THE FUNCTION OF COMMUNAL ROOSTS: RELEVANCE OF MIXED ROOSTS

Zahavi (1971, 'Ibis' 113: 106-109) has recently reviewed the problem of the functional significance of communal roosting in birds. He is inclined to the view that efficiency in food location promoted by the communal roosts acting as information centres (Ward 1965, 'Ibis' 107: 173-214) is the primary function of communal roosts, while the adaptations against predation are a response to increased predation pressure consequent on the assemblage of birds. I think that a consideration of the phenomenon of mixed communal roosts, and an examination of the significance of communal roosts in the light of Hamilton's (1971, 'J. theor. Biol.' 31: 295-311) suggestion regarding the adaptive significance of flocks, are pertinent in this context and suggest that predator avoidance may be an important function of communal roosts in its own right.

A review of the habit of communal roosting in Indian birds shows that a significant proportion of these roost in close associations of two or more species. Whistler (1935, 'Popular handbook of Indian birds') notes that the White Wagtail Motacilla alba and the Yellow Wagtail M. flava commonly roost together and so do the House Crow Corvus splendens, Common Myna Acridotheres cristis, and Rose-ringed Parakeet Psittacula krameri. The Rosy Pastor Pastor roseus often joins the Common Myna at its roosts. I have observed mixed communal roosts of the House Crow, the Jungle Crow Corvus macrorhynchos and the Common Myna, and associations of the Cattle Egret Ardeola ibis, Little Egret Egretta garzetta and Common Myna. P. Gole (pers. comm.) has observed a mixed communal roost of the House Crow, Jungle Crow, Common Myna, Rose-ringed Parakeet and Cattle Egret on a single Peepal Tree Ficus religiosa in a well-wooded area and was told by the local inhabitants that the roost was probably very old. The association of the two or more species when participating in a mixed roost is very close, though the associates tend to remain discrete by being concentrated in different parts of the roosting tree, or by occupying separate trees if more than one roosting tree is needed to accommodate the roosting population. Nonetheless, they aggregate in as small an area as possible and will not occupy two separate roosting trees leaving some unoccupied in between.

If there were no positive advantage accruing to communally roosting birds through predator avoidance, it is difficult to see how such associations could have evolved. The increased numerical strength and diversity of the mixed roost renders it all the more conspicuous, at least to the ornithologist. I have been observing a mixed roost of House Crows, Jungle Crows and Common Mynas for the past several months. The Jungle Crows gather on a hill near this roost from as long as an hour before sunset and indulge in pre-roosting aerial displays there. The Common Mynas arrive largely during the half-hour before sunset and display on the ground or in trees close to the roost, while the House Crows fly in mostly after sunset directly to the roosting trees. There is therefore a lively activity of birds for almost an hour and a half and over a large area near the mixed roost every evening. During the period of observation the mixed roost became split on one occasion. The House and the Jungle Crows moved together to a roost about 300 m from the old roost, while the Common Mynas stayed on at the old roost. Each of the two separated roosts was definitely less conspicuous to me. However, this state lasted for only about four weeks after which the Common Mynas shifted their roost to precisely that occupied by the two species of crows. The unified mixed roost was again as conspicuous as before the split.
A priori there appears little possibility of any information about the location of food being communicated amongst birds of different species, especially as none of the associates mentioned above appear to form mixed flocks for feeding. Such information exchange is clearly out of the question when the associates are of such different feeding habits as the Cattle Egret and the Rose-ringed Parakeet. However, the House and the Jungle Crow and the Common Myna are all three omnivorous and there could have been some communication amongst the three species as to the location of food sources. I therefore watched the three species leave the mixed communal roost at dawn. The timings of their departure from the roost were as distinct as the timings of their arrival at the roost and the birds left in parties restricted to single species. We can therefore definitely rule out the possibility of increased efficiency of food location as a function of the interspecific association.

It would then appear that the function of these mixed roosts must relate to predator avoidance. Exploration of this problem will be facilitated by an explicit definition of the various parameters involved in predation at a communal roost. Let $p(N)$ be the probability of an individual which is a member of a communal roost of strength $N$ being detected by a predator, and $q(N)$ be the probability of a member of a roost of strength $N$ being captured once it has been detected. Then, $p(1)$ is the probability of a solitary rooster being detected, and $q(1)$ is the probability of such an individual being captured following its detection. If we leave aside considerations of how large a feeding range can be covered by individuals from a communal roost and so on for the moment, then the optimal roost size $\hat{N}$ is that at which $p(N)q(N)$ reaches a minimal value.

It is generally claimed that $p(N)$ increases as $N$ increases, i.e. the probability of an individual being detected increases as that individual becomes a member of a communal roost of a larger and larger size. However, the theoretical argument developed by Hamilton (op. cit.) suggests that this need not necessarily be so. The argument is based on the fact that $p(N)$ is not to be regarded as the probability of the whole group being detected, but must be interpreted as the probability of a given individual being detected. An increased probability of a whole group being detected need not imply an increased probability of a particular individual being detected. In fact prey animals may hide by seeking cover among other animals of the same species. Zahavi (op. cit.) cites good evidence that $q(N)$ decreases as $N$ increases, i.e. a given individual, once detected, has a better chance of escaping predation when it is a member of a larger roost because of the warning that may be conveyed to it by the other members of the roost. There is therefore no a priori reason to believe that a decrease in $q$ may not be sufficiently large to compensate for an increase in $p$, and thereby confer an advantage to a communal roost towards predator avoidance.

Although it is not possible to make exact statements at this stage about the roost size at which $p(N)q(N)$ will reach a minimum, we can suggest certain trends. If these trends are verified empirically, then the argument that predator avoidance is an important function of communal roosting will be strengthened. If $p(N)$ increases rapidly with $N$, then larger communal roosts will be strongly disfavoured, and the optimal roosts size will be small; whereas if $p(N)$ does not increase rapidly with $N$, then the optimal roost size will be large. The latter condition will hold for birds roosting in large protected locations such as large crevices or chimneys. The communal roosting of the Chimney Swift Chaetura pelagica may provide an example of this. Similarly, birds which inhabit open country may not be able to render themselves very inconspicuous even when roosting solitarily, and therefore may not lose much by roosting in large groups. The House and the Jungle Crows and the Common Myna cited above as communal roosters are in fact birds of very open country.

Also, the steeper the decline in $q(N)$ with an increase in $N$, i.e. the more effective the warning system, the larger would be the optimal size of the communal roost. The more
social species would be expected to have evolved the most effective systems of warning each other against predation. We would therefore expect the species which normally feed socially to show a propensity towards roosting socially. It is therefore difficult to distinguish between efficiency of food location or predator avoidance as functions of communal roosting for the species which feed socially throughout the year. However, if predator avoidance is the major function of communal roosting, then a species which feeds socially only for a part of the year should not cease to roost communally during the season of solitary feeding, unless some special conditions such as breeding prevail. Zahavi (op. cit.) cites much data bearing on this problem.

It therefore appears plausible that predator avoidance is a function of communal roosting in many species which do not form mixed roosts, and highly probable that it is the function of communal roosting in those species that associate with other species in forming mixed roosts. If individuals of one species can respond to the warning signals of individuals of the other species they associate with in the mixed roost, then the advantage of communal roosting towards predator avoidance will be augmented and mixed roosting favoured. The advantage would be particularly great if the other species is one like the House Crow which will not only warn, but actively drive away the predator. The advantage could also derive from some sort of a threshold phenomenon. Suppose that considerations of feeding range limit the size of a communal roost for any one species below some threshold of numbers such that if the population were higher than this threshold, at least one individual would be awake at any one time throughout the night. Then this threshold population may be exceeded by the formation of mixed roosts.

However, mixed roosting need not be mutually beneficial to all the species involved. Thus the Common Myna may benefit from the association of the more aggressive crows, but from the viewpoint of the crows the advantage conferred by the mynas in warning of the approach of predators may not compensate for the disadvantage of making the roost more attractive to predators. In the case of the observations cited above this may perhaps have been the reason why the crows changed their roosting site, only to be followed by the mynas.

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