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NEST ATTRIBUTES, AGGRESSION, AND BREEDING SUCCESS OF GULLS IN SINGLE AND MIXED SPECIES SUBCOLONIES

JULIE C. ELLIS[1,3] AND THOMAS P. GOOD[2]

[1]*Department of Ecology and Evolutionary Biology, 80 Waterman St., Brown University, Providence, RI 02912*
[2]*Conservation Biology, Northwest Fisheries Science Center, National Marine Fisheries Service,*
2725 Montlake Boulevard East, Seattle, WA 98112

Abstract. We investigated attributes of nests, aggressive interactions, and reproductive success in mixed and single species subcolonies of Great Black-backed Gulls (*Larus marinus*) and Herring Gulls (*L. argentatus*) on Appledore Island, Maine. Distances to the nearest neighboring nest were smaller for *L. argentatus* than *L. marinus*, with greatest distances between nests at edges of subcolonies in both species. More *L. argentatus* nests had natural screens (vegetation or rock >30 cm tall) adjacent to them than did *L. marinus* nests, but screen presence did not differ among nest positions within the colony. Clutch size did not differ between species; however, hatching success (number of chicks hatched per nest) was higher in *L. argentatus* than *L. marinus*. Fledging success (number of chicks fledged per nest) of *L. marinus* was greater at nests with heterospecific neighbors, whereas the opposite was true for *L. argentatus*. For both species, the frequency of aggressive interactions was lower at nests with *L. argentatus* neighbors. Overall, *L. marinus* nesting near *L. argentatus* experienced less aggression and greater reproductive success than those nesting among conspecifics, where intraspecific aggression was relatively high. *L. argentatus* nesting near *L. marinus* experienced more aggression and lower reproductive success than those nesting among conspecifics, where intraspecific aggression was relatively low. The costs and benefits of nesting in mixed species colonies may depend on the relative size and aggressiveness of the heterospecifics. Interactions with *L. marinus* in mixed species colonies may be contributing to the current declines of *L. argentatus* throughout New England.

Key words: aggression, interspecific competition, Larus argentatus*,* Larus marinus*, mixed species colonies, nest characteristics, population trends.*

Atributos del Nido, Agresión y Éxito Reproductivo en Subcolonias Mixtas y Uniespecíficas de *Larus marinus* y *Larus argentatus*

Resumen. Investigamos los atributos de los nidos, interacciones agresivas y el éxito reproductivo en subcolonias mixtas y de una sola especie en *Larus marinus* y *L. argentatus* en la Isla Appledore, Maine. Las distancias al nido vecino más cercano fueron menores para *L. argentatus* que para *L. marinus*, y las distancias más grandes entre los nidos estuvieron localizadas a las orillas de las subcolonias. Un mayor número de nidos de *L. argentatus* tuvieron cobertura natural (vegetación o roca de más de 30 cm de altura) junto a ellos comparado con nidos de *L. marinus*; sin embargo, la presencia de cobertura no fue diferente entre las distintas posiciones de los nidos dentro de la colonia. El tamaño de la nidada no fue diferente entre las especies, pero el éxito de eclosión (número de polluelos que eclosionaron por nido) fue mayor en *L. argentatus* que en *L. marinus*. El éxito de emplumamiento (número de volantones por nido) de *L. marinus* fue mayor en nidos que tuvieron vecinos heteroespecíficos, mientras que lo opuesto sucedió para *L. argentatus*. Para ambas especies, la frecuencia de interacciones agresivas fue menor en nidos que tuvieron individuos de *L. argentatus* como vecinos. En general, los individuos de *L. marinus* que anidaron cerca de *L. argentatus* experimentaron una menor agresión y un mayor éxito reproductivo que los individuos que anidaron entre nidos de coespecíficos, en donde las agresiones intraespecíficas fueron relativamente altas. Los individuos de *L. argentatus* que anidaron cerca de *L. marinus* experimentaron una mayor agresión y un menor éxito reproductivo que los que anidaron cerca de coespecíficos, en donde las agresiones intraespecíficas fueron relativamente menores. Los costos y beneficios de anidar en colonias mixtas pueden depender del tamaño relativo y la agresividad de los individuos heteroespecíficos. Las interacciones con *L. marinus* en colonias mixtas puede estar contribuyendo a la actual disminución de *L. argentatus* a través de Nueva Inglaterra.

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[3] Present address: Shoals Marine Laboratory, G-14 Stimson Hall, Cornell University, Ithaca, NY 14853. E-mail: jce4@cornell.edu

INTRODUCTION

Colonial nesting in birds can have associated costs and benefits, including increased competition for food or mates, disease transmission, predator defense, and information about good foraging sites (reviewed in Wittenberger and Hunt 1985, Clode 1993). Recent hypotheses of how coloniality evolved are mechanistic and focus on habitat and sexual selection (Danchin et al. 1998, Wagner et al. 2000). These latter hypotheses form a general framework for the study of coloniality that emphasizes habitat and conspecifics as commodities that drive choices resulting in coloniality (Danchin and Wagner 1997).

The choice of nesting habitat and proximity to nesting aggregations can be critical for colonially nesting seabirds. Dense nesting in colonies can lead to increased aggressive interactions among neighboring pairs (Butler and Trivelpiece 1981, Butler and Janes-Butler 1982). However, structure around the nest site can mitigate levels of aggression (Cezilly and Quenette 1988, Vermeer et al. 1988) and reduce predation on adults, eggs, and chicks (Bukacińska and Bukacińksi 1993, Good 2002).

Generally, competitive and aggressive interactions are less intense between heterospecifics than conspecifics (Tinbergen 1953), due in part to species-specific food or nesting requirements (Burger and Gochfeld 1990, Good et al. 2000) or breeding phenology (Götmark 1989). Birds nesting in mixed species colonies may have the added benefit of protection against predators from outside the colony (Götmark and Andersson 1984, Götmark and Åhlund 1988). Benefits derived from nesting with heterospecifics may thus lead to the persistence of mixed species colonies (Burger 1981).

Gulls and terns (Laridae) frequently nest in mixed colonies. While some species may benefit from nesting with larids (Tufted Ducks [*Aythya fuligula*], Vaananen 2000), there can be considerable costs (Burger 1979, Pius and Leberg 1997). For example, gulls have been implicated in population declines of puffins (Russell and Montevecchi 1996, Finney et al. 2003), auklets (Wilson 1993), terns (Becker 1995, Nocera and Kress 1996, Whittam and Leonard 1999), skimmers (O'Connell and Beck 2003), and other gulls (Castilla 1995, Borboroglu and Yorio 2004).

Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*) breed in mixed species coastal colonies from Maine to New York (Pierotti and Good 1994, Good 1998). Breeding populations of *L. argentatus* have declined steadily over the last 25 years (Cavanagh 1992, Brown et al. 2001, Robertson et al. 2001). These declines are usually attributed to improved sanitation and closing of landfills (Buckley and Buckley 1984) with which *L. argentatus* are strongly associated (Wells 1994), and to reduced fish offal and discards resulting from closures of ground fisheries in the early 1990s (Howes and Montevecchi 1993, Chapdelaine and Rail 1997). Populations of *L. marinus* have steadily increased during the 20th century (Borror and Holmes 1990, Brown et al. 2001). Their larger size and greater aggressiveness confer a competitive advantage over *L. argentatus* for fisheries discards and marine invertebrates (Furness et al. 1992, Rome and Ellis 2004), and their earlier nesting chronology confers a competitive advantage for nest sites in colonies (Pierotti and Good 1994, Good 1998).

In this study, we investigated intra- and interspecific interactions between *L. marinus* and *L. argentatus* in breeding colonies on Appledore Island, Maine. Specifically, we tested the null hypotheses that nest attributes, aggression, and breeding success of *L. argentatus* and *L. marinus* do not differ between mixed and single species subcolonies. We predicted that nests would provide more protective cover, aggression from congeners would be greater than from conspecifics, and breeding success would be lower for *L. argentatus* in mixed species subcolonies than single species subcolonies, and that nests would provide less protective cover, aggression from congeners would be lower than from conspecifics, and breeding success would be higher for *L. marinus* in mixed species subcolonies than in single species subcolonies.

METHODS

STUDY SITE AND SPECIES DESCRIPTIONS

We conducted our study on Appledore Island, ME (42°58′N, 70°37′W) in the Isles of Shoals archipelago, located approximately 10 km from the coast of New Hampshire in the Gulf of

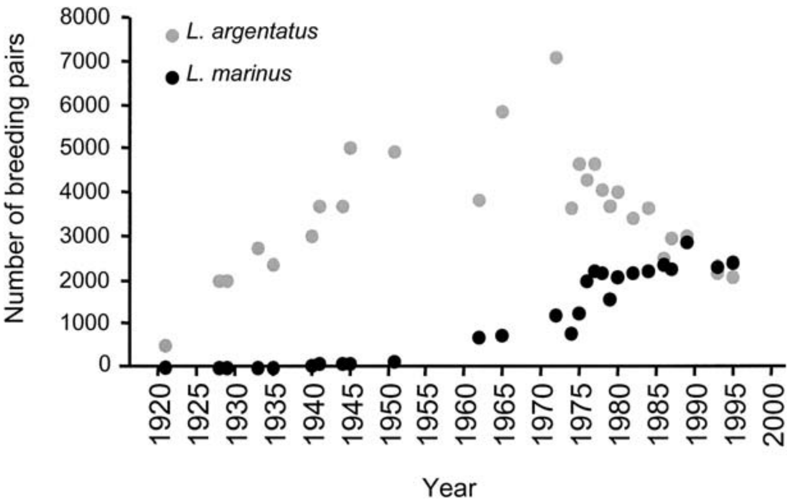

FIGURE 1. Changes in the number of *L. argentatus* and *L. marinus* pairs breeding at the Isles of Shoals, Maine and New Hampshire, USA, 1920–2000. Each data point represents the total number of pairs of each species in the year they were censused.

Maine. *L. marinus* and *L. argentatus* breed on Appledore Island in a variety of habitats—on exposed inland ridges, cobble beaches, bare rock ledges on the island's periphery, around shrubs, and near buildings of the Shoals Marine Laboratory. Both species inhabit Appledore Island from March through September, however *L. marinus* begin nesting approximately two weeks earlier than *L. argentatus* and move to the mainland two–four weeks prior to *L. argentatus* (JCE and TPG, pers. obs.).

Trends in gull populations on the Isles of Shoals are representative of those throughout New England. Neither *L. marinus* nor *L. argentatus* bred on the Isles of Shoals at the turn of the century. By 1972, *L. argentatus* had increased to over 7000 breeding pairs, and *L. marinus* had increased to over 1100 breeding pairs (Drury 1973). Since 1975, the number of breeding *L. argentatus* has steadily declined, while the number of breeding *L. marinus* has increased (Borror and Holmes 1990). A 1995 census showed *L. argentatus* had decreased to fewer than 2100 pairs, while *L. marinus* had increased to over 2400 pairs (A. C. Borror, pers. comm.; Fig. 1).

NEST ATTRIBUTES

In 1991, we marked 60 active *L. argentatus* nests and 55 active *L. marinus* nests with painted and numbered rocks. A nest was considered active if it contained at least one egg on the first visit in May. To minimize differences among pairs in nesting chronology, we collected data only from subcolonies on the northeastern "North Head" of Appledore Island, where breeding in both species is most synchronous (TPG, unpubl. data).

We categorized each marked nest as part of a mixed species or single species subcolony, as well as its location relative to other nests (McGill-Harelstad 1985): "core" nests had only conspecific neighbors, generally within 6 m, "edge" nests were at the periphery of a conspecific subcolony and lacked neighbors on at least one side due to the presence of dense vegetation or proximity to the shoreline, and "interface" nests had at least one heterospecific neighbor within 6 m. To determine whether nest density and attributes of nests varied with respect to nest position in either mixed or single species subcolonies, we collected data on nearest-neighbor distance and nest attributes, particularly natural screens (vegetation or rock >30 cm in height adjacent to the nest cup; Cezilly and Quenette 1988). We recorded data on natural screen size (angular extent from 0–360°) to determine the proportion of nests in the subcolony with vegetation or rock adjacent to the nest cup and the proportion of nests with adjacent vegetation or rock that screened or blocked the view of the nearest neighbor.

BREEDING SUCCESS

We checked nests weekly from the period of egg-laying and incubation in May until chicks fledged in August by walking through the colony, and recorded the number of eggs or chicks at marked nests during each nest visit. From these data, we calculated clutch size, hatching success (mean number of chicks hatched per nest), and fledging success (mean number of chicks fledged per nest) as indices of breeding success.

INTRA- AND INTERSPECIFIC AGGRESSION

To determine whether frequency of aggressive interactions differed between gull species and among colony positions, we conducted behavioral observations of nests during the breeding season (May to August) of 2000. Sixty nests were categorized as either "core" or "interface" for both species, and marked with numbered 12″ × 1″ sections of PVC pipe driven into the ground.

We randomly selected one to two subcolonies for observations per day; whether observations occurred in the morning or afternoon was also randomly determined. All observations were made between 08:00 and 20:00 EST. From within an observation blind about 10 m from the colony, nests were randomly chosen in each subcolony area and observed for 30 min with binoculars. Typically, between two and four nests were observed simultaneously. During observations, we recorded the duration of aggressive interactions between pairs and recorded the identity of both participants. Ritualized aggressive vocalizations observed in the two gull species (described in Good 1998, Pierotti and Good 1994) are Long Call, Long-call Note, Mew Call, and Warning Call. Ritualized aggressive displays (Good 1998, Pierotti and Good 1994) are: Upright Posture, Facing-Away, Grass-Pulling, Choking, and Charge.

STATISTICAL ANALYSES

We used two-factor General Linear Models (SPSS® version 13, SPSS 2004) to test the effects of gull species and nest position within the subcolony (edge, core, or interface) on nearest neighbor distances (log-transformed) and natural screen size (transformed using the equation arcsine ($\sqrt{[(\text{angular extent}/360^\circ)]}$) + 0.5).We tested for significant differences among colony positions using *post-hoc* Tukey-Kramer HSD tests. We used binomial logistic regressions (JMP® version 5.1; SAS Institute 2003) to test the relationship between gull species and colony position on nest characteristics (presence or absence of a natural screen; presence of a natural screen that blocked views of the nearest neighbor). We used a generalized estimating equation (Norton et al. 1996, SAS® version 9.13, SAS Institute 2005) to test the relationship between species and among nest positions within the subcolony on clutch size, hatching success, and fledging success; data used in these analyses were the number of chicks successfully hatched or fledged from each nest. Values reported are means ± SE.

To analyze the behavioral data, we tallied the total number of aggressive displays or vocalizations that occurred during each 30-min observation bout, and adjusted the total to the number of aggressive displays occurring per hour. We used two-factor ANOVAs to analyze the effects of species and nest position within the subcolony (core and interface only) on frequency of aggressive interactions. The number of aggressive interactions per hour was transformed using the equation log $(x + 1.1)$ prior to analysis. Because we selected nests for observation randomly, a few pairs of birds were observed more than once during the breeding season. We treated these observations as independent, because interactions were unlikely to be dependent on previously recorded observations due to changes in neighbor identities and reproductive status over the course of the breeding season (Pius and Leberg 1997).

RESULTS

NEST ATTRIBUTES

Overall, distances among nearest neighbors were significantly smaller in *L. argentatus* than *L. marinus* (two-factor GLM, species: $F_{1,110} = 67.2$, $P < 0.001$; Fig. 2). In both species, nearest neighbor distance was significantly greater among edge nests compared to core nests; neither was significantly different from interface nests (colony position: $F_{2,110} = 4.6$, $P = 0.01$; Tukey-Kramer HSD, $P < 0.05$). In *L. argentatus*, distances were smallest among core nests, whereas in *L. marinus* there was very little difference between interface and core nests, but the interaction of species*nest position within

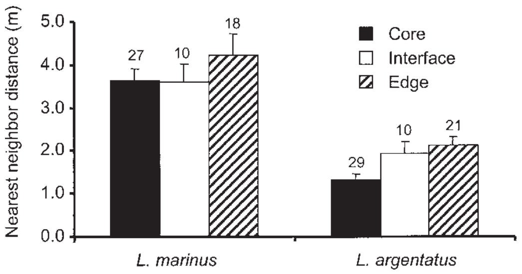

FIGURE 2. The effect of nest location (core, edge, or interface) on mean (± SE) distance to the nearest neighbor (in meters) in *L. argentatus* and *L. marinus*. "Core" nests had conspecific neighbors within ~6 m, "edge" nests were at the periphery of a conspecific subcolony and lacked neighbors on at least one side, and "interface" nests had at least one heterospecific neighbor within 6 m. Sample sizes are given above each bar.

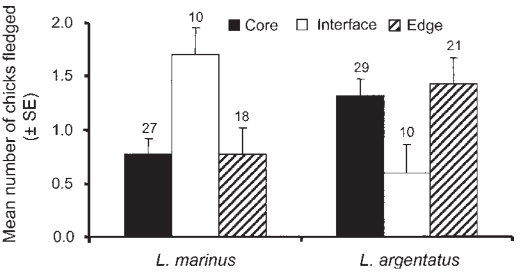

FIGURE 3. The effect of nest position within the subcolony (core, edge, and interface) on mean (± SE) number of chicks fledged per nest in *L. argentatus* and *L. marinus*. "Core" nests had conspecific neighbors within ~6 m, "edge" nests were at the periphery of a conspecific subcolony and lacked neighbors on at least one side, and "interface" nests had at least one heterospecific neighbor within 6 m. Sample sizes are given above each bar.

the subcolony was not significant ($F_{2,110} = 1.7$, $P = 0.19$).

Proportionally more *L. argentatus* nests had natural screens (87%) than did *L. marinus* nests (62%; logistic regression, species: $\chi^2_1 = 6.0$, $P = 0.01$), but there was no effect of nest position within the subcolony (core: 72%, interface: 80%, edge: 77%; $\chi^2_2 = 0.4$, $P = 0.80$) or species*nest position interaction ($\chi^2_2 = 0.2$, $P = 0.91$). Natural screen size did not differ significantly between *L. argentatus* (149° ± 13.8) and *L. marinus* nests (141° ± 17.9; two-factor GLM: $F_{1,110} = 0.12$, $P = 0.73$), or among nest positions within the subcolony (core: 128° ± 15.4, interface: 171° ± 25.9, edge: 157° ± 20.3; $F_{2,110} = 1.0$, $P = 0.35$); nor was there a species*nest position interaction ($F_{2,110} = 0.1$, $P = 0.94$). The proportion of nests having a natural screen that blocked views of the nearest neighbor did not differ between *L. argentatus* (52%) or *L. marinus* (45%; logistic regression, $\chi^2_1 = 0.4$, $P = 0.52$). In both species, more interface nests (65%) had screens that blocked the nearest neighbor than did edge (41%) or core (47%) nests, but the trend was not significant ($\chi^2_2 = 3.0$, $P = 0.23$), nor was the interaction of species*nest position ($\chi^2_2 = 1.2$, $P = 0.56$).

BREEDING SUCCESS

Clutch size did not differ between *L. argentatus* (2.8 ± 0.1) and *L. marinus* (2.8 ± 0.1; $\chi^2_3 = 0.01$, $P = 0.99$) or among nest positions within the subcolony (core: 2.7 ± 0.1, interface: 2.8 ± 0.1, edge: 2.8 ± 0.1; $\chi^2_6 = 0.6$, $P = 0.99$), and there was no species*nest position interaction ($\chi^2_6 = 5.4$, $P = 0.99$). Mean hatching success (number of chicks hatched per nest) did not differ significantly between *L. argentatus* (2.1 ± 0.1) and *L. marinus* (1.8 ± 0.1; $\chi^2_1 = 1.6$, $P = 0.2$), there was no effect of nest position within the subcolony on hatching success (core: 1.9 ± 0.1, interface: 1.9 ± 0.2, edge: 2.0 ± 0.2; position: $\chi^2_2 = 1.1$, $P = 0.6$), nor was there a significant species*nest position interaction ($\chi^2_2 = 1.8$, $P = 0.4$). Mean fledging success (number of chicks fledged per nest) did not differ significantly between *L. argentatus* (1.2 ± 0.1) and *L. marinus* (0.9 ± 0.1; $\chi^2_1 = 0.1$, $P = 0.75$), and there were no significant differences among nest positions within the subcolony (core: 1.0 ± 0.1, interface: 1.1 ± 0.2, edge: 1.1 ± 0.2; $\chi^2_1 = 0.8$, $P = 0.96$; Fig. 3). However, there was a significant interaction between species and nest position within the subcolony ($\chi^2_1 = 11.3$, $P = 0.003$). For *L. marinus*, fledging success was greatest at interface nests, whereas for *L. argentatus*, fledging success was lowest at interface nests.

INTRA- AND INTERSPECIFIC AGGRESSION

There were no significant differences in aggression between species (two-way ANOVA: $F_{1,88} = 1.0$, $P = 0.32$) or between nest positions within the subcolony ($F_{1,88} = 2.1$, $P = 0.15$), but there was a significant interaction between the two factors ($F_{1,88} = 42.8$, $P < 0.001$; Fig. 4). The number of aggressive interactions per hour

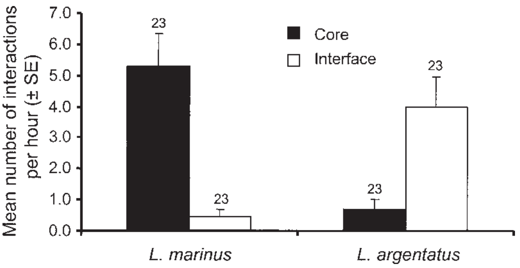

FIGURE 4. The mean (± SE) number of aggressive interactions (vocalizations, displays) per hour in *L. argentatus* and *L. marinus*. "Core" nests had conspecific neighbors within ~6 m and "interface" nests had at least one heterospecific neighbor within 6 m. At nests located in the core of a subcolony, aggression was directed at conspecifics; aggression was directed at congeners at interface nests. Sample sizes are given above each bar.

was significantly lower at *L. marinus* interface nests (0.5 ± 0.2) than at core nests (5.3 ± 1.0) whereas the number of aggressive interactions per hour was significantly lower at *L. argentatus* core nests (0.7 ± 0.3) than at interface nests (4.0 ± 0.9; Tukey-Kramer HSD, $P < 0.05$).

DISCUSSION

Our results strongly suggest that *L. marinus* and *L. argentatus* experienced different cost-benefit profiles associated with mixed species nesting. Whether the nearest neighbor was conspecific or heterospecific influenced the frequency of aggressive interactions, some nest-site characteristics, and breeding success. *L. marinus* nesting near *L. argentatus* experienced less aggression and higher reproductive success than those nesting near conspecifics, whereas *L. argentatus* nesting near *L. marinus* experienced more aggression and lower reproductive success than those nesting near conspecifics. Given such asymmetric consequences of nesting in mixed species colonies, the increases in *L. marinus* populations observed in northeastern U.S. colonies have likely negatively affected *L. argentatus*, and may have contributed to the latter species' decline. Surveys of coastal Maine islands have often documented *L. argentatus* declines in association with increases in *L. marinus* (Erwin and Korschgen 1979, Andrews 1990).

On Appledore Island, *L. argentatus* declined and *L. marinus* increased in number during the 1970s and 1980s. During this time, *L. marinus* displaced *L. argentatus* from prime nesting habitat on inland grassy ridge tops and increased its use of the rocky habitat to which *L. argentatus* had been relegated. In the mid-1900s, *L. argentatus* dominated grassy ridgetops, but by 1980, only 4% of 318 *L. argentatus* nests were found in grassy ridgetop habitat, compared with 70% of 190 *L. marinus* nests (McGill-Harelstad 1985). By 1993, *L. argentatus* on the North Head of Appledore Island nested almost exclusively in rocky habitat (98% of 470 nests), and *L. marinus* had expanded from grassy ridgetop areas into rocky habitat (55% of 143 nests; TPG, unpubl. data).

L. marinus may usurp nesting territories by breeding earlier than *L. argentatus* (Good 1998) and through direct confrontation. McGill-Harelstad (1985) documented a disproportionate number of adult *L. argentatus* carcasses (93%) on Appledore Island in 1980, and pecked and eaten carcasses were found in the vicinity of *L. marinus* nests 85% of the time. In our study, *L. argentatus* were also the dominant carcasses (90%) observed in the colony, and observations indicated that some pairs of *L. marinus* hunted and consumed adult *L. argentatus* during the early part of the breeding season (JCE, pers. obs.).

Aggression by *L. marinus* may also result in mortality of juvenile *L. argentatus*. Fledging success in *L. argentatus* was significantly lower at interface nests. We also observed dozens of *L. argentatus* fledglings being eaten by *L. marinus* when *L. argentatus* adults and fledglings foraged in rocky intertidal zones. *L. marinus* attacked and drowned *L. argentatus* fledglings, and then fed them to *L. marinus* chicks waiting on the nearby shore (JCE and TPG, pers. obs.). This predatory behavior has been observed in a few pairs for many years (A. C. Borror, pers. comm.), and is now widespread around Appledore and surrounding islands within the Isles of Shoals (JCE and TPG, pers. obs.). High rates of predation on juvenile *L. argentatus* may contribute to decreased numbers of adults returning to nest.

Changes in the distribution of *L. marinus* and *L. argentatus* nests may have altered patterns of nearest neighbor identity. For *L. marinus*, interface nests increased from 20% in 1980 to 48% in 1993, while core nests declined from 60% to 16% over the same period, whereas for

L. argentatus, core nests changed little (60% to 61%), while interface nests increased from 19% to 23% (McGill-Harelstad 1985; TPG, unpubl. data). Interface nests of both species were more likely to have natural screens blocking views of the nearest neighbor, however in contrast to other mixed species gull colonies (Good 2002, Good et al. 2000) we found natural screens did not influence predation on nests. Natural screens may have had little consequence in our study because they are more effective at preventing egg than chick predation (Butler and Janes-Butler 1982, Good 2002), and the latter is more common on Appledore Island.

In gulls, higher densities of nesting pairs usually increase the frequency of aggressive interactions (Butler and Trivelpiece 1981, Butler and Janes-Butler 1982, Pierotti 1987, Marin et al. 1995). In our study, densities of both species were higher than those found in other studies (mean nearest-neighbor distance, *L. marinus*: 4.7 m, Butler and Trivelpiece 1981; 5.6 m, McGill-Harelstad 1985; 30.9 m, Götmark 1982; 3.8 m, this study; *L. argentatus*: 4.0 m, Pierotti 1982; 4.1 m, McGill-Harelstad 1985; 6.5 m, Götmark 1982; 1.7 m, this study). However, while the density of *L. argentatus* nests was higher in the middle of single species (core nests) than mixed species groups (interface nests); the frequency of aggressive interactions was much lower among core than interface nests. Thus, the identity of the nearest neighbor was a better predictor of time spent in aggressive interactions than was nearest-neighbor distance.

Competition and aggression among heterospecifics in mixed species colonies have reduced reproductive output and led to population declines in several seabird species. For example, predation by skuas has resulted in decreases in petrels (Weidinger 1998) and kittiwakes (Phillips et al. 1999). Our results indicate that interactions with *L. marinus* may be contributing to the decline of *L. argentatus* populations in the northeastern U.S.

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