 70° 37′ W), is located in the Isles of Shoals, a 9-island archipelago approximately 10 km from the coast of New Hampshire. Herring Gulls have nested on Appledore Island since the turn of the 20th century, and Herring Gulls and Great Black-backed Gulls have nested together on Appledore Island since the 1940s (Ellis and Good 2006). The population of Herring Gulls peaked in the mid-1970s and has declined steadily since then (Borror and Holmes 1990). In the past 5 years, the population has remained fairly stable at approximately 650 breeding pairs (J. C. Ellis, unpubl. data.).

REPRODUCTIVE SUCCESS AND GROWTH RATES

In the summer of 2009, we randomly selected 60 focal nests during the incubation stage. Thirty of these nests were relatively isolated from other nesting gulls (mean distance of closest three neighboring nests 19.5 ± 1.4 m [SE], range 7.8–45 m, the "loose subcolony" context). The other 30 nests were located in relatively dense subcolonies (mean distance of closest three neighboring nests 4.2 ± 0.2 m, range 1.8–7. 3 m, the "dense subcolony" context). Nests selected in the loose subcolony were in a variety of locations: in or under shrubs, along paths, and near buildings and other structures, and under porches. Nests in the dense subcolony were located on the relatively exposed, rocky periphery of the island. We labeled the nests and recorded the maximum width, length, and mass of each egg on the first visit.

We checked each focal nest daily between 06:00 and 12:00 and recorded its contents. On the day of hatching (day 1), we designated each chick A, B, or C in the order it hatched and colored a small portion of its underside with a permanent marker for individual identification. Each chick was weighed to the nearest 0.5 g with a 300-g Pesola scale. The exposed

culmen and head + bill length were measured with calipers to the nearest 0.1 mm. We used these measures because they are good descriptors of overall size in the Herring Gull (Coulson et al. 1983, Bogdanova and Nager 2008). To generate growth curves, we remeasured each chick on days 3, 5, 7, and 9. After day 9, the chicks became too mobile to catch and measure, and further measurement increased the risk of chicks moving between nests and artificially inflating chick mortality. We monitored survival of each chick daily from hatching through first flight (day 35–40). After its first flight, we considered a chick fledged and departed from the nest site and did not monitor its subsequent survival.

STATISTICAL ANALYSIS

To test for potential differences between productivity of pairs nesting in dense subcolonies and those nesting in more isolated locations, we compared clutch size, egg size, hatch weight, and hatching date in the two contexts. We tested for differences in clutch size with a Poisson-distributed model in PROC GLIMMIX in SAS (SAS Institute 2003). To test for differences in egg size, we compared an estimate of egg volume, calculated as maximum length × maximum width^2 (Hipfner and Gaston 1999), for the two contexts with a mixed linear model (PROC MIXED) with nest number as a random effect because we measured multiple eggs in each nest. Similarly, we tested for differences in the weight of chicks at hatching while controlling for position in the hatch order by using nest as a random variable and by including an interaction between nest context (dense or loose subcolony) and weight at hatching. Because all eggs hatched in the month of June, we used day since June 1 as the response variable when testing the influence of nest context on hatch date. We designated hatch date as the date when the first egg in a clutch hatched. We used generalized linear mixed models to test for differences in growth rates over time, where the response variables were weight, culmen length, and head + bill length. Explanatory variables included the influence of nest context (categorical: dense or loose subcolony) and chick age (categorical: 1, 3, 5, 7, or 9 days). We set chick identity as a random variable in all models because chicks we measured repeatedly over time. We tested for normality of residuals with PROC UNIVARIATE; no data transformations were required. All analyses were run in SAS version 9.1.3. Significance was defined at $\alpha = 0.05$. All values presented under Results are means ± SE, unless otherwise indicated.

Our initial observations indicated that the availability of cover in the dense and loose subcolonies differed widely. The loose subcolonies had more cover (e.g., vegetation, man-made structures) than the dense subcolonies, which might create differences in detectability. Therefore, we used a mark–recapture approach, using program MARK (White and Burnham 1999), to assess differences in reproductive success between the contexts. This approach has been used in previous studies of survival rates and reproductive success and has revealed outcomes different from those suggested by studies based on traditional analyses (Nichols et al. 1998, White and Burnham 1999, MacKenzie et al. 2002). Mark–recapture models account for variation in detectability among different groups (in this case different nest densities) and help equilibrate survival estimates between chicks hatched in the dense and loose subcolonies. To normalize the encounter histories and make them the same length for each chick, every encounter history began on 4 June, the date the first chick in the sample hatched, and continued daily until 10 July ($n = 37$ days). To test the influence of nest density, hatch weight, and hatch date on chick survival, each encounter history included several covariates: nest context (categorical), hatch weight (continuous), and hatch date (continuous).

Because order in which a chick hatches influences survival in species hatching asynchronously (Graves et al. 1984, Pierotti and Bellrose 1986, Hario and Rudbaeck 1999, Lif et al. 2005), we analyzed each position in the order (A, B, or C) separately. For each position, we tested a set of 15 candidate models, including all combinations of the covariates of interest (Table 1). From this model set, we ran the MARK analyses to determine which factor (or factors) had the greatest influence on chick survival. Because Julian hatch date is a time-varying covariate, we did not test any fully time-dependent models (Cooch and White 2007). We ranked approximating models by the Akaike information criterion, corrected for sample size (AIC$_c$; White and Burnham 1999). In cases of more than one competing model (ΔAIC < 2), we used a model-averaging function to generate survival estimates (Φ).

RESULTS

During this study, we monitored 168 total eggs and 137 chicks belonging to 60 nests from hatching to fledging. Comparison of nest contents in the dense and loose subcolonies revealed no significant differences in clutch size, egg volume, hatching success, or hatch dates (Table 2). Mean weights of chicks at hatching differed according to position in the hatch order, with first chicks being largest (A, 66.19 ± 0.89 g; B, 64.13 ± 0.74 g; C, 59.45 ± 1.09 g, $F_{2,79} = 16.29$; $P < 0.001$), but it did not differ by whether the nest was in a dense or loose subcolony (Table 2). These measures are typical of similar studies of the Herring Gull (Pierotti 1982, Götmark 1982, Risch and Rohwer 2000).

Chicks from the dense subcolony gained more weight in the first 9 days after hatching than did chicks from the loose subcolony ($F_{1,406} = 66.67$, $P < 0.001$, Fig. 1A). On day 9, the mean weight of a chick from the dense subcolony (210.39 ± 4.32 g) was 49.61 g (31%) greater than that of a chick from the loose subcolony (160.78 ± 6.97 g). Similarly, rates of growth of the culmen of chicks from the dense subcolony were greater than those of chicks from the loose subcolony

TABLE 1.   Models and model-selection results for chick survival, by order of hatching (chick A, B, or C). Only results of models with the greatest support (ΔAIC $\leq$ 2) are shown. The following models were included in all chick-survival analyses, but are not presented in the table because they had little support in the data (ΔAIC $\geq$ 2): Φ(group + Julian) p(.); Φ(group + weight)p(.); Φ(group + weight + Julian)p(.); Φ(group + weight + Julian)p(group); Φ(weight)p(group); Φ(weight + Julian)p(.).

Order of chick	Model[a]	K	ΔAIC	Weight	Deviance
First (A)	Φ(.)p(.)	2	0.0[b]	0.23	176.6
	Φ(weight)p(.)	3	0.8	0.16	175.4
	Φ(group)p(.)	3	1.5	0.11	176.0
	Φ(Julian)p(.)	3	2.0	0.08	176.6
Second (B)	Φ(Julian)p(group)	4	0.0[c]	0.19	233.4
	Φ(.)p(.)	2	1.0	0.11	238.6
	Φ(weight + Julian) p(group)	5	1.9	0.07	233.2
Third (C)	Φ(group)p(group)	4	0.0[d]	0.39	121.0
	Φ(group)p(.)	3	2.0	0.14	123.1
	Φ(group + Julian) p(group)	5	2.0	0.14	120.9
	Φ(group + weight) p(group)	5	2.0	0.14	120.9

[a]Models test for the influence of nest context (group), hatch weight (weight), and date (Julian).

[b]AIC_c = 180.6.

[c]AIC_c = 241.6.

[d]AIC_c = 127.3.

(Fig. 1B; day 9 $\bar{x}_{\text{dense subcolony}}$ = 24.76 $\pm$ 0.32 mm, $\bar{x}_{\text{loose subcolony}}$ = 23.41 $\pm$ 0.33 mm; $F_{1,406}$ = 20.94, $P < 0.001$). The rate of growth of head + bill was also greater for chicks from the dense subcolony, but this result was not statistically significant (Fig. 1C; day 9 $\bar{x}_{\text{dense subcolony}}$ = 65.14 $\pm$ 0.46 mm, $\bar{x}_{\text{loose subcolony}}$ = 62.96 $\pm$ 0.62mm; $F_{1,406}$ = 3.64, $P = 0.06$).

Of the 137 chicks that hatched, 60 (44%) died by day 20. The first (A) chick to hatch in each nest had a distinctly greater probability of surviving to fledging (Φ = 0.59 $\pm$ 0.10) than the last (C) chick (Φ = 0.19 $\pm$ 0.22). Model-selection results indicated that mortality in the two contexts of nesting was not evenly distributed (Table 1). For the A and B chicks, models receiving the greatest support did not always have group (nest context) in the Φ parameter; in fact, the null model was among the top set of models for both the A and B chicks. Conversely, for the C chicks, the top eight models (with >99% of the total probability) had a group effect in the Φ parameter, indicating that nest context had a marked effect on the expected survival

TABLE 2.   Measures of investment in reproductive effort, hatch dates, and hatching success for Herring Gulls nesting in loose and dense subcolonies on Appledore Island, Maine.

	Loose subcolony (n = 30)		Dense subcolony (n = 30)		F	P
	Average	SE	Average	SE		
Clutch size	2.83	0.069	2.77	0.092	0.02	0.88
Egg volume[a]	55.89	0.27	55.49	0.27	1.14	0.29
Hatch weight	64.01	0.846	63.67	0.698	0.05	0.82
Hatch date	11 Jun	0.798	12 Jun	0.841	1.06	0.31
Number hatched	2.37	0.148	2.2	0.194	0.12	0.73

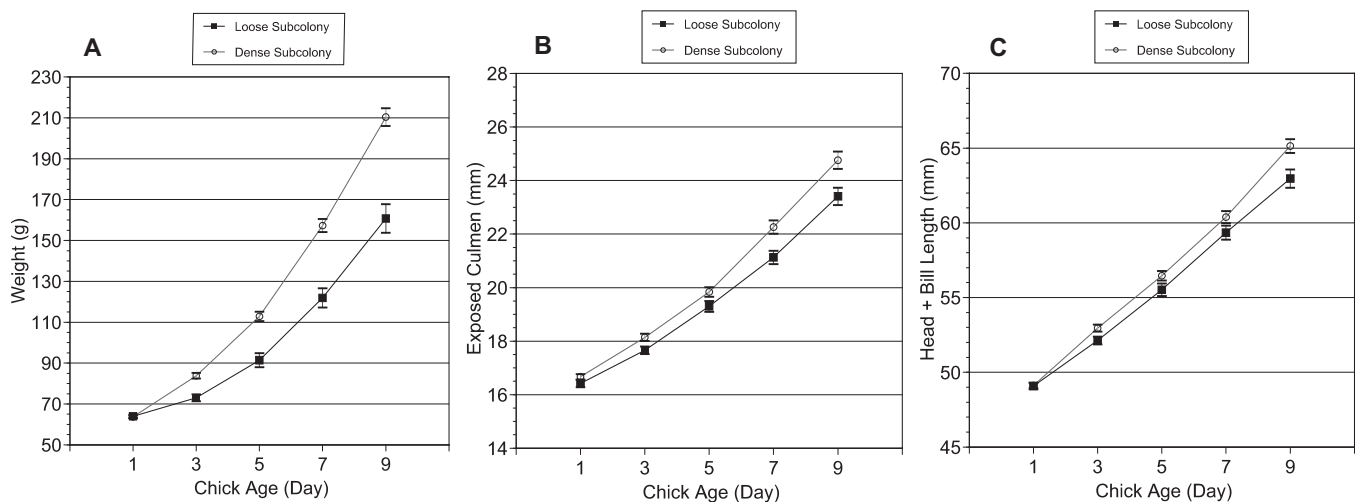[a]Calculated as maximum length $\times$ maximum width^2.

FIGURE 1.   Rates of growth of Herring Gull chicks reared in loose and dense subcolonies on Appledore Island, Maine. (A) Changes in weight over time ($F_{1,406}$ = 66.67, $P < 0.001$). (B) Changes in length of exposed culmen over time ($F_{1,406}$ = 20.94, $P < 0.001$). (C) Changes in length of head + bill measurements over time ($F_{1,406}$ = 3.64, $P = 0.06$).

of the C chicks. Although the probabilities of survival of A and B chicks were similar in the two contexts, in the dense subcolony C chicks were far more likely to survive to fledging ($\Phi = 0.50 \pm 0.22$) than those in the loose subcolony ($\Phi = 0.02 \pm 0.25$, Fig. 2). The number of C chicks hatched in the dense ($n = 16$) and loose ($n = 15$) subcolonies was almost identical, but survival in the two contexts differed greatly (10 and 2, respectively).

DISCUSSION

Colonial nesting is a widespread strategy with numerous potential drawbacks (Watanuki 1988, Tella et al. 2001, Clancy et al. 2006, Varela et al. 2007) and benefits (Götmark 1990, Hernandez-Matias et al. 2003, Antolos et al. 2006, Ashbrook et al. 2008). To be conserved, however, this strategy must allow birds nesting in colonies to contribute more offspring to future generations than birds nesting in a more solitary context. Indeed, we confirmed that chicks hatched in a dense colony grew faster and that third chicks had a greater probability of surviving to fledging in dense subcolonies than did third chicks hatched in more isolated situations on the same island. This pattern may seem counterintuitive because the chicks born and reared in the loose subcolonies had more cover (e.g., vegetation, man-made structures) in which to hide from potential predators. Nevertheless, our MARK analysis indicated that individuals nesting in the dense subcolony had greater reproductive success than conspecifics nesting in the loose subcolony.

   At each age interval (days 1, 3, 5, 7 and 9), chicks from dense subcolonies weighed more, on average, than those from loose subcolonies. The gap in average chick weight increased with each successive interval (Fig. 1A). A chick's growth rate can be used as a proxy for its success at fledging and long-term survival (Pierotti 1982, Pierotti and Good 1994), suggesting that nest context is an important determinant of reproductive success and, ultimately, fitness. However, since we did not measure the chicks after day 9, it is possible that the chicks in the loose subcolony may have gained the weight necessary for fledging later in the nestling period after we had stopped measuring every chick.

   Differences in reproductive investment between the contexts did not arise in the early stages of the reproductive cycle. We detected no differences in egg size, clutch size, date of hatching, weight at hatching, or number of chicks hatched per nest. We found no difference in either parental investment in the clutch or egg loss between dense and loose subcolonies. These results differ from those of a similar study of the Herring Gull by Pierotti (1982), who found that parental investment differed by nest context and presumably had an influence on the differences in survival and growth of chicks observed. Our detecting no difference in parental investment between nest contexts makes the differences in chick-growth rate and survival we observed all the more noteworthy.
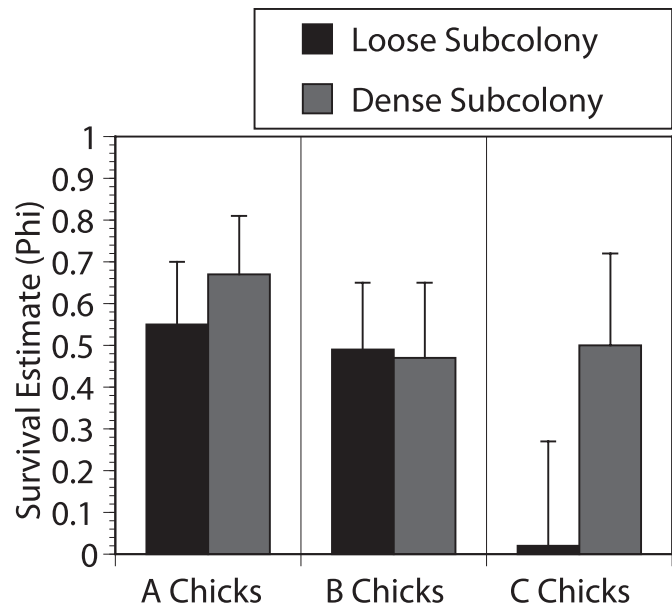

FIGURE 2.   Differences in expected survival for first (A; dense subcolony, $\Phi = 0.67 \pm 0.14$; loose subcolony, $\Phi = 0.55 \pm 0.15$), second (B; dense subcolony, $\Phi = 0.47 \pm 0.18$; loose subcolony, $\Phi = 0.49 \pm 0.16$), and third (C; dense subcolony, $\Phi = 0.50 \pm 0.22$; loose subcolony, $\Phi = 0.02 \pm 0.25$) chicks, from hatching to fledging, by context of nest. These results indicate a significant difference in expected survival of third chicks, with those hatched and reared in the dense subcolony (gray bars) having a significantly higher expected survival, from hatching to fledging, than chicks in the loose subcolony (black bars).

   Survival analyses indicated that in the dense subcolonies third chicks were far more likely to survive to fledging than those at more isolated nests (Fig. 2). Interestingly, adults in the dense subcolony were not more likely to lay or hatch a third egg than those individuals in the loose subcolony, but of the third chicks that hatched, survival from hatching to fledging was much greater in the dense subcolonies. These results demonstrate that nest density is a critical predictor of reproductive success within a Herring Gull colony. Furthermore, the extent that our results reflect differences between sites rather than differences in the quality of breeders between sites suggests that variability in reproductive success between nest contexts is dependent upon the success or failure of the third chick in the nest. This potential increase in reproductive output of 33% in the dense subcolonies over that in isolated situations is nontrivial and raises the question of why any Herring Gull chooses to nest in relative isolation. Future studies that span multiple breeding seasons may shed light on whether these patterns are consistent over time.

   The quality as parents of birds nesting in loose and dense subcolonies may differ, but such potential differences must be quantified through analysis of the physical attributes, behavior (e.g., food-provisioning rates, nest defense), and prior experience or age of the birds. Nesting experience could play a role in nest location and, ultimately, reproductive success.

Anecdotally, we noted that a higher proportion of gulls retaining subadult plumage were nesting in more isolated situations, suggesting that age may affect nest-site selection. This observation deserves formal investigation. Growth, survival, and fledging success of Herring Gull chicks have been negatively correlated with age of the parents (Risch and Rohwer 2000, Bogdanova et al. 2007). Egg predation is significantly higher when the incubating adult is a young individual, and the survival rate in broods raised by young gulls is markedly lower, even when egg quality is controlled for by cross-fostering clutches (Bogdanova et al. 2007).

Agonistic interactions between adults may have also influenced the observed trends in chick growth and survival. In studies of chick growth and survival in mixed-species colonies of gulls, it is important that intraspecific and interspecific agonistic behaviors be considered because heterospecific gulls are commonly the main predators of chicks (Watanuki 1988, Borboroglu and Yorio 2004). Preliminary quantification of agonistic interactions revealed that aggressive interactions between adults (mostly intraspecific) were more frequent at nests in the dense subcolony than at the more isolated nests, a pattern described previously (Butler and Janes-Butler 1982, Pierotti 1987). However, while frequent high-intensity agonistic behaviors (e.g., fighting; Tinbergen 1960) could have negative consequences for chick growth and survival through adults not being able to forage as successfully (i.e., spending all their time guarding chicks), frequent low-intensity agonistic behaviors (e.g., long call, *kek/yeow* call; Tinbergen 1960) might suggest an increased level of vigilance that could have a positive effect on chick survival.

The causes and consequences of coloniality in seabirds, and in larids in particular, have been studied for several decades (Tinbergen 1960, Hunt and Hunt 1976, Götmark 1982, Oro 1996, Hernandez-Matias et al. 2003). Overall, this study showed that the reproductive success of Herring Gulls nesting in dense colonies is increased through an increased rate of chick growth and greater probability of survival of the third chick. Even though a few previous studies have used mark–recapture models to examine survival of adult larids (Allard et al. 2006, Ratcliffe et al. 2008), to our knowledge, this is the first study to use such models to examine survival of larid chicks. This analysis enabled us to demonstrate that differences in reproductive success were not due to differences in our ability to detect chicks in dense and loose subcolonies (which differed substantially in cover). Further research is required to quantify the effects of parental quality and age, nesting habitat, agonistic behavioral interactions, and proximity to nesting Great Black-backed Gulls on reproductive success.

ACKNOWLEDGMENTS

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