Avocetta N° 28 (1): 5-8 (2004)

Aggression and microhabitat segregation among nesting common terns *Sterna hirundo* and Mediterranean gulls *Larus melanocephalus*

LUCA CANOVA, MAURO FASOLA

Dipartimento di Biologia Animale, Università di Pavia, Piazza Botta 9, I-27100 Pavia, Italy (canova@unipv.it)

Abstract - We studied aggressive behaviour in a mixed colony of Mediterranean gulls and common terns. The two species bred syntopically but selected different reproductive microhabitats. Common terns were more aggressive than Mediterranean gulls, and aggression rate was higher towards heterospecifics than conspecifics. In both species, aggression rates were higher during the incubation phase, fell to a minimum when chicks rested in nests and increased again when chicks were able to wander inside the colony. High aggression rates during the pre-hatching phase are in agreement with theories of parental investment, while those involving adults during the chick wandering phase could be explained by a higher encounter rate with non-familiar adults, that induced an increase of aggressions between territory holders. The lower aggression in the "early chicks" phase can be explained by the increased food demand by chicks and the consequent reduction of adult density foraging out of the colony; however, selection of differing reproductive microhabitat can be considered as a further factor promoting coexistence, enhancing chicks survival immediately after hatching.

Riassunto - *Aggressività e segregazione del microhabitat riproduttivo in sterne comuni* Sterna hirundo *e gabbiani corallini* Larus melanocephalus. Sono state studiate le interazioni aggressive, sia a livello intraspecifico che interspecifico, in una colonia mista di gabbiano corallino e sterna comune. Le specie nidificano in condizioni di sintopia ma in microhabitat differenti. La sterna comune risulta più aggressiva rispetto al gabbiano corallino sia nei confronti di questo che dei conspecifici, ma in generale il tasso di aggressività è maggiore a livello interspecifico che intraspecifico. La frequenza delle interazioni aggressive è più elevata nella fase di cova e quando i pulcini sono in grado di abbandonare il nido, mentre è minima, in entrambe le specie, subito dopo la schiusa. Elevati tassi di aggressività nella fase precedente la schiusa sono in accordo con la teoria dell'investimento parentale, mentre nella fase di escursione dei pulcini entro la colonia l'aggressività è probabilmente favorita dall'alto tasso di incontro con adulti non familiari. La riduzione dell'aggressività nella fase intermedia è probabilmente spiegabile con la diminuzione di adulti nella colonia, dovuta alle accresciute necessità alimentari dei pulcini. La selezione di differenti microambienti riproduttivi può tuttavia giocare un ruolo nel favorire la coesistenza, incentivando la sopravvivenza dei pulcini nella fase immediatamente successiva alla schiusa, attraverso la riduzione della loro visibilità.

Introduction

Colonial breeding is considered adaptive since it improves nest defence, reduces predation on chicks and perhaps increases feeding efficiency through information exchange among individuals (Krebs 1974, Veen 1977, Wittenberger and Hunt 1985). However, coloniality may imply costs for individuals, since it may favour: a) increased predation on adults (Veen 1977), b) competition, aggression and cannibalism among conspecific and/or heterospecific neighbours (Hunt and Hunt 1976), and c) increased vulnerability to ectoparasites and diseases (Duffy 1983).

Aggressive behaviour, both at the interspecific and intraspecific level, is then one of the most important outcome of colonial breeding: for this reason, costs and benefits of aggressive behaviour have been extensively studied in gulls and terns (Burger and Gochfeld 1991, Brown and Brown 2001). Aggressive interactions in colonial breeding birds are ultimately due to limited resource supplies bringing about competitive behaviour, and to defence of eggs or chicks (antipredator behaviour). Interference competition and depletion of neighbours productivity is an important competitive strategy enhancing the contribution of own alleles to future generations (Pierotti 1980).

Colonial gulls and terns usually select different nesting microhabitats when breeding syntopically, and this segregation may be adaptive in reducing direct contacts among neighbours (Buckley and Buckley

Received 19 December 2003, accepted 19 February 2004 (Assistant editor: D. Rubolini).

1980). Another, though not alternative, explanation is that the structural features of nesting microhabitats enhance chick survival in relation to their size (Blokpoel *et al.* 1978, Fasola and Canova 1992).
The aims of our study were: 1) to describe aspects of aggressive behaviour in a mixed colony of Mediterranean gulls *Larus melanocephalus* and common terns *Sterna hirundo* in relation to breeding phases of adults; and 2) to understand the role of differing reproductive microhabitat selection in promoting local coexistence between the two species.

Methods

The study was carried out in the Valli di Comacchio (NE Italy), an ancient lagoon located along the Adriatic coast (further details in Fasola and Canova 1991), in the periods 4-6 June 1991 (incubation phase), 9-11 June 1991 (early chicks) and 14-16 June 1991 (wandering chicks). Data were recorded in a mixed-species colony in which Mediterranean gulls and common terns were breeding together with gull-billed terns *Sterna nilotica*, black-headed gulls *Larus ridibundus*, and little terns *Sterna albifrons*. Only the first two species were studied since the others bred in low numbers or joined the colony during the study period. The nesting microhabitats of these two species were characterised by measuring the main three variables which segregate nesting shorebirds in the Comacchio lagoon (details in Fasola and Canova 1992): 1) percentage of bare mud or sand within 1 m of the nest, 2) percentage of vegetation cover within 1 m of the nest, and 3) height of vegetation (maximum height in cm of the nearest clump of grass or forbs).
Behavioural observations were made from a hide overlooking the colony at a height of 3 m; a portion of the colony, including 23 Mediterranean gull and 27 common tern nests, was observed for a total of 12 hours (480 nest-hours) during each of the three phases of the breeding period. Observation periods lasted 240 minutes and were conducted between 08:30 and 14:30 each day; we used 10-min scan samplings to record aggressive behaviour, alternated with 10-min breaks. Overall, 46 scan samplings were recorded during each phases. We recorded the frequency of attacks and fights, i.e. intrusions of an individual into the territory of another, followed by physical contact. Several kinds of aggressive interactions could be identified at our colony: chase = one or more individuals running after an intruder; mobbing = several individuals flying over an intruder; attack = an aggressive encounter between an intruder and a challenger, aimed to strike the former and usually resulting in a physical contact. Since we considered only dyadic encounters, i.e. interactions between two individuals, chase and mobbing behaviour were excluded from analyses. Thus, our data refers to attacks occurring between adults, followed by physical contact. The frequency of attacks was expressed as attack rate (no. of attacks/10 min period); overall, data refers to 138 scan samplings. Data are expressed as mean and SE.

Results

The microhabitat around nests differed significantly between common terns and Mediterranean gulls (Tab. 1): Mediterranean gulls chose nest sites characterised by high vegetation cover, low bare ground and lower vegetation, while common terns choose sites with reduced vegetation cover but higher vegetation.
Figure 1 shows the frequency of interspecific aggressive interactions according to reproductive stages: the rate of interspecific aggression fluctuated widely between reproductive phases, mean attack rates ranging from 2.58 ± 0.46 ("early chicks") to 3.67 ± 0.33 ("wandering chicks") in common terns, while in Mediterranean gulls interspecific attacks ranged from 0.84 ± 0.17 ("early chicks") to 1.70 ± 0.18 in the pre-hatching phase. Aggression rate by common terns towards Mediterranean gulls was significantly higher than the reverse in all reproductive phases ($F_{1,136}$ = 48.3, P < 0.0001), i.e. common terns were more aggressive. Both species showed a similar variation in aggression rate in relation to nesting phase, i.e. attack rates were higher in the pre-hatching phase, fell to a minimum when chicks were laying in the nest, and then increased again when the chicks were more than five days old and were able to wander through the colony (Fig. 1).
The frequency of intraspecific aggressions was constantly lower than that of interspecific aggressions in both species: in common terns, the mean intraspecific aggression rate was significantly lower than the

Table 1. Mean (± SE) of three microhabitat variables measured around 23 Mediterranean gull and 27 common tern nests of the same colony. Statistics refer to Mann-Whitney *U* tests.

	Mediterranean gull	Common tern	Statistics
Sand cover %	20.4 ± 1.0	39.5 ± 1.6	Z = -5.83, N = 40, P < 0.001
Vegetation cover %	79.6 ± 1.0	60.5 ± 1.6	Z = -5.83, N = 40, P < 0.001
Vegetation height cm	25.0 ± 1.5	51.7 ± 2.2	Z = -5.91, N = 40, P < 0.001

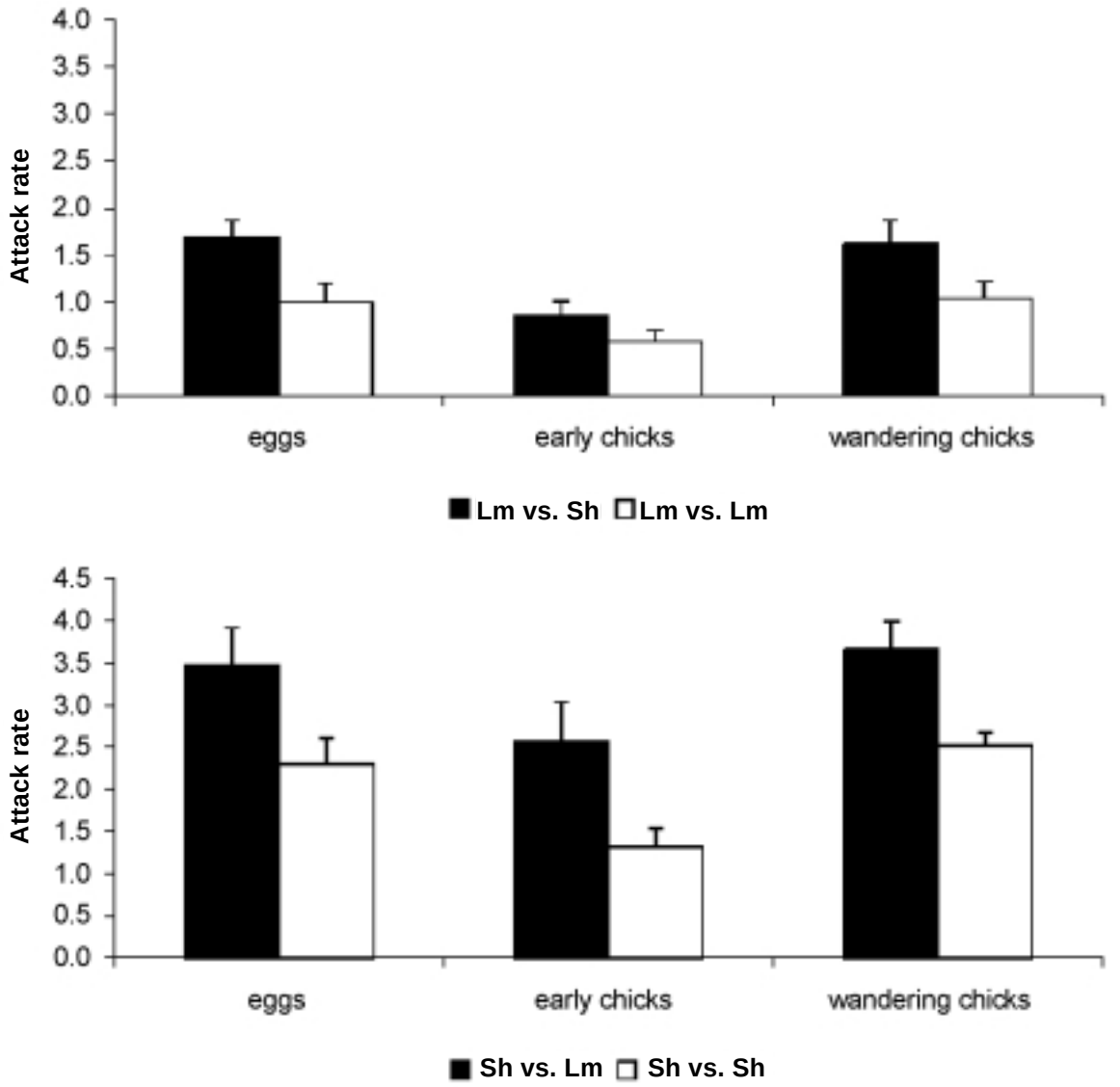

Figure 1. Inter- and intraspecific attack rates (no. of attacks/10 min, mean ± SE) according to reproductive phase in a mixed colony of Mediterranean gulls (Lm) and common terns (Sh).

interspecific one (2.11 ± 1.2 vs. 3.31 ± 1.9; $t = 4.27$, $N = 136$, $P < 0.001$), and the same pattern was observed in Mediterranean gulls (0.90 ± 0.1 vs. 1.43 ± 0.1; $t = -3.26$, $N = 136$, $P = 0.001$).

Discussion

Aggressive behaviour is one of the most important outcome of colonial breeding and its costs and benefits have been extensively studied in gulls and terns (Burger and Gochfeld 1991, Brown and Brown 2001). Aggressive interactions in colonial breeding birds are ultimately due to limited resource supplies, such as display grounds and suitable reproductive habitat, bringing about competitive behaviour, and to defence of eggs or chicks (antipredator behaviour); the interpretation of the resulting interference competition may have a great importance from an evolutionary viewpoint. The main results of our study were: 1) aggressiveness strongly differed between reproductive phases and species and 2) the frequency of aggressive interactions towards heterospecifics was higher than towards conspecifics in both species.

It is well known that aggressive behaviour reaches a maximum in colonial birds during the hatching phase (Andersson *et al* 1980, Burger 1984, Shealer and Burger 1992); according to the theory of parental investment, the rate of aggression among breeding birds should increase from laying to fledging of young (Dawking and Carlisle 1976, Boucheer 1977, Cote 2000). Our data only partially agree with this traditional pattern, since the frequency of aggression does not increase constantly during chick development, but shows two distinct peaks, in the incubation phase and when chicks are wandering away from the nest (Fig. 1). The high rate of aggression during the incubation phase in our case supports Barash's (1975) hypothesis that traditional parental investment theory should apply only to altricial birds, while in precocial birds a high degree of aggressiveness in territorial defence would be reduced later on in the breeding season since chicks are able to protect themselves (Andersson *et al.* 1980, Burger 1984, Kilpi 1987, Shealer and Burger 1992). However, the presence of a second peak in the aggression rate contrasts with Barash's (1975) hypothesis: wandering of chicks in the colony, although probably reducing the need for aggressive defence of the nest by parents, may on the other hand induce aggressive behaviour by parents towards foreign chicks. The low rate of aggression during the "early chicks" phase may partly be explained by the reduction of parent density in the colony, as a result of the increased amount of time devoted to foraging by the parents, which should reduce the opportunities for encounters.

A more general synthesis of our results is summarised as follows: it seems clear that parental defence did not increase directly with increased investment and that, contrary to findings by Burger and Gochfeld (1991), chicks experienced a minimum of aggression when they are more vulnerable and lay in the nest. Thus, defence response appears to be influenced not only by previous investment or chicks vulnerability, but is probably induced by movement of chicks within the colony.

The frequency of aggressive interactions among species can be reduced by selection of different nesting microhabitats (Blokpoel *et al.* 1978), and vegetation structure influenced both types and frequency of aggressive encounters (Bukacinska and Bukacinski 1993). Since the proximal factor influencing aggressiveness inside a colony is a visual cue, the observed differences in microhabitat selection could be considered, in addition to the reduced density of adults immediately after hatching, as a further factor promoting coexistence between common terns and Mediterranean gulls. As previously stated (Fasola and Canova 1992), selection of differing reproductive microhabitat can enhance chick survival soon after hatching, by reducing their visibility to neighbouring.

Acknowledgements - We wish to thank the Società Itticoltura Valli di Comacchio (SIVALCO) for access permission and facilities.

References

Andersson M, Miklund C G, Rundgren H 1980. Parental defence of offspring: a model and an example. Animal Behaviour 28: 536-542.

Barash D P 1975. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. Wilson Bulletin 87: 367-373.

Boucher D H 1977. On wasting parental investment. American Naturalist 111: 367-373.

Burger J 1984. Pattern, mechanism and adaptive significance of territoriality in the herring gull *Larus argentatus*. Ornithological Monograph 34: 1-92.

Blokpoel H P, Catling M, Haymes G T 1978. Relationship between nest sites of common terns and vegetation on Eastern Headland Toronto Outer Harbour. Canadian Journal of Zoology 56: 2057-2061.

Brown C R, Brown M B 2001. Avian coloniality. Progress and Problems. In: Van Nolan J, Thompson C F (eds). Current Ornithology. Vol. 16. Kluiver, New York, pp. 1-82.

Bukacinska M, Bukacinski D 1993. The effect of habitat structure and density of nests on territory size and territorial behaviour in the black-headed gull *Larus ridibundus*. Ethology 94: 306-316.

Buckley F G, Buckley P A 1980. Habitat selection and marine birds. In Burger J, Olla B L, Winn H E (eds). Behaviour of Marine Animals. New York, Plenum Press, pp. 1-141.

Burger J, Gochfeld M 1991. The common tern. Its breeding biology and social behavior. Columbia University Press, New York, pp. 1-413.

Cote S D 2000. Aggressiveness in king penguins in relation to reproductive status and territory location. Animal Behaviour 59: 813-821.

Dawkins R, Carlisle T R 1976. Parental investment, mate desertion and a fallacy. Nature 262: 131-133.

Duffy D C 1983. The ecology of tick parasitism on densely nesting Peruvian seabirds. Ecology 64: 110-119.

Fasola M, Canova L 1991. Colony site selection by eight species of gulls and terns breeding in the Valli di Comacchio (Italy). Bollettino di Zoologia. 58: 261-266.

Fasola M, Canova L 1992. Nest habitat selection by eight syntopic species of Mediterranean gulls and terns. Colonial Waterbirds 15: 169-178.

Hunt G L, Hunt M W 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. Ecology 57: 62-57.

Kilpi M 1987. Do herring gull *Larus argentatus* invest more in offspring defence as the breeding season advances? Ornis Fennica 64: 16-20.

Krebs J R 1974. Colonial nesting and social feeling as strategies for exploiting food resources in the great blue heron *Ardea herodias*. Behaviour 51: 99-134.

Pierotti R 1980. Spite and altruism in gulls. American Naturalist 114: 290-300

Shealer D A, Burger J 1992. Differential responses of tropical roseate tern aerial intruders throughout nesting cycle. Condor 94: 712-719.

Veen J 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern *Sterna sandvicensis*, L Behaviour Supplement 20: 1-193.

Wittenberger J L, Hunt G L 1985. The adaptive significance of coloniality in birds. In: Farner D S, King J R, Parker K C (eds). Avian Biology. Academic Press, New York, pp. 1-79.