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THE EFFECT OF DAYTIME, TIDES AND OTHER FACTORS ON SOME ACTIVITIES OF LESSER BLACKED-BACKED GULLS, LARUS FUSCUS

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Résumé

L'observation du comportement du goéland brun au nid (Larus fuscus) a permis d'observer l'effet à long terme de nombreux facteurs sur le lissage des plumes, le sommeil et d'autres activités non déterminées. Le nombre des animaux observés augmentait en raison directe de l'avancement de la saison et en raison inverse des minima thermiques quotidiens. Les maxima thermiques quotidiens sont en corrélation positive avec la proportion quotidienne moyenne d'oiseaux endormis. Des oscillations thermiques quotidienne régissent les pourcentages d'animaux qui dorment, mais non pas la proportion de ceux qui se lissent les plumes. De même les marées influent sur la proportion de goélands endormis et aussi, dans ce cas, sur la proportion de ceux qui se lissent les plumes. Le calcul des intercorrélations résiduelles entre les variables du comportement indique que la proportion de ceux qui se lissent les plumes est constante et indépendante de la proportion des oiseaux endormis ou qui se comportent autrement. Une autre série d'observation a montré de plus que des perturbations qui abaissent la proportion d'oiseaux endormis et qui au début font également baisser la proportion d'oiseaux qui se lissent les plumes, sont suivies d'augmentations tardives mais prononcées des activités de lissage.

Summary

By sampling the behaviour of nesting Lesser Black-backed Gulls (Larus fuscus) the effect of a number of longterm factors on sleeping, preening and other, non-specified, activities was investigated. It was found that the number of birds observed increased with the advance of the season and that it depended inversely on daily minimum temperatures. The daily maximum temperatures correlated positively with the mean daily proportion of birds asleep. Strong symmetrical diurnal cycles affected the percentages of birds sleeping and birds engaged in other activities, but not the proportion of birds preening. Similarly, weak symmetrical tidal cycles affected the percentage of gulls asleep and engaged in other behaviour. However, the proportion of birds preening is in this case also affected by a trend similar to that of gulls sleeping. The residual intercorrelations between the behavioural variables indicated that the proportion of gulls preening is constant and independent of the variations in the proportions of birds sleeping and behaving otherwise, but its variability is increased when the proportion of gulls sleeping is low. An additional series of sampling observations showed that disturbances which depress the proportion of birds sleeping and which initially also depress the per-

centage of gulls preening, are followed by delayed and marked increases of preening activity. Finally these results are related to additional but less systematic observations and then discussed in the light of more general considerations.

INTRODUCTION

During observational and physiological studies on the behaviour of Lesser Black-backed and Herring Gulls (Larus fuscus and L. argentatus by R. G. B. Brown (1967 a,b,c) and myself (Delius, 1967, 1970, in prep) we came to suspect that the occurrence of many of the behaviour patterns which interested us were affected by a number of longterm factors which, while not of direct interest to us, clearly had to be taken into account as sources of non-stationarity interfering with the rigorous analysis of behavioural sequences (Delius, 1968). The present paper is an attempt to assess the effect of some of these factors on selected behavioural activities in a quantitative way.

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METHODS

The study was carried out at a large breeding colony comprising approximately 20,000 pairs of Lesser Black-backed Gulls and Herring Gulls, situated on Walney Island, Lancashire, England. Most observations, aided by the use of 10 $\times$ 50 binoculars mounted on a tripod, were made from a tower overlooking a section of the colony containing nearly 250 nesting Lesser Black-backed Gull pairs, during a period lasting from the 31st of April to the 15th of May 1967. Additional observations were made at various times over two breeding seasons, some from hides placed close to nesting birds.

Two types, of observation schedules were followed. One consisted of sessions at hourly intervals in everyone of which it was attempted to watch some 120 birds for 3 to 4 seconds each in quick succession and record whether they were preening, i.e. drawing feathers through their beak, sleeping, i.e. resting their head on the back with the eyes closed, or engaged in other behaviour. 1 to 8 sessions were carried out every day and their timing was staggered from day to day so that over 3 days the whole daylight period had been sampled, and this was continued until each full daytime hour had been recorded on 5 different days.

When these observations were done the gulls had just begun to lay eggs. To avoid that the onset of incubation should modify their activity patterns too radically to allow an assessment of the factors of interest, their eggs were removed everyday. This caused them to relay in a continous way throughout the observation period. The strong site binding which sets in with the egg laying guaranteed that a stable number of resident birds were present in the area during the observation sessions.

The second schedule consisted of 12 series of 10 observation sessions, each taken in quick succession every 2 minutes and only involving recording the behaviour of some 50 birds. On the third session, following two undisturbed ones, the birds were frightened by the observer stepping out of the lookout and waving his arms until a considerable proportion of the gulls under observation flew up. The observations were then resumed for a further 7 sessions.

Weather records were obtained from the Walney Southend Lighthouse and the Barrow Gas Works, both situated a short distance away from the colony. Details about the tides were derived from the Barrow Harbour tide tables.

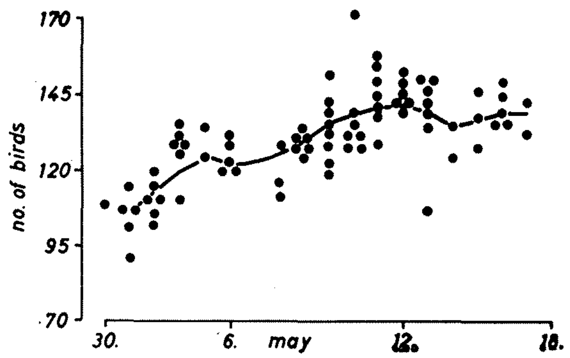


Figure 1

Seasonal trend in the number of gulls observed. Each point indicates an observation session.

RESULTS

The analysis of the data obtained by means of the first schedule yielded the following results :

Seasonal effects.

Although an effort was made to keep the birds in a stable state in the breeding cycle, the data were examined for seasonal trends. None could be detected in the percentages of birds preening, sleeping or engaged in other activities, only the daily mean number of birds recorded in the sessions showed a marked trend (Fig. 1). These numbers of course depended on the effort made by the observer but since a deliberate effort was made to record 120 birds on each occasion, the rise in the numbers actually recorded indicates that the number of birds present rose throughout the observation period. This in fact accords well with more casual observation of the colony as a whole.

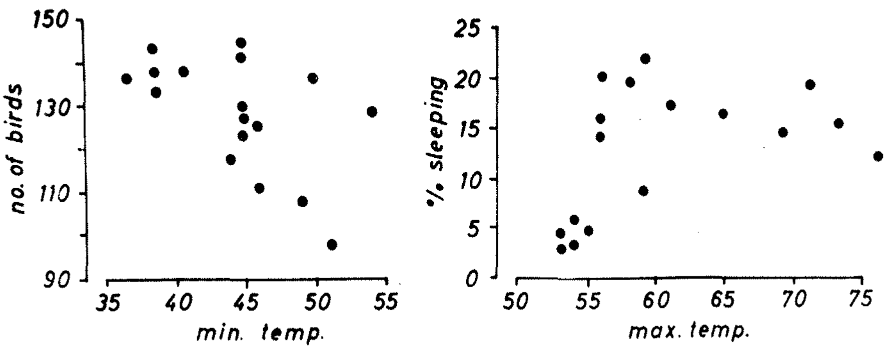
Weather

Although no persistent trends could be detected other than in the number of birds recorded, some day to day fluctuations did exist and it seemed likely that these were due to variations of weather conditions. Therefore the daily mean proportion of birds sleeping, preening and doing neither, as well as the number of birds recorded, were related to the daily maximum and minimum temperatures, mean daily visibility scores, mean daily wind scores, daily barometric pressures, daily rainfall and also daily tidal amplitudes, the latter of course closely connected with the moon cycle. Except for the correlations discussed below none of these proved to be significant.

A positive correlation between the mean daily proportion of birds sleeping ant the daily maximum temperatures (Fig. 2) ($r_s = + 0.51$, $p < 0.05$), suggests that high temperatures are soporific to gulls as they generally are assumed to be to humans.

Figure 2

Correlations between daily temperatures and the daily mean number of gulls observed and the daily mean percentage of gulls asleep.



There was a significantly positive correlation between the mean daily number of birds counted and the daily tide amplitude. But a partial correlation analysis reveals that this is a spurious association. arising in the following way. Only a partial moon cycle had been sampled so that tidal amplitudes were correlated with the date. Since the number of birds recorded was correlated with the date, this also resulted in a correlation between number of birds and tidal amplitude. This is however, an artefact.

Between the mean daily number of birds observed and the daily minimum temperature there was a negative correlation (Fig. 2) ($rs = -0.54$, $p < 0.05$). As a partial correlation analysis showed, this is not due to a correlation between the advancing dates and daily minimum temperatures, and the rising number of birds with date described earlier.

Daytime

No diurnal trend in the number of birds observed was found, even when the number of birds had been corrected for the advance of season effect described earlier. This is somewhat surprising in view of the clear cut impression gained from extended but more casual observations that birds were present in maximal numbers early in the morning and left the colony towards mid-morning, and only begun to gather there again during late evening. That this cycling was not detected must be due to the effort made to observe the same number of birds in each session. This, however, opens the questions of how the seasonal trend mentioned earlier could be detected, although according to impressions it was less pronounced than the diurnal one just described.

The proportion of birds sleeping depends markedly on daytime, being low in the early morning, increasing slowly towards the afternoon and then declining rapidly towards the evening (Fig. 3, the trend is significant by the Kruskal Wallis test, $p < 0.001$). Observations on the behaviour of the gulls at night supplement this picture. The behaviour seems then to depend on the illumination levels: on clear, moonlit nights a good proportion of the birds were quite active while on darker nights most birds could be made out to be sleeping.

The percentage of gulls preening seems to be hardly affected by the time of day, there being no significant trend. Consequently the proportion of birds engaged in other activities is a function of daytime, and is a mirror image of the proportion observed sleeping. This trend is again significant by the Kruskal Wallis test, $p < 0.001$.

Tidal Cycles

While no relation to the tidal cycle could be discerned in direct plots of the percentages of gulls sleeping and engaged in other activities, this was partly due to the considerable scatter introduced by the diurnal rhythms just discussed. When the mean values from the corresponding curves shown in Fig. 3 were subtracted from each datum and these deviations from the mean were plotted against the tide cycle, there were slight trends, with a maximum at high tide, and a minimum just before low tide in the case of the proportion of birds sleeping, and a mirror image thereof in the case of gulls engaged in other activities (Fig. 4). Both trends are significant according to Kruskal Wallis tests ($p < 0.001$).

A direct plot of the proportion of gulls preening against the tide cycle, (and here, as mentioned before, there is no problem with an interfering diurnal cycle), also shows a slight trend which although similar to that of birds sleeping has a maximum sometime after low tide. The trend is also significant at the $p < 0.01$ level according to a Kruskal Wallis test.

The number of birds observed did not vary with the tidal cycle and this accords with more casual observations: only during the highest spring tides was the number of birds on the nesting grounds noticeably increased, probably because no resting places were available on the beach.

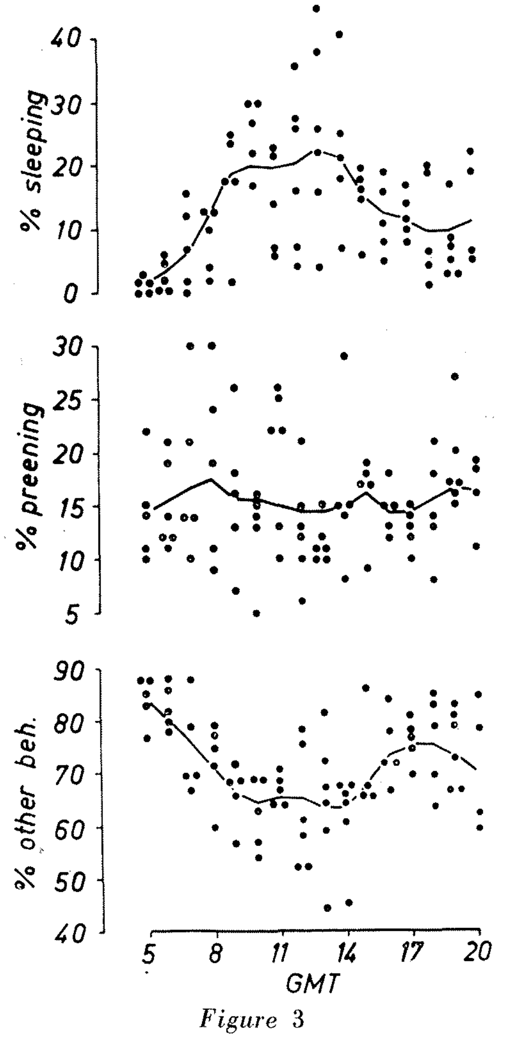


Figure 3

Diurnal trend in the proportions of gulls sleeping, preening and showing other behaviour. The trend lines are sliding averages over three hour intervals. Each point represents observations of over 100 birds. The abscissa is in hours Greenwich Mean Time.

Intercorrelations

It remains to examine whether intercorrelations between behavioural measures, after corrections have been made for the effect of the factors so far discussed, indicate the presence of further factors affecting them. For this purpose the percentages of birds preening, sleeping and engaged in other behaviour activities were

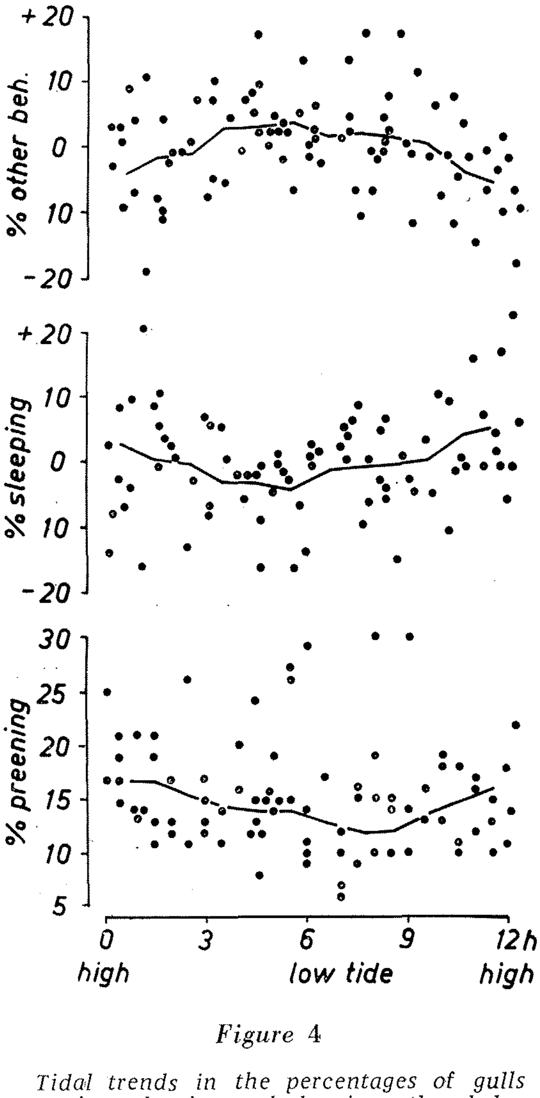


Figure 4

Tidal trends in the percentages of gulls preening, sleeping and showing other behaviour. The trend lines are sliding averages over three hour intervals. Each point is based on observation of over 100 birds.

corrected for the effect of diurnal and tidal influences and plotted, (as is adequate for such proportional measures), on a triangular co-ordinate system (fig. 5). This shows that the number of preening birds is virtually constant, with varying proportions of birds sleeping and engaged in other activities, these being inversely related to each other. Further we observe

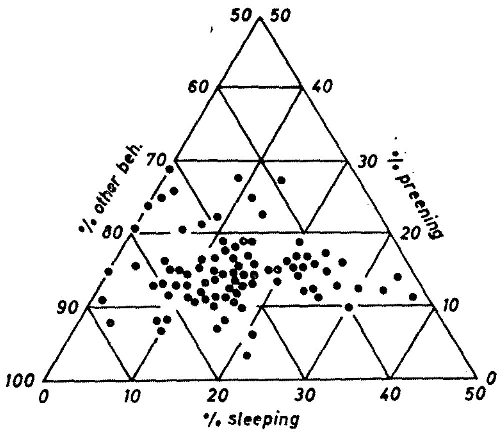


Figure 5

A correlogram of the percentages of gulls sleeping, preening and behaving otherwise. Each point indicates an observation of over 100 *birds.*

that at lower percentages of birds sleeping, that is at higler percentages of birds behaving otherwise, there is an increased scatter in the proportion of birds preening. Some casual observations suggested that this might be due to transient decreases and increases in the number of birds preening when disturbing events tended to arouse the birds from the baseline behaviour. More systematic observations to test this are described in the next section.

Disturbances

During the observations which led to the preceding results it was repeatedly noticed that even short lasting disturbances caused by persons, cattle, or predatory mammals like weasels and stoats moving through the colony, or sometimes even violent fights between some gulls, caused more than transient changes in the behaviour of the birds. For this reason a series of observations was made, following the second schedule described in the methods section. The results are schown in Fig. 6 were the proportion of birds sleeping, preening and engaged in other activities during each session are plotted as a function of time. The proportions of birds sleeping drops to zero during the disturbance and then recovers slowly to normal over the next 14 minutes, and this is what one might expect. The delayed peak in the proportion of birds preening, occuring some 4 minutes after the disturbance, and its slow decay to normal not complete some 14 minutes later, is however striking. The proportion of birds engaged in other activities shows a peak during the disturbance itself and decays to a normal level over the next 10 minutes and possibly then overshoots to a sub-normal level during the 12th and 14th minute after the upset. All the trends are significant at $p < 0.001$ according to Kruskal Wallis tests.

DISCUSSION

The results suggest that weather conditions do not affect the behaviour of the birds in any decisive way, except for the findings that the proportion of sleeping gulls correlated positively with the daily maximum temperatures, and that the number of birds recorded correlated negatively with the daily minimum temperature. The first finding seems to agree with the general assumption that higher temperatures are soporific. Additional casual observations lend support to this for the case of gulls.

The increased number of birds observed at lower temperatures is less easily explained. Under bad weather conditions birds in the colony were generally unwilling to fly even after disturbances. This circumstance may be responsible for the correlation. It is surprising that a number of birds did not correlate with such factors as wind, visibility and rain, since general observations showed these factors to have the same bad-weather effect. However, the observations did also suggest that only extreme weather conditions markedly affected the behaviour of gulls. Such did in fact not occur during the period of this study.

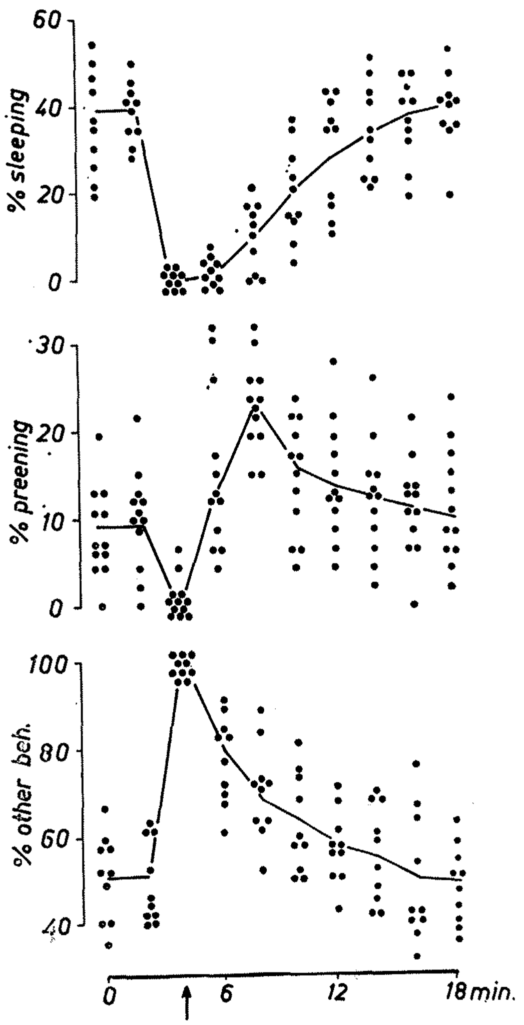


Figure 6

The behavioural response of gulls to a disturbance (indicated by an arrow). Each point represents observations on 50 birds.

The increase of the number of birds observed with the advance of the season fits well with observations that the site tenacity and attendance of gulls increases markedly during the egg laying period, probably due to hormonal factors functionally adapted to insure a prompt beginning of incubation. It is somewhat surprising though, that the advance of season did not affect the other behaviour measures, since Brown (1967) has described a number of changes in behaviour occurring with the advance of the season. However, the behaviours he dealt with were all closely related with reproductive functions, whereas those I am concerned with here are not.

A strong effect of daytime on the proportion or birds sleeping and engaged in other activities agrees well with general experience. The fact that the percentage of gulls preening is not affected is, by the same criterion, somewhat unexpected. Whether the diurnal cycles are endogenously or exogenously determined can of course not be decided from these results, but it seems likely that they are the compound action of both. In any case it is clear that the various behaviours of gulls are differentially affected by diurnal rhythms and this is in accordance with findings on a number of other species (Aschoff 1965, Delius 1963, 1968).

The relatively small influence of the tide cycle on the Lesser Black-backed

Gulls's behaviour recorded here, is somewhat surprising in view of the fact that these gulls have a relatively marine habitat in comparison with Herring Gulls, for which Drent (1967) has described a marked influence of tidal cycles on behaviour. On the other hand they are not coastal but rather open sea feeders and this may make them less tide dependent. It must be remembered though that none of the measures taken were related to feeding (compare Boecker, 1968). Even so, all three behaviour measures were affected, if only in a slight way, by the tidal cycle and this opens the question of whether these rhythms are determined by external or internal factors. The fact that the cycles were detected in gulls observed away from any immediate tidal influences is suggestive that internal rhythms play a role.

A more general question is whether these observations made at the bird's nesting sites are representative for the colony population as a whole, since during the egg laying period, an average of one third of the gulls were estimated to be away from their nests at any one time : some of them foraging, some resting, usually on the mud flats close to the colony. Extensive but unsystematic observations of these latter gulls suggest that while the proportion of birds sleeping and preening was on average higher there than at the nesting site, the diurnal and tidal variations were similar at and away from nesting site.

It must also be borne in mind that some of the effects described might be subject to seasonal changes, the present observations having been obtained during a restricted period of the annual cycle. Season changes in diurnal rhythms have in fact been repeatedly demonstrated in other species (Aschoff and Wever, 1965, Delius 1963).

The persistence with which disturbances alter the behaviour of the gulls merits underlining, the more so as it is my definite impression that the behavioural changes are more complex than those indicated here. It was obvious for example, that immediately after the disturbances and before the onset of the peak in preening activity there is a considerable increase in aggressive behaviour. Following the peak there is, in turn a quite consistent rise in courtship and sexual activities, the most striking component of this being a burst of copulatory mounting some 10 minutes after the disturbance. Even though this is not reflected in the measures taken here, there could be little doubt that the gulls did not return to baseline behaviour until some 30 minutes after the disturbance.

I earlier suggested (Delius, 1967) that the preening of gulls is a characteristic behaviour of a specific dynamic stage in the sleep-wake continuum, corresponding to the transition from a high level to a low level of arousal. The results just reported accord with this view. It should be added that similar results were obtained in two further experiments in which less drastically arousing stimuli were presented to incubating gulls in one case, and caged juvenile gulls in the other. A statistically significant delayed peak in the occurence of preening behaviour and other comfort behaviour was present in both cases (Delius, in prep.). This response pattern occurs in other species (voles : Fentress, 1968 ; rats : Bindra and Spinner, 1958) and in fact is probably widespread among vertebrates if our unsystematic observations on a variety of species can be relied upon. Why this should be so I have attempted to explain elsewhere (Delius, 1970).

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