



# Evidence for social facilitation of preening in the common tern

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## ABSTRACT

Social facilitation of reproductive behaviour has been studied extensively in gulls and terns, but social facilitation of preening has been reported only anecdotally, and has not been previously quantified. We studied a common tern, *Sterna hirundo*, colony during the summers of 1996 and 1997 to test for socially facilitated preening. Scan sampling provided evidence of spatial and temporal synchrony of preening behaviour. Preening occurred more often than expected in groups of three or more neighbours. Breeding pairs also preened simultaneously more often than expected. In loafing (resting) areas, the proportion of preeners present increased with tern density. Behavioural observations suggest that preening spread from neighbour to neighbour. The observed clumping in preening behaviour could not be explained by differences in date, time of day or weather. Social facilitation of preening and other maintenance behaviour may be an important aspect of group living that is often overlooked.

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Maintenance behaviour constitutes a substantial proportion of the time-activity budgets of birds and mammals, yet has probably received the least study of any major category of vertebrate behaviour (Cotgreave & Clayton 1994). Preening in birds serves many functions, including feather care and the removal of dirt and ectoparasites (Andrew 1956; Van Iersel & Bol 1958; Van Rhijn 1977; Clayton 1991; Cotgreave & Clayton 1994), and can also occur as a displacement activity (Andrew 1956; Van Iersel & Bol 1958). In this study, we examined preening in the common tern, *Sterna hirundo*, to test for social facilitation of this behaviour.

Social facilitation is any increase in the frequency or intensity of a behaviour (except that due to learning) caused by the presence of conspecifics performing the same behaviour (Clayton 1978; Gochfeld 1980; Nicol 1995). Social facilitation is an important aspect of group living, as the behaviour of one individual can induce similar behaviour in other group members. Social facilitation can enhance the benefits of group living by contributing to foraging success, antipredator defence, and reproductive synchrony within social groups (Clayton 1978). The synchrony resulting from social facilitation is at a finer scale than synchrony resulting from environmental stimuli, and thus enhances cohesion of social groups (Clayton 1978).

The adaptive benefits of socially facilitated preening are not obvious, and synchronous preening could actually be maladaptive if it decreases antipredator vigilance. However, possible functions for the social facilitation of preening exist. Preening aids in the removal of ectoparasites (Clayton 1990, 1991; Cotgreave & Clayton 1994), which at increased levels, are a cost associated with living in groups (Alexander 1974). Social facilitation of preening should lead to an increased proportion of time spent preening in group-living species, and thus could partially compensate for the increased parasite load. Cotgreave & Clayton (1994) found no larger proportion of time allocated to preening and related behaviour in colonial than in semicolonial or noncolonial birds, but their comparative study extended across taxa differing in many aspects other than the degree of coloniality. Preening in the presence of other preeners may also serve a social function. In stump-tailed macaques, *Macaca arctoides*, autogrooming near conspecifics had the same social effects as allogrooming with conspecifics (Goosen 1974). Among birds, evidence for a social function of synchronized preening comes from a reported tendency for preening to spread from dominant to subordinate individuals (Nguyen-Clausen 1975; Van Rhijn 1977), perhaps signalling dominance status. Synchronous preening among mates (Caryl 1976) is also suggestive of communicative function.

Tests for the social facilitation of preening are extremely rare and are restricted to studies of captive birds. Nguyen-Clausen (1975) demonstrated that preening in a group of six mynahbirds, *Acridotheres cristatellus*,

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coincided more frequently in time than expected at random, and he often observed preening behaviour spreading from the dominant individual to the rest of the group. Other studies of preening are merely suggestive of social facilitation. Gauthier & Cyr (1990) found preening to be more common among red-winged blackbirds (*Agelaius phoeniceus*) in groups than when they were alone, and Nicol (1989) found that domestic hens, *Gallus gallus domesticus*, preened more often when familiar pen mates were placed in close proximity than when they were placed 1 m apart. Preening occurred simultaneously among neighbouring Bengalese finches, *Lonchura striata domestica*, more often than expected (Birke 1974), and was more strongly synchronized between pair-bonded than among nonpair-bonded zebra finches, *Taeniopygia guttata* (Caryl 1976). Evans (1970) demonstrated weak, but significant, synchrony of preening in another finch, the red avadavat, *Amandava amandava*. In a test of mate choice in rock doves, *Columba livia*, Clayton (1990) found a significant correlation among male stimulus pairs in the proportion of time spent grooming. However, synchronous preening alone does not necessarily imply social facilitation (Crook 1961; Birke 1974; Gochfeld 1980; Clayton 1990), as activity cycles, weather and social stimulation may also synchronize maintenance behaviour.

Colonial birds are ideal for the study of social facilitation in the field, as many individuals can be observed simultaneously in a fixed location. Social facilitation of reproductive behaviour, aggressive encounters and predator mobbing have been previously demonstrated in colonies of gulls and terns (Southern 1974; Gochfeld 1980; Burger & Gochfeld 1991). Reports of socially facilitated preening among gulls and terns (Laridae) are largely anecdotal. Preening has been observed spreading from neighbour to neighbour in common terns (Palmer 1941), black terns, *Chlidonias niger* (Goodwin 1959), herring gulls, *Larus argentatus* (Van Rhijn 1977) and great black-backed gulls, *Larus marinus* (B.G. Palestis, personal observation). However, social facilitation of preening behaviour has not been quantitatively tested in any larid species. In this study, we quantified preening behaviour in the common tern to test for social facilitation of preening and to rule out other synchronizing factors. We selected common terns for study, because anecdotal evidence for socially facilitated preening exists for this species (Palmer 1941) and other aspects of common tern preening have been described in detail (Van Iersel & Bol 1958). We tested the null hypotheses that there is no synchrony in preening; alternatively, that any synchrony in preening results from factors other than social facilitation.

## METHODS

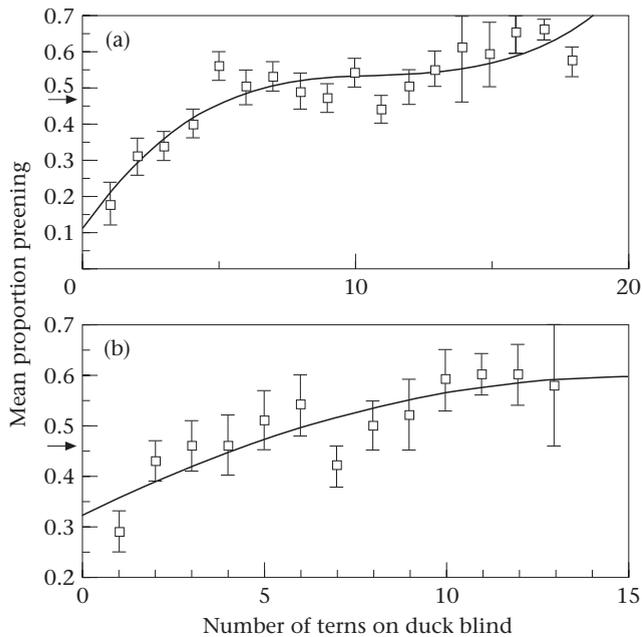
This study took place during the summers of 1996 and 1997 on Pettit Island, a 0.3 hectare salt marsh island in Manahawkin Bay in New Jersey. The island is more than 90% covered with *Spartina* grasses (Burger & Gochfeld 1991). Approximately 70 and 50 pairs of common terns nested on Pettit Island in 1996 and 1997, respectively.

The terns nested on wrack (mats of dead vegetation) along the edges of the island, and often loafed on three duck blinds (1.2 × 3.2 m wooden boxes) present on the island. We made observations with binoculars from a small boat anchored approximately 20 m from the island, or occasionally from a canvas blind in the centre of the island. Within 5 min after our arrival, the terns settled down and appeared to be undisturbed by our presence. We made observations from 6 June to 2 August in 1996 and from 26 May to 2 July in 1997, covering nearly the entire breeding cycle in 1996. The distribution of observation times throughout the day was approximately evenly spread between 0800 and 1500 hours, with observations between 1500 and 1930 hours occurring less frequently. We collected quantitative data via scan sampling (see below). We also recorded behavioural observations ad libitum between scans and between blocks of scans. We collected information on the effect of tern density on preening only from terns that were resting on duck blinds, as the blinds provided a fixed area where density increased with the number of individuals present.

To estimate accurately the frequency of a particular behaviour with instantaneous sampling, it is necessary to use interscan intervals as short as is practical (Martin & Bateson 1993). On the other hand, when scan samples are used as independent data points the interval must be longer than the duration of the behaviour of interest (Martin & Bateson 1993). We performed instantaneous sampling at 2-min intervals to measure the frequency of preening among adult terns. Because we calculated the proportion of individuals preening within a particular block of scans (see below) and within a particular treatment (nesting versus loafing areas, tern density), we obtained only one frequency data point per treatment per block of scans. Whenever we treated individual scans as independent data points, however, we only used scans separated by 8 min or more. To ensure that 8 min was a reasonable interval length, we timed 17 preening bouts with a stopwatch. The longest bout recorded lasted 7.5 min, and the median length of preening bouts was only 128 s. Additionally, although we did not keep track of individual terns, it was apparent that there was usually considerable turnover of individuals within 8 min, particularly in loafing areas. Therefore it is unlikely that we repeatedly sampled the same individuals from one scan to the next.

We performed 1129 and 572 scans in 1996 and 1997, respectively, each from left to right along an edge of the colony across at least 10 nesting territories and one or two duck blinds. We divided scans into blocks by the hour of the day in which they were performed (61 blocks in 1996 and 52 in 1997). Because we calculated the frequency of preening as the mean proportion of stationary (i.e. not flying or walking) terns preening, the values obtained overestimated the actual frequency of preening in the colony.

Because we performed scans from neighbour to neighbour, we were able to observe both the spatial and the temporal clumping of preening. Scan sampling provides a conservative test for synchronous preening because tern



**Figure 1.** The mean ( $\pm$ SE) proportion of terns preening (on duck blinds) versus the number of terns present in (a) 1996 and (b) 1997. The grand mean proportion of terns preening on duck blinds for each year is indicated by an arrow. Note that the range of values along the X-axis is smaller in 1997 than in 1996, which may partially explain the difference between years in the shape of the curve.

preening bouts are frequently interrupted by brief periods of vigilance (Van Iersel & Bol 1958; Roberts 1996; this study). For example, if two neighbours were both engaged in preening bouts, but one was vigilant at the time of a scan, then preening would only be recorded in one individual. Scan sampling could therefore lead to some synchronous preening being overlooked.

## RESULTS

The mean ( $\pm$ SE) proportion of stationary adult terns in the colony that were engaged in preening behaviour at a given time was  $0.35 \pm 0.01$  ( $N=61$  blocks of scans) in 1996 and  $0.31 \pm 0.02$  ( $N=52$ ) in 1997. In other words, terns with an opportunity to preen (i.e. not flying or walking) spent approximately 30–35% of their time preening during the 1996 and 1997 breeding seasons. Terns loafing on duck blinds preened more frequently than those on or near nests. In 1996, the frequency of preening was  $0.47 \pm 0.03$  ( $N=43$ ) on duck blinds and  $0.28 \pm 0.02$  ( $N=61$ ) in nesting areas (Wilcoxon signed-ranks test:  $Z=4.65$ ,  $P<0.0001$ ). In 1997, the frequency of preening was  $0.46 \pm 0.02$  ( $N=52$ ) on duck blinds and  $0.22 \pm 0.01$  ( $N=52$ ) in nesting areas ( $Z=5.88$ ,  $P<0.0001$ ). However, the mean frequency of preening by lone terns on duck blinds was only  $0.18 \pm 0.06$  ( $N=24$ ) in 1996 and  $0.29 \pm 0.04$  ( $N=33$ ) in 1997 (Fig. 1). Therefore, when only one tern was present on a duck blind, the frequency of preening was similar to that observed in nesting areas in 1997 (Mann–Whitney  $U$  test:  $Z=0.68$ ,  $P=0.495$ ), and was

**Table 1.** Synchronous preening in breeding pairs\*

	1996		1997	
	Expected	Observed	Expected	Observed
Both preen	22	38	7	21
One preens	83	50	42	15
Neither preens	79	95	61	75

\*The observed and expected frequencies of simultaneous preening among mated pairs are shown for 1996 and 1997. Expected numbers are calculated based on the proportion of these individuals that were observed preening in 1996 (0.34) and in 1997 (0.26).

significantly lower than the frequency of preening in nesting areas in 1996 ( $Z=2.11$ ,  $P<0.05$ ).

Within a fixed area (the tops of rectangular duck blinds), the proportion of individuals preening increased greatly with the number of terns present. When only one tern was present on a duck blind, the frequency of preening was low (see above). The relationship between tern density and the per capita frequency of preening was best described with a third-degree polynomial in 1996 ( $Y=0.075+0.14X-0.14X^2+0.004X^3$ ;  $F_{3,309}=20.21$ ,  $P<0.0001$ ), as preening increased, then levelled off, and then increased again at the highest tern densities (Fig. 1). In 1997 the range of tern densities observed was not as great as in 1996, and preening simply increased and then gradually levelled off with increasing tern density (Fig. 1;  $Y=0.297+0.049X-0.002X^2$ ;  $F_{2,200}=8.54$ ,  $P<0.0005$ ). The proportion of individuals preening on duck blinds was highly variable, and tern density explained little of this variation ( $r^2=0.165$  in 1996 and 0.070 in 1997).

When both members of a breeding pair were present in a territory, the pair tended to synchronize preening. Breeding pairs preened simultaneously more often than expected by chance (1996:  $X^2_2=28.00$ ,  $P<0.0001$ ; 1997:  $X^2_2=48.57$ ,  $P<0.0001$ ; Table 1). Expected numbers were generated based on the proportion of these individuals that were preening, 0.34 in 1996 and 0.26 in 1997. These proportions were similar to the mean frequencies of preening obtained in nesting areas (see above).

The size of exclusive clumps of preeners (i.e.  $N$  individuals in a row, from left to right across an edge of the colony, all preening but surrounded by nonpreeners) differed significantly from the expected distribution if no social facilitation occurred (1996:  $X^2_4=849.36$ ,  $P<0.0001$ ; 1997:  $X^2_3=274.11$ ,  $P<0.0001$ ; Table 2). We calculated this expected distribution using the mean proportion of stationary terns preening simultaneously, 0.35 in 1996 and 0.31 in 1997 (see above). The probability of preening occurring in  $N$  consecutive individuals equalled  $0.35^N$  (or  $0.31^N$ ). The probability of a group of preeners of size  $N$  occurring was therefore  $0.35^N$  minus the probabilities for groups larger than  $N$ . Lone preeners occurred less frequently than expected, while groups of three or more preeners in a row were more common than expected (Table 2).

The observed synchrony in preening could not be explained by time of day, date or weather. Time of day

**Table 2.** The observed and expected frequencies of groups of *N* neighbouring individuals that preened while being surrounded by nonpreeners\*

Number of consecutive preeners	1996		1997	
	Expected	Observed	Expected	Observed
1	997	473	560	310
2	173	169	86	110
3	40	90	18	48
4	11	46	4	14
5	3	27	1	8
6	1	8	0	3
7	0	5	0	2
8	0	2	0	0
9	0	2	0	0
10	0	0	0	1

\*Expected frequencies are based on the mean frequency of preening in 1996 and 1997. We combined observations of five or more consecutive preeners in 1996 and observations of four or more consecutive preeners in 1997 to avoid inflating  $\chi^2$  values.

did not have a significant effect on the frequency of preening in either year (1996: ANOVA,  $F_{11,44} = 0.95$ ,  $P = 0.508$ ; 1997:  $F_{9,42} = 1.71$ ,  $P = 0.117$ ). The mean ( $\pm$  SE) proportion of individuals preening tended to be highest around noon ( $0.38 \pm 0.02$ : 1100–1300 hours in 1996;  $0.35 \pm 0.03$  in 1997), but much variation existed (SD = 0.14 in 1996, 0.12 in 1997). Although the frequency of preening behaviour varied from day to day, there was no correlation between preening frequency and date of observation (1996:  $F_{1,26} = 0.030$ ,  $P = 0.863$ ; 1997:  $F_{1,16} = 0.37$ ,  $P = 0.551$ ), indicating no trend within the breeding season. There was also no correlation between preening and ambient temperature (1996: no data; 1997:  $F_{1,16} = 0.22$ ,  $P = 0.647$ ), approximate per cent cloud cover (1996:  $F_{1,21} = 1.46$ ,  $P = 0.241$ ; 1997:  $F_{1,16} = 0.75$ ,  $P = 0.400$ ), or precipitation (1996:  $F_{2,26} = 2.28$ ,  $P = 0.123$ ; 1997:  $F_{2,19} = 0.88$ ,  $P = 0.429$ ), but we made very few observations during severe weather.

Behavioural observations also suggested that preening is socially facilitated. Preening appeared to spread from neighbour to neighbour, but not to neighbours facing away from the preener. For example, in one observation, five individuals were present on a duck blind and one was preening. Within 2 min, four of the five terns were preening, and one tern, which was facing away from the other four terns, was not preening. Preening in one individual, however, did not always induce preening in a neighbour even when neighbours were looking at each other. In another example, six terns were on a duck blind and none was preening. One individual began to preen, and within 1 min four were preening, but preening did not spread to the other two terns.

## DISCUSSION

We found evidence of socially facilitated preening in common terns. Preening appeared to spread from neighbour to neighbour, and was more synchronous than expected by chance. Breeding pairs synchronized their

preening, and groups of three or more consecutive neighbours preened more often than expected by chance. Additionally, preening increased in frequency as tern density increased. Even though environmental variables were not correlated with the frequency of preening, variables such as weather would act at a much larger spatial and temporal scale than the synchrony reported here (Clayton 1978).

Much of the evidence for social facilitation of preening comes from terns loafing on duck blinds, but preening occurs more frequently in loafing areas than in nesting areas (Palmer 1941; Van Iersel & Bol 1958; this study). Therefore, before social facilitation can be discussed, the possibility that terns simply go to duck blinds to preen must be considered. Parental care, territorial defence and nest maintenance do not occur in loafing areas, and some of the individuals present may be individuals returning from bathing to preen (Van Iersel & Bol 1958). When only one individual was present on a duck blind, however, the frequency of preening was low. The frequency of preening by lone terns on duck blinds was similar to that seen in nesting areas in 1997, and was actually significantly lower than the frequency of preening in nesting areas in 1996. Social facilitation may therefore play a large role in increasing the frequency of preening in loafing areas. On duck blinds, no vegetation is present to decrease visibility, and individuals are in close proximity to each other. In contrast, within the colony, vegetation is quite dense and neighbours are more distant from each other. The difference in the frequency of preening between loafing and nesting areas may be smaller in beach colonies, where little vegetation is present to decrease visibility among neighbours.

Terns preened more often as the number of individuals present in a fixed area (the tops of the duck blinds) increased. As the number of individuals increases, the likelihood that at least one will happen to preen will increase, perhaps allowing preening to spread more frequently to neighbours. With increased density, individuals are also in closer visual contact with each other. This result could also simply be an effect of crowding and displacement preening. Displacement preening seems an unlikely explanation for the increase in preening with density, however, because preening bouts rarely resembled the quick bouts characteristic of displacement preening (Van Iersel & Bol 1958). Rapid, incomplete preening bouts are less likely to be recorded by scan sampling because of their short duration. Additionally, displacement preening among common terns is most frequent during nest relief (Van Iersel & Bol 1958), and may explain some of the observed synchrony in preening among breeding pairs, but not among individuals on duck blinds. It is also unlikely that the increase in preening with increased tern density resulted from aggressive display. Van Iersel & Bol (1958) found displacement preening to be common during aggression only when terns left their nests during territorial disputes. Aggression on duck blinds consisted of simple displacements, not territorial disputes.

Socially facilitated preening may be common to group-living birds, but this phenomenon has received very little

quantitative study. Much research has focused on the social functions of allogrooming and allopreening, and social facilitation provides another mechanism whereby grooming behaviour may play an important role in the interactions among members of social groups. Further study is needed to determine the adaptive value, physiological mechanisms, ontogeny and spatial and temporal scale of the occurrence of socially facilitated preening.

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