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Competition for Nest Sites Between Kelp Gulls (*Larus dominicanus*) and Terns (*Sterna maxima* and *S. eurygnatha*) in Patagonia

FLAVIO QUINTANA[1] AND PABLO YORIO
[2]*Centro Nacional Patagónico, CONICET, Boulevard Brown s/n 9120, Puerto Madryn, Chubut, Argentina; and Wildlife Conservation Society, New York, New York 10460, USA*

Seabirds frequently nest in mixed-species colonies (Burger 1985). Several studies have shown differences in habitat and nest-site use among seabirds (Buckley and Buckley 1980, Croxall and Prince 1980, Fasola and Canova 1992). However, some degree of overlap in habitat and nest-site requirements may exist between species, resulting in interspecific competition that often leads to nest-site displacement or even the replacement of one species by another (Buckley and Buckley 1980, Burger 1985). Spatial interactions between seabirds can be more intense in areas where habitat is limited or when the population of one of the species is expanding (Burger and Shisler 1978, Trivelpiece and Volkman 1979, Duffy 1983, Ainley 1990).

At many mixed colonies of larids, larger species often displace smaller species from their territories, occasionally forcing them to abandon the breeding area (Burger and Shisler 1978, Burger 1985). In addition, larger larids generally arrive at breeding sites earlier (Morris and Hunter 1976, Burger 1985), which gives them a competitive advantage over smaller species. Gulls (*Larus* spp.) frequently have been involved in the displacement of other species from breeding habitats (Thomas 1972, Burger 1979, Bradley and Monaghan 1986, Furness and Monaghan 1987). Terns appear to be one of the most affected seabirds, and some tern populations have decreased as a result of population expansion by gulls (Thomas 1972, Nisbet 1973, Greenhalgh 1974, Courtney and Blokpoel 1983, Parnell et al. 1988, Ainley and Hunt 1991, Blokpoel and Scharf 1991).

At Punta León, Argentina, Royal Terns (*Sterna maxima*) and Cayenne Terns (*S. eurygnatha*) breed intermingled in a dense cluster of nests within a Kelp Gull (*Larus dominicanus*) colony. The Kelp Gull colony increased in size from 3,200 pairs in 1982 to 6,500 in 1995, and gulls currently occupy almost all of the available nesting space (Yorio et al. 1994). Given the overlap in nest-site use and the current expansion of Kelp Gulls, we expected that competition for nesting space could result in negative effects on both species of terns. In this paper, we document spatial interactions between Kelp Gulls and Royal and Cayenne terns at Punta León, Patagonia. We quantify their temporal and spatial patterns of settlement, describe and quantify gull aggressive behavior toward terns, and determine the allocation of nesting space as a result of spatial interactions among these species.

Study area and methods.—Punta León (43°04'S, 64°02'W) is located 10 km south of the mouth of Golfo Nuevo, Chubut, Argentina. The coast in this area is characterized by gravel beaches with extensive cliffs 30 to 100 m high. A silt platform seaward of the cliffs and covered by vegetation (mainly *Suaeda divaricata, Atriplex lampa,* and *Lycium chilense*) is used as a nesting site by several seabird species, including Kelp Gulls (6,500 pairs), Royal Terns (650 pairs), Cayenne Terns (1,150 pairs), Imperial Cormorants (*Phalacrocorax atriceps*; 2,650 pairs), Neotropic Cormorants (*P. olivaceus*; 100 pairs), Rock Shags (*P. magellanicus*; 1 pair), and Guanay Cormorants (*P. bougainvillii*; 2 pairs; numbers from Yorio et al. 1994).

During 1990 to 1992, we obtained information on temporal and spatial settlement patterns of Royal Terns, Cayenne Terns, and Kelp Gulls. To determine settlement patterns by terns, we counted the number of nests every two to three days from mid-September to early November, using spotting scopes (20 to 45×) from an observation point on the cliffs 50 to 70 m from the colony. We monitored the growth of the colony by mapping its size and shape at intervals of two to four days. We obtained settlement patterns of Kelp Gulls from late August to mid-November through weekly counts of breeding individuals at a study area close to the tern colony and during 1990 and 1991 by monitoring 53 and 40 marked nests, respectively, every two to three days. The 20 × 20 m study area used to monitor gull settlement was located in the southern part of the Kelp Gull colony.

To study the effects of Kelp Gull territorial behavior on tern settlement, during 1990 we conducted 23 one-hour observations during which we scanned the colony for settling terns (n = 73 groups). When a group of settling terns was detected, we recorded whether the terns were attacked and whether they were totally or partially displaced by territorial gulls. We defined "settling terns" as a variable number of birds of both tern species that tried to settle at the colony periphery. Most pairs of terns build nests and lay their eggs on the same day that they settle in the colony site (Quintana and Yorio 1997). We de-

[1] E-mail: quintana@cenpat.edu.ar
[2] Address for correspondence.

fined "settled tern" as any bird sitting on a nest, with or without eggs. We defined a gull "attack" as any behavior consisting of a short chase by a peripheral territorial gull (and on occasion a peck without establishing physical contact) that resulted in the flight of the group of settling terns or of an incubating tern adjacent to that gull territory. We defined a peripheral territorial gull as any bird holding a territory, with or without a nest, located at a distance of less than 3 m from the tern colony.

To quantify Kelp Gull territorial behavior (gull attacks) toward terns, we made observations with spotting scopes and binoculars from the observation point on the cliff throughout the daylight hours (0700 to 2100 EST) during most of the tern breeding cycle. During each hour (n = 307), we quantified the rate of gull attacks directed at settling or incubating terns. During 1991 and 1992, we analyzed the difference in territorial behavior between gulls nesting near settling terns versus those nesting near settled terns.

To document the displacement of nesting pairs of Kelp Gulls by settling terns, we monitored at two-day intervals 38 and 40 gull pairs breeding at the tern colony periphery during 1991 and 1992, respectively. During each nest check, we recorded the presence of gulls at the nest, the state of the breeding cycle, and the estimated distance of the nest to the tern colony periphery. If the gull nest disappeared (loss of nesting material and eggs), we recorded whether the site was occupied by a nesting tern.

Results.—Kelp Gulls settled at the colony over a two-month period (Yorio et al. 1994). Gulls arrived at the colony and selected territories that were dispersed throughout the area. Late arrivals settled between existing territories. Kelp Gull nesting density was variable, ranging from 0.002 to 0.75 nests/m^2 (Yorio et al. 1994). Colony formation by Royal and Cayenne terns was initiated by a group of about 100 to 150 individuals that settled on available bare ground among Kelp Gull nests, and the colony grew through the settlement of new groups of both species at the colony periphery (Quintana and Yorio 1997). The resulting nesting density for both tern species combined ranged between 9 and 11 nests/m^2 (Yorio et al. 1994). During all study years, Kelp Gulls settled more than a month earlier than the terns. Gulls started claiming territories during late August and early September, but both tern species did not settle at the colony site until the second or third week of October. However, given the asynchrony in timing of breeding, some Kelp Gull pairs settled adjacent to the tern colony during and after the tern laying period. Both gulls and terns started laying in mid-October (Yorio et al. 1994, Quintana and Yorio 1997).

Although Kelp Gulls settled in the nesting area before the terns, both tern species were able to establish and breed among gull territories in all three seasons. The growth of the tern colony through the settlement of groups of birds at the colony periphery was mainly

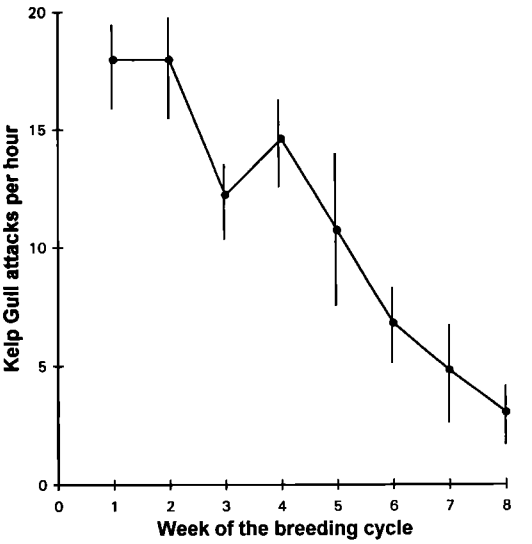

FIG. 1. Seasonal variation in rate of Kelp Gull attacks ($\bar{x}$ ± SD) on Royal Terns and Cayenne Terns during 1990 (week 1 = 18 to 24 October), Punta León, Patagonia.

in the direction of vegetated ground and in areas without gull territories. We did not quantify gull nesting densities at the time of tern settlement to avoid disturbance to gulls and terns. However, qualitative observations showed that during all years, sections of the gull colony had lower nest densities than the sections where terns bred. Moreover, during 1991, terns changed the location of their colony to an area of higher gull density than that used in the previous seasons. This new area had one of the highest nesting densities of Kelp Gulls on the entire colony (0.50 nests/m^2; Yorio et al. 1994). Terns continued to breed in this part of the colony for the next three years.

The settlement of tern groups ($\bar{x}$ = 25.7 individuals, range 5 to 120, n = 73) at the colony was affected by the presence of territorial Kelp Gulls, with and without nests, at the periphery of the colony. During 1990, 79.4% (n = 73) of the tern groups that we followed during settlement were attacked by peripheral gulls. Attacks by Kelp Gulls frequently forced groups of settling terns to take flight, on occasion causing the group to leave the colony. Of 58 groups that were attacked, 31% were forced to leave the site and 53.4% were partially driven away by gulls by the end of the observation period. In 15.6% of the cases, we could not determine the results of the interaction.

The mean number of Kelp Gull territorial attacks per hour toward tern groups was 13.8 ± SD of 8.8 (n = 121) in 1990. The number of attacks per hour decreased significantly as the season progressed (Spearman correlation, $r_s = -0.98$, $P < 0.01$; Fig. 1). Most spatial interactions between gulls and terns oc-

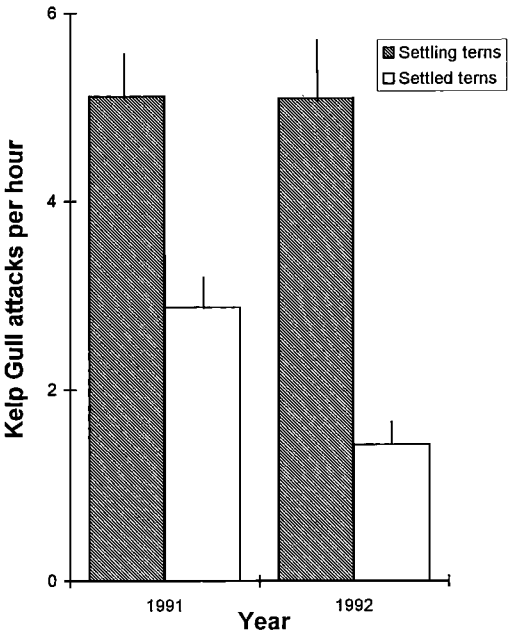

FIG. 2. Rate of Kelp Gull attacks ($\bar{x} \pm$ SD) toward settling and settled Royal Terns and Cayenne Terns during 1991 and 1992, Punta León, Patagonia.

curred during the period of tern settlement, and the highest rate of gull attacks was during the first two weeks of the terns' breeding cycle (Fig. 1). The average number of gull pecks and chases per hour during 1991 and 1992 was significantly higher toward settling than settled terns (Wilcoxon test; 1991, $Z = 3.43$, $P < 0.001$; 1992, $Z = 4.56$, $P < 0.001$; Fig. 2).

Even though some Kelp Gull pairs also settled after terns had selected the colony site, gulls were never observed displacing terns that had already laid eggs. In only a few occasions, gull territorial behavior forced an incubating tern to leave the egg exposed for several minutes. In contrast, gull territories that had nests, some of them with eggs, were taken over by settling terns during all three years of the study. In 1991 and 1992, 28.9% ($n = 38$) and 20% ($n = 40$), respectively, of the Kelp Gull pairs nesting in the vicinity of the tern colony lost their territories and nests to settling terns. Gull nest displacement occurred as the tern colony grew and groups of settling terns intruded into the territories of gulls, taking over the nesting space. On occasion, Kelp Gull nests were gradually surrounded by tern pairs, and incubating gulls retained their nests for some time before abandoning them. Displacement of nesting gulls by terns occurred even after gulls had started laying eggs. During 1991 and 1992, 54.5% ($n = 11$) and 87.5% ($n = 8$), respectively, of the displaced gulls had already started laying before they were displaced.

Discussion.—Even though gulls and terns at Punta León exhibit overlap in habitat use (Quintana and Yorio 1997), and the larger Kelp Gulls arrive at the colony earlier, Royal Terns and Cayenne Terns were able to form breeding colonies by displacing the gulls. Aggressive behavior by Kelp Gulls toward terns seems to be related to defense of breeding space, as suggested by the significantly higher rate of attacks toward settling versus settled terns.

The settlement and nesting strategies of Royal Terns and Cayenne Terns appear to be important determinants of competitive interactions with gulls. Although large body size and early timing of settlement can be important determinants of the outcome of spatial interactions (Burger and Shisler 1978, Duffy 1983, Burger 1985), settlement in dense groups may allow smaller birds to displace larger and earlier settling birds that nest at lower densities (Burger 1985). At Punta León, Royal Terns and Cayenne Terns settle at the colony in relatively large and dense groups that are able to displace nesting Kelp Gulls. Similar observations have been reported for other tern species, such as Sandwich Terns (*Sterna sandvicensis*) nesting with Black-headed Gulls (*Larus ridibundus*; Taverner 1970, Smith 1975, Veen 1977), Elegant Terns (*Sterna elegans*) nesting with Heerman's Gulls (*Larus heermanni*; Barrie 1975), and Arctic Terns (*Sterna paradisaea*) nesting with Herring Gulls (*Larus argentatus*; Bianki 1977). In this respect, the nesting traits of the crested tern group give them an advantage over other tern species, many of which are or have been affected as a result of expanding gull populations (Thomas 1972, Nisbet 1973, Courtney and Blokpoel 1983, Ainley and Hunt 1991, Blokpoel and Scharf 1991).

Even though we found no evidence that terns at Punta León currently are affected by spatial competition with Kelp Gulls, an increase in gull nesting density due to population expansion may interfere with tern settlement in the future. In addition, Royal Terns and Cayenne Terns may pay a cost by nesting among Kelp Gulls owing to delayed breeding, energy loss from territorial behavior, and/or prolonged exposure of eggs during territorial interactions. Any such costs probably will increase with increasing densities of nesting gulls. During 1991, for example, the location of the tern colony changed to an area of higher gull density. During that season, the growth of the tern colony was slower than in previous seasons (Quintana and Yorio 1997). Unfortunately, it cannot be determined whether the delay in settlement was a direct consequence of territorial interactions between gulls and terns, a result of lower food availability, or a combination of these factors. Given the potential negative effects on terns of an increase in nesting densities of Kelp Gulls, we recommend the establishment of a monitoring program to allow the early detection of conflicts between these species.

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