The daily cycle of feeding activity of the Greater Flamingo in relation to the dispersion of the prey *Artemia*

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Introduction

The salinas of the Camargue (Delta of the Rhône, southern France) are the only regular breeding locality of the Greater Flamingo *Phoenicopterus ruber roseus* in Europe (Johnson 1975). During the summer a group of non-breeding birds, or of failed breeders, numbering from 1000 to over 4000 individuals normally appears in the high salinity areas of the salinas, where they undergo moult. Breeding birds flight into and out of the colony at dawn and dusk, either to relieve the incubating partner or to feed young, and some feeding activity takes place at all hours of day and night. The non-breeding birds, however, which are not constrained to visit the colony, feed almost exclusively at night and roost during the daytime at a traditional site where there was formerly a breeding colony, (last used in 1969). In the evening the majority of these birds fly 1 to 5 km to lagoons with a higher salinity (150 to 250 g/l NaCl) where an undescribed brine shrimp species of the genus *Artemia,* is virtually the only prey available. Examination of the stomach contents of birds killed by collision with overhead wires confirm that *Artemia* comprises practically all the diet. Small numbers of Diptera larvae *(Ephydra bivittata:* Ephydridae and *Thinophilus achilleus:* Dolichopodidae) occur in the lagoons and have occasionally been found in flamingo faeces, but they almost certainly comprise a negligible proportion of the diet.

Some preliminary observations on *Artemia* suggested that they were more abundant in net samples taken at night in the upper 5 to 10 cm of water, than in similar samples taken during the daytime. In addition, *Artemia* could not be seen near the surface during the daytime. These preliminary findings, plus the occasional observation of flamingos feeding at night by surface "skimming" (Rooth, 1965), lead to a hypothesis that *Artemia* was undergoing a vertical diurnal migration and was concentrating near the surface at night where it would be highly vulnerable to flamingo predation. A study of the diurnal changes in the dispersion of *Artemia* was therefore undertaken in order to determine whether the night time feeding activity of flamingos was indeed an adaptation to foraging during the period when their prey was most accessible.

Methods

Daily time budgets of flamingo activity were established by scan sampling (Altmann 1974) of flocks every 15 minutes throughout the 24 hr, recording the proportion of birds involved in feeding and other activities. Night-time observations were made using an image intensifier, but, even with this equipment, poor visibility restricted observations to moonlight conditions (within 5 days of full moon). The number of birds under observation at any one time varied greatly, and was generally higher in daytime than at night.

Vertical movement in *Artemia* in the water column was studied using a zooplankton net of rectangular cross-section divided into seven horizontal shelves each 10 cm deep (water depth was 40 cm in sampling locations so that only four shelves were actually used). The net was placed on cylindrical plastic rails embedded 30 cm apart in the bottom substrate, which prevented the bottom shelf from filling with mud. The net was gently pushed forward through the water for a distance of 4.5 m at a slow walking speed, the entrance being closed by a vertically sliding plate when the sampler was lowered into and lifted out of the water. *Artemia* did not appear to be able to avoid the sampler, so that the collections probably give an unbiased representation of the vertical distribution. Samples collected by the net were passed through a sieve of 1 mm mesh which retained all adult and subadult stages (Heath 1924), and only these were counted. Some preliminary samples in which all stages were counted indicated that larval *Artemia* showed similar basic trends in vertical movement over the diurnal cycle as adults, but were always more randomly dispersed, presumably because they are less capable of swimming against weak wind-induced currents.

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Cladocera (Stearns 1975) and *Artemia* show reduced activity in darkness which might make them more susceptible to predation by flamingos at night. In order to test this possibility, *Artemia* were sampled using a hand-operated peristaltic pump with a flow rate of approximately 2 l/min. This compares to a water clearance rate of 0.5 l/min measured for the Lesser Flamingo *Phoeniconaias minor* which has a body weight approximately half that of the Greater Flamingo (Vareschi 1978). The pump was operated in a way to mimic flamingo feeding. The intake consisted of a plastic funnel 5 cm in diameter mounted on a pole which was moved backwards and forwards in an arch through the water column as the operator walked slowly forward. Samples were taken at eight points on a transect across a lagoon, five replicates being taken at each point during the daytime and two at night.

Results

Flamingo feeding activity

Non-breeding flamingos feeding in high salinity lagoons showed a consistent pattern of feeding activity over the 24 hr cycle. The data presented (Fig. 1) are for one 24 hr period. The results of other observation periods in the summer months are similar, but less complete.

During the hours of darkness 70–100% of the birds under observation were feeding (heads down and bills partially or fully immersed), but during the day little or no feeding took place, and the time was spent in sleeping and comfort activities. There is some indication, confirmed by other data, that the majority of birds cease feeding during the period between first light and sunrise, and birds are vigilant (head raised, frequent calling) during this time. Some

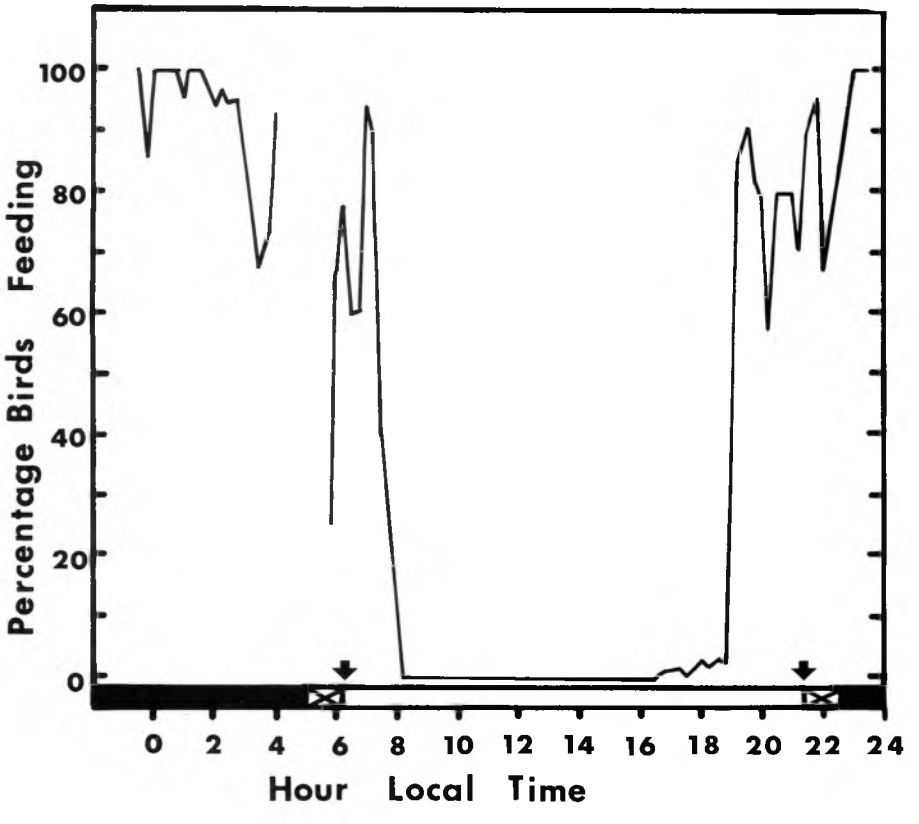

Figure 1. Percentage of Flamingos under observation indulging in feeding activity over a 24 hr period on 26–27 June 1979. The number of birds varied from 16 to 1400 individuals. The times of sunrise and sunset are indicated by arrows and the period of darkness by a black horizontal line.

feeding activity resumes after sunrise before birds fly off to the daytime roost. Flamingos start feeding again up to two hours before sunset as they progressively leave the roost and begin to occupy the feeding lagoons, and by nightfall all birds are feeding again.

Artemia distribution

The results of eight series of samples taken with the zooplankton net in two of the feeding lagoons during both day and night between May and August 1980 all show similar patterns of diurnal change in vertical distribution. The data presented (Fig. 2) show a typical pattern under conditions of low wind velocity.

During daylight hours most *Artemia* aggregated in the bottom 10 cm, evidently because of a negative phototaxis as described by Manouvriez (1977). Contrary to expectations, at night there was no surface aggregation and under most conditions *Artemia* were dispersed in the water column, though there was a tendency for the top 10 cm to be avoided. This became more pronounced under windy conditions. The distribution of *Artemia* in the remaining depth strata at 20.00 hr and at 04.00 hr on 5–6 May (Fig. 2) does not depart from an even distribution (for 20.00 hr $x^2=1.78$, and for 04.00 hr $x^2=4.67$; d.f.=2, $p>0.05$). The presence or absence of moonlight appeared to have no effect on the night time vertical distribution.

The peristaltic pump caught more *Artemia* in the day than at night (mean day = 14.0 indiv./l; mean night = 6.8 indiv./l). There were, however, enormous variations between samples, so the difference is marginally not significant (Mann-Whitney U test on means for each sampling location, $p = 0.052$). Thus there is no evidence that the reduced activity by *Artemia* at night results in a greater ease of capture by flamingos, and the differences in the densities recorded can be explained by the greater vertical dispersion of *Artemia* in the water column. Night-time catches in shallow areas of the lagoon where the water depth was only 10 cm, tended generally to exceed those in the same location during the day. Extremely high catches were obtained by day in deeper areas (depth 40 cm), indicating a horizontal displacement over the daily cycle. These results suggest that the optimal daytime strategy for flamingos would be to feed during the day in the deepest part of the lagoon.

Discussion

The diurnal pattern of feeding activity shown by non-breeding flamingos in the Camargue is in agreement with that of Rooth (1965) in the Caribbean and Studer-Thiersch (1972) in Spain, who also report low levels of feeding activity by *Phoenicopterus ruber* during the daytime, with increases towards dawn and dusk. These authors, however, lack extensive

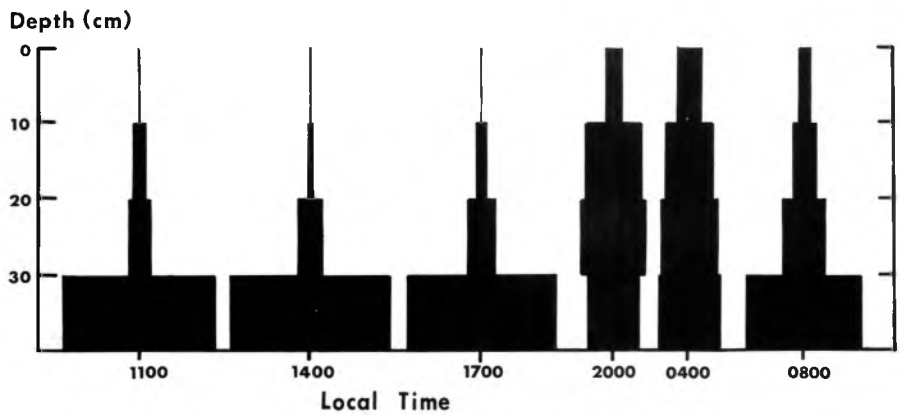

Figure 2. Vertical percentile distribution of adult and sub-adult *Artemia* at six sampling times over a 24 hr period on 5–6 May 1980. Samples taken at 20.00 hr and 04.00 hr were in darkness. Salinity approximately 110 g/l NaCl.

data showing that feeding is concentrated in the hours of darkness. In neither study was the diet of the birds recorded, but *Artemia* were absent from the lagoons studied by Rooth.

Feeding activity at night would appear to be mal-adapted to efficient foraging on *Artemia*, but it is possible that this behaviour serves other functions related either to predator avoidance or to thermoregulation.

Many Anatidae have similar cycles of feeding activity to that shown by flamingos. In these species night time feeding is thought to be an adaptation to avoidance of diurnal predators, especially raptorial birds (Tamisier 1970, 1972; Willi 1970). Fledged flamingos, however, now have no natural predators in their Palearctic range, and the Greater Flamingo is now a protected species, although some birds continue to be shot illegally. This is therefore not likely to be a major mortality factor. Hunting pressure in the salinas is relatively low and the period of observation was in the closed season when there was no hunting. Under most circumstances in the Camargue flamingos continue to be wary of man and are also susceptible to disturbance from low-flying aircraft. The lagoons used for feeding are mostly smaller (mean 68 ha) than that in which the day roost is situated (230 ha) so that disturbance from human activity on the shoreline is more likely in the former. Night-time feeding could thus in part be an adaptation to avoid human disturbance.

An alternative explanation of night time feeding by flamingos is that it serves a thermoregulatory function. Feeding is an energetically demanding activity for a flamingo, not only because of the mechanical work involved in filtration (Pennycuick & Bartholomew 1973), but also because of the energy expenditure for food assimilation. This energy expenditure increases in the domestic chicken at temperatures above the temperature for thermoneutrality, i.e. about 18°C (Calder & King 1974). Kendeigh (1969) estimated that the capacity for useful work in House Sparrows *Passer domesticus* declined at temperatures above the thermoneutrality temperature, which is about 22°C in this species, because of problems in dissipating the mechanical heat produced. Thermoneutrality temperatures have not been measured in the Greater Flamingo, but ambient temperatures are sufficiently high in Camargue (mean daily maximum for July = 28.6°C), to suggest that it may be advantageous for birds to feed at night in summer and spend the daytime in non-demanding comfort activities. Even in winter, when temperatures are consistently below the thermoneutrality temperature, and energy must be expended to maintain body temperature, it may still be advantageous to devote the colder part of the 24 hr cycle to feeding activity and spend the daytime in energy conserving activities such as sleeping. In winter, when *Artemia* are absent from the salinas and food densities are lower than in summer, flamingos spend a larger proportion of the day feeding, but still with a tendency for reduced activity, while most birds feed continuously at night (Johnson 1983).

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Summary

Non-breeding adult Greater Flamingos *Phoenicopterus ruber* filter-feeding on the brine shrimp *Artemia* in the salines of the Camargue, France, feed almost exclusively at night and roost during the daytime. *Artemia* undertakes a diurnal vertical migration and is concentrated near the bottom during the daytime, but is dispersed at night. Night-time feeding is thus non-adaptive in terms of foraging efficiency but may serve an anti-predatory or thermoregulatory role.

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