Breeding Ecology of Birds

Why do Some Species Nest Singly While Others are Colonial ?

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One of the most fascinating aspects in the life of birds is their breeding phase, which is intimately tied to the distribution and abundance of food resources in their environment. However, food is not evenly distributed in space and time, and this is thought to have been one of the factors affecting the evolution nesting strategies. To understand how birds have evolved different types of nesting patterns ornithologists have used a variety of approaches, the most useful of which have been to build simple models based on optimality principles.

Birds are a familiar feature of our environment and everyone notices them. It is small wonder then that bird-watching is such a popular pastime the world over. Due to their varied life styles, conspicuousness, diurnal habits, and interesting plumage and calls, birds are also regarded as good subjects for exploring a number of questions of ecological and conservation significance. One of the most fascinating aspects in the life-cycle of birds is their breeding phase. It is a common observation that different species of birds breed at particular times of the year. For instance, over much of India, come spring and the hot weather, a flurry of activity is to be seen in the bird world. One of the commonest sights then is that of sparrows building their untidy nests in the cups of ceiling fans.

Broadly speaking, food is believed to be one of the most critical resources for the survival and reproduction of animals. A well-known theory in ecology known as the 'food availability-breeding time' hypothesis suggests, rather logically, that most birds breed at that time of the year when plenty of food is available for their chicks. Seen in the light of behavioural ecology, which attempts to explain animal behaviour in terms of direct or

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indirect enhancement of their reproductive success (Darwinian fitness), this theory makes sense and has fairly wide applicability. However, several exceptions have also been noted and these can be explained by the fact that in some cases birds have to make trade offs and balance the conflicting pressures of other forces in their environment. These may include pressure from predation, punishing weather regimes, or competition for nesting sites.

Figure 1. A Coppersmith Barbet. Barbets are highly territorial birds and advertise their territories by their ringing, metallic calls which sound like a hammer working in an ironsmith's workshop. Their calls are said to possess ventriloquistic qualities.

The availability and distribution of food is linked to a host of factors. For instance, for many frugivorous birds such as barbets, parakeets and others, the time when trees come into fruiting and flowering may be synchronized with climatological patterns. However, over much of India it is the monsoon which exerts a key influence over the food cycles of birds. Salim Ali, in a beautiful essay on the nesting habits of Indian birds entitled 'Stopping by the woods on a Sunday morning', writes "The monsoon is the breeding season par excellence of insectivorous birds, and also of the numerous others who, though when adult, subsist principally on grain, yet require soft food in the nature of juicy grubs and caterpillars to nourish their young in the nest".

To understand how birds have evolved different types of nesting patterns, ornithologists have used a variety of approaches, the most useful of which have been to build simple models based on optimality principles. In this article I will discuss some of these approaches in the hope that they will be interesting to biologists and non-biologists alike, and also illustrate the general principles for building simple behavioural ecology models. To make my task easier I shall restrict myself to two contrasting types of nesting patterns found in the world of birds, namely solitary nesting and colonial nesting. A number of birds such as barbets, owls (see *Figures* 1 and 2), hornbills, sparrows, mynas and bulbuls build nests in isolation. On the other extreme is group-nesting or colonial-nesting, as exemplified by some water-birds. Their colonies, known as

Figure 2. A Spotted Owlet is another solitary nester.

Box 1. Indian Heronries: a Habitat in Peril

One of the best examples of colonial nesting in birds is heronries but, interestingly, the term heronry itself is a bit of a misnomer. In England, the tree on which herons nest is known as a 'heronry' and it makes perfect sense to call it so because only herons are found on such trees. However in India, which has a much greater diversity of colonial water-birds, a heronry is seldom composed of nests of only herons as other birds such as storks, ibises, spoonbills, cormorants and egrets may also nest on the same tree. Since the pioneering work on Indian birds was carried out by Englishmen, one would suspect that the term 'heronry' has just stuck on and not been replaced for want of a better word.

Heronries have often been written about in slightly disparaging terms by ornithologists. For instance, their nests have been described as 'rude' or placed 'cheek by jowl'. Terms like 'mohulla', 'bazaar', etc. have also been used for describing them. Considering that heronries are inhabited by fish-eating birds, they are often not regarded as an altogether pleasant place to be in, with fishy odors emanating from them! Due to this reason, local people sometimes resent heronries in their neighborhood and may even cut heronry trees or drive the birds away. However, the droppings of the birds provide a rich source of fertilizer and this is generally valued by the local people.

India is well-endowed with heronries with some states such as Gujarat and Karnataka having large numbers of recorded heronries. Since heronries are a highly clumped breeding effort in space and time they are also vulnerable to destruction. Since many heronries lie outside the protected areas network, for example in or around village ponds (*Figure* A), they are at the mercy of local sentiments where considerations of convenience and commerce often come first and conservation generally takes a back seat. Thus, a tree with nests of herons, storks, pelicans can easily come under the axe to fulfill local timber or energy demands. Since heronry birds are dependent upon wetlands for their food, an additional threat comes from the fact that wetlands are themselves under threat. Unfortunately, wetlands are generally regarded as wastelands, breeding grounds for mosquitoes and thus a source of malaria, and from the viewpoint of administrators and land developers, they are thought to be fit only for land reclamation. Due to these reasons a number of heronry birds of India are under severe threat and require urgent protection.

Figure A. Many heronries in India are located in village ponds such as the one shown in this picture of a village pond in Gujarat.

heronries (*Box* 1), can be seen in most places around water (*Figure* 3), but to see really impressive ones you will need to travel to a bird sanctuary such as Keoladeo Ghana National Park at Bharatpur in Rajasthan, Ranganthitoo bird sanctuary near Mysore in Karnataka, or Vedanthangal sanctuary near Chennai in Tamil Nadu.

Figure 3. A colony of Painted Storks.

The Economic Defendability Model

Our starting premise for this model is that resources (primarily food) are not evenly distributed in space and time. In fact, only three situations are possible, as shown in *Figure* 4. The first situation, with resources being randomly distributed (A), is not very realistic because resources like food, nesting material or availability of mates are generally not randomly distributed. Typically, resources are tied to physico-geographic features of the landscape and are distributed along certain well-defined patterns in the natural world across all scales. Therefore the second situation (B) in which resources are regularly distributed is perhaps more realistic. Consider a forest in which there are a number of trees attracting insects, birds and other fauna due to their fruits, flowers or the insects, in turn, attracted to them and also the substrate which the trees themselves offer in terms of a habitat (say, for nesting). The distribution of the trees will not be random because they are themselves distributed along some well-defined gradients of soil, moisture and the like. The third situation (C) is one in which resources are clumped in their distribution. Imagine schools of fish in an ocean. Such resources are neither distributed randomly nor

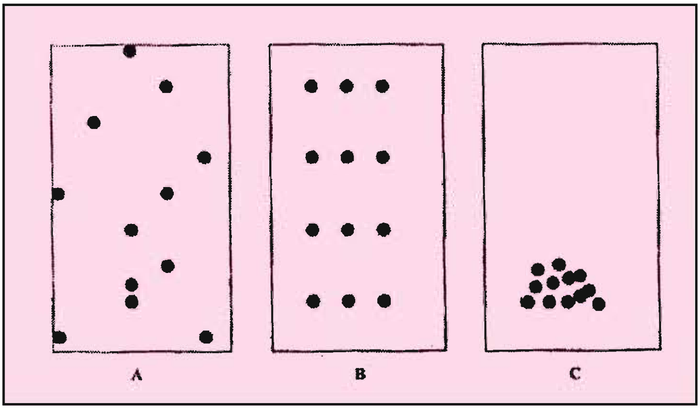

Figure 4. The basic patterns of resource distribution. Each black dot represents one unit of a resource. A, random; B, regular; C, clumped.

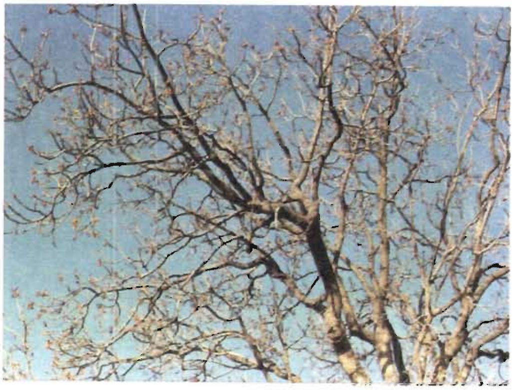

Figure 5. Resources can be clumped in time . The picture shows a tree in flowering phase, which may happen only once a year.

regularly. There are vast empty spaces where there will be no fish and then suddenly a school is encountered. From the view point of a predator, say, a sea-bird, vast distances have to be covered to track and locate these localized food resources but once sighted, there is no real scarcity because of the local supra-abundance of fish. Besides being localized in space, food or other resources can also be clumped in time. For instance, imagine a forest bird which depends upon the nectar of flowers, which, in turn, depends upon the time when the tree comes into the flowering phase (*Figure* 5). Since this may happen only at a particular time of the year, the resource, from the point of view of the bird, is localized in time.

Given these basic patterns of resource distribution, we can now ask the question: what sort of nesting patterns should evolve in different environments? In *Figure* 6, again consider the black dots as resources and assume that in any area a pair of birds require 6 units (dots) of resources to survive and reproduce. In situation A, the resources are densely and fairly uniformly distributed. Consequently, five pairs of birds can survive in this area, each with a small territory (outlined with dotted lines) that can be defended with ease. However, in situation B, with resources distributed sparsely and somewhat spaced out, only

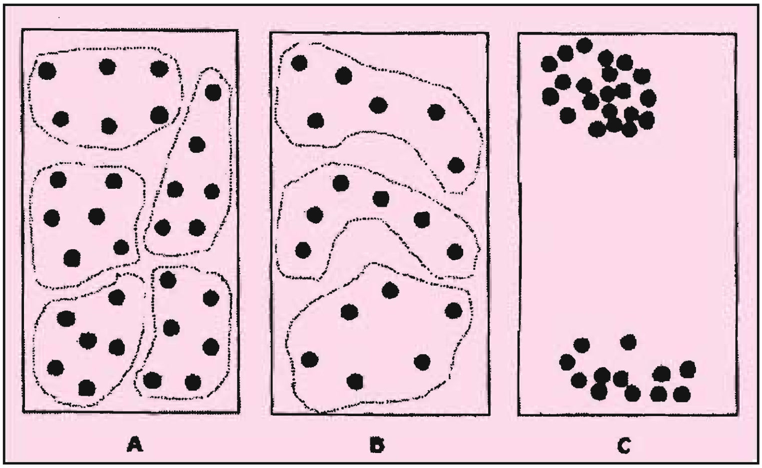

Figure 6. The formation of territories in relation to resource distribution. A. An abundance of resources leads to several individuals forming small, compact territories; B. Due to the scarcity of resources fewer territories are possible, leading to significant demographic changes; C. When resources are clumped in their distribution, defense of territory is meaningless and territoriality breaks down.

three pairs of birds will be able to survive and each will have a comparatively larger territory perimeter to defend. The effort (in terms of energy and time) needed for this defense, however, may not always be justified by the amount of resources preserved by the defense. *Figure* 6 C presents a situation in which the resource distribution is highly clumped. If a pair of birds decided to defend this superabundance of resources and was successful, much of the resources would go unutilized. Moreover it would also be pointless to defend this resource if it was located far away from the nest as in the middle of a large water body, for example.

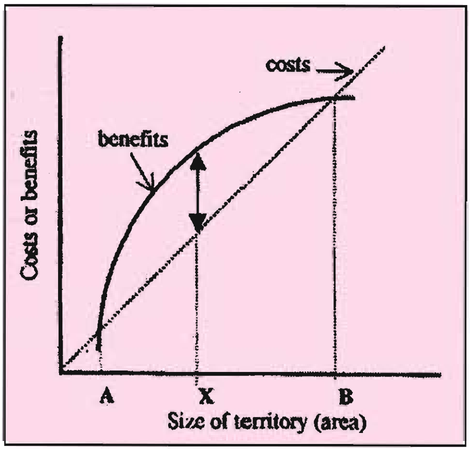

Figure 7. A graphical presentation of Jerram Brown's economic defensibility model. As territory size increases both the costs and benefits increase, but in a different manner. The costs, such as energy needed for the defense of territory increase in a linear manner with increasing territory size. However, the benefits, say, the amount of food, increase very rapidly at first but level off after a certain territory size. According to the model, territories of size between A and B are worth defending, and the optimum territory size is at X where the benefit:cost ratio is maximum.

(Redrawn from Perrins & Birkhead, 1983).

Another way to look at this situation would be to ask the question: what should be the optimal territory size for a bird? This is best described by the economic defendability model proposed by Jerram Brown in 1969 (*Figure* 7). The model hypothesizes that as territory size increases, both the costs and the benefits increase, but in different ways. The costs may be in terms of energy used to defend the territory from conspecifics and the benefits may include the reserves of food or nesting material that can be obtained with ease within a defined area. The model makes the assumption that the costs increase more or less linearly but the benefits increase rapidly at first and then level off.

The Economics of Solitary and Colonial Nesting

So far we have learnt that different patterns of nesting behaviour are likely to evolve according to the type of resource distribution. For a barbet inhabiting a forest, where resources are more or less regularly distributed, a territorial system may evolve. It is not uncommon to hear the tut-tut-tut calls of barbets on hot summer afternoons. As you walk along you hear the familiar metallic call of a barbet, sounding like a hammer working in an ironsmith's workshop, advertising his territory. But just as soon as one individual has started his advertisement, another one starts calling almost as if to say, 'Hey, I know you have a territory but I have one too'. Very soon the woodland or the forest is ringing with the calls of barbets. In contrast to this situation, if the food is highly clumped in space and time, territoriality can break down. Imagine a flock of gulls prospecting for a school of fish in the sea. Once the school is located the gulls get busy harvesting this resource. Since food is abundant there is no point in defending this resource, which is also anyway impossible to defend by virtue of it being in the middle of the sea. Also, since the food is located at a place where the nest cannot be built (all birds are terrestrial animals and require land for nesting purposes) the nesting and feeding areas are far apart. Brown's model would thus predict a total collapse of the territorial mode of nesting and this leads to the situation in which birds start nesting in colonies. Some field tests of the model are discussed in *Box* 2.

Some interesting ideas have been advanced by ecologists to explore the advantages which birds could derive from nesting in colonies and the most persuasive of these is the geometric model

Box 2. Field Tests of the Economic Defendability Model

The economic defendability model can be tested in a number of ways. One way to do this is to adopt a comparative approach and study the spacing behaviour of birds. A study of weaverbirds demonstrated that for those species whose food resource (insects) was predictable in space and time, the birds spaced out and defended all-purpose territories. Such territories are also known as Type A or 'all-inclusive' territories and provide for all the requirements of the nesting pair. In a sense this is somewhat similar to living in a large farm where everything including water and food is available and the owner does not have to go to the market for anything. Another interesting comparative study used data on body weight and territory sizes for a variety of different birds to show that the size of the territory was directly proportional to the bird's body weight. A positive correlation between territory size and body weight is exactly what Brown's model would predict because if territories have evolved as a means of defending food resources, large birds would need more resources than smaller ones and hence their territory size would be proportionally greater. Another type of testing which the model lends itself to is a comparison of how individuals of the same species adopt different strategies in different environmental situations. One would expect that when food is abundant the territory size would be small and as food becomes scarce, the territory size will increase. Evidence in support of such a hypothesis has come from a study of ovenbirds in which territory size was indeed seen to be related to food availability and abundance.

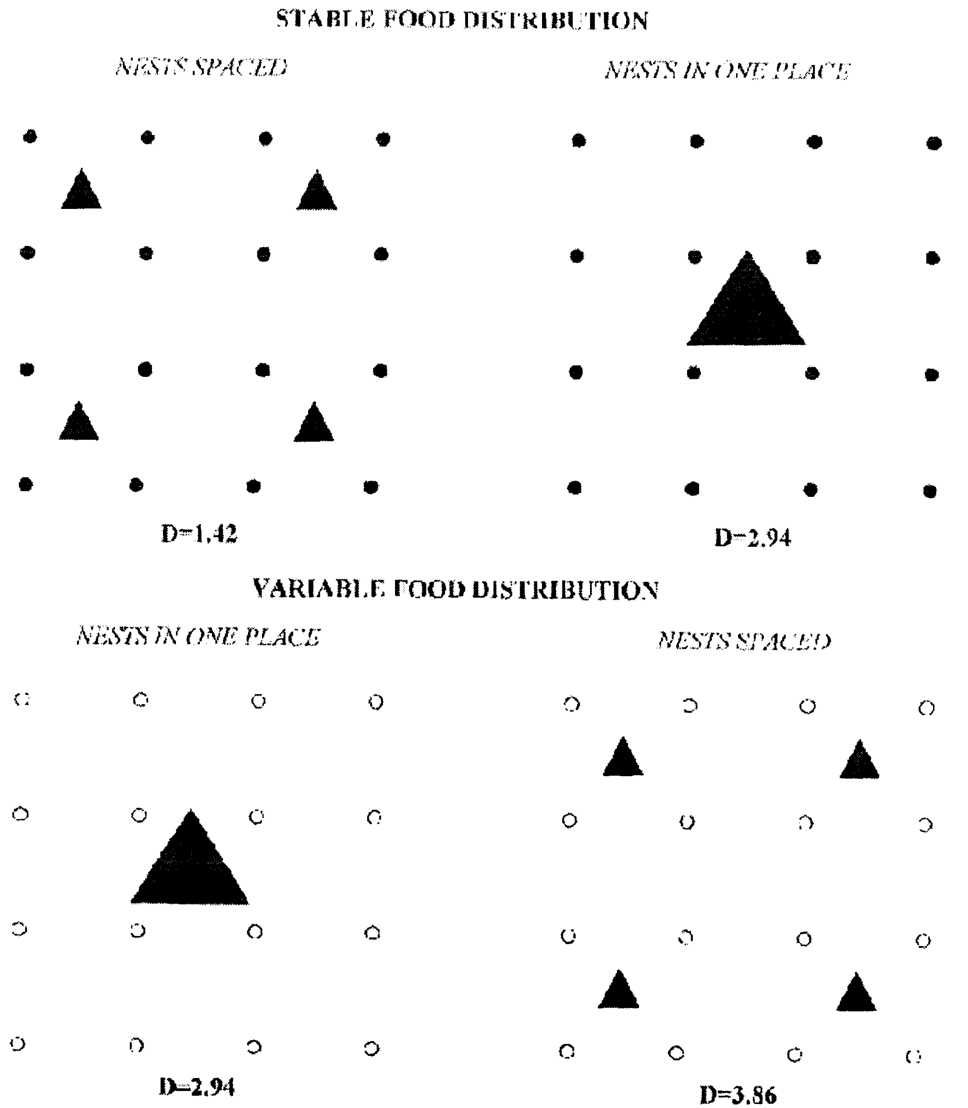

Figure 8. The geometrical model for avian coloniality. The solid circles represent resources that are continuously available. The open circles represent food resources that are variable in space or time, each of which must be exploited to an equal extent during the course of the breeding season. Small black triangles represent single nests and the larger ones represent colonies with four nests. The model presents the mean travel distance for food (D) in different situations. D is lowest for dispersed nesters if the food distribution is stable, i.e. uniformly distributed and continuously available. But when the food distribution is variable in time and space then D is the lowest for colonial (central site) nesters. For more details see text.

(Redrawn from Wittenburger and Hunt, 1985).

It has been postulated that some amount of information transfer about food resources takes place in a colony and if one bird is able to locate a food resource, others can then follow suit.

(*Figure* 8). This model estimates the distance that will be traveled by a hypothetical bird to collect food in different situations. The model assumes two contrasting types of food distribution patterns, the stable food distribution pattern and the variable pattern. Coming to the example mentioned earlier, the stable food situation could be a forest that has a number of trees, which a bird can exploit for food. Since all the requirements of a nesting pair can be met by, say, four trees, it would be a sensible strategy to nest solitarily with a small all-purpose territory to defend, inside which only a certain distance has to be traveled for harvesting resources. In this example, a total of four nests can be made and in terms of average foraging distance this would be economically feasible compared to a situation in which all the four nests were located in the geometric center of the patch (the average distance to be traveled in the latter case being much higher, $D=2.94$ units of distance). However, the situation changes somewhat if the food distribution is variable. Seen purely in terms of the distance that needs to be covered for harvesting these resources, having all the nests placed in the geometric center of the colony is advantageous ($D=2.94$) as compared to having nests spaced out ($D=3.86$). Given such a situation, colonial-nesting will be favored.

Evolution of Coloniality

Like other forms of nesting, coloniality has its advantages and disadvantages for the individuals who choose to adopt this strategy. A common approach has been to list out all the advantages and the disadvantages but the problem has been that many variables can enter the argument both as costs and benefits almost simultaneously. For example, energetics can enter the argument as a benefit because colonial nesting is certainly believed to enhance food finding and foraging efficiency. It has been postulated that some amount of information transfer about food resources takes place in a colony and if one bird is able to locate a food resource, others can then follow suit. In fact, some ornithologists have gone to the extent of suggesting that the plumage patterns of certain water-birds may have evolved to facilitate increased communication regarding food location. This may perhaps explain why many colonial species of herons, storks, etc. are uniformly coloured in white or black. However, the energetic aspects of food finding can also enter the argument as a cost because some amount of competition, including stealing of food, occurs at the food patch and at the nesting site. Another pressure on nesting birds is predation and this too can enter the argument both as a cost and a benefit. For instance, group-living certainly increases group-defense against predators. W D Hamilton, the famous evolutionary biologist (see *Resonance* Vol 6, No.4, pp.4-5, 2001), discussed how the chances of an individual being predated upon decrease when it lives in flocks or groups. But group-living has its disadvantages too, and one of them is increased visibility to predators. One of the unique aspects of colonial species is that colonies may be the only place where they can find mates because in the non-breeding season, each individual bird, whether male or female, leads a solitary existence. At the colony site there are a number of other benefits too (such as the ease with which nesting material can be stolen from neighboring nests) but the benefits come with a price tag attached.

Group-living certainly increases group-defense against predators, but group-living has its disadvantages too, and one of them is increased visibility to predators.

Wittenburger and Hunt, in their review on the evolution of coloniality, consider the net effect of coloniality on each significant variable. They argue that coloniality should evolve when:

$$N_p + N_e + N_m + N_i > 0,$$

where N_p is the benefit from enhanced defense minus the cost of increased attraction of predation (net effect on vulnerability to predation), N_e the benefit from enhanced foraging efficiency minus the cost of increased competition (net energetic effect), N_m the benefit of increased access to mates minus the cost of increased competition for mates (net effect on mating opportunities) and N_i the increased opportunities to exploit or disrupt neighbors (for example, steal nest material or kill chicks) minus the increased degrees of interference perpetrated by neighbors. Interestingly, not all cases of group-nesting are instances of 'active coloniality'. In certain cases, a critical factor, say, nesting substrate, may be limiting or very patchily distributed in space. In such a situation, colonies would form but they would be due to the fact that nesting substrates are too few and not necessarily because of the selective advantages of nesting in colonies. This can easily arise in the case of sea-birds that nest on islands in the sea. Since there may be only a few islands that are suitable for nesting (some may be unsuitable due to say presence of predators or due to human disturbance) birds may be forced to nest together because of a lack of options. This is a case of 'passive coloniality'.

In many parts of India, it is a common sight to see mynas and crows roosting together. In fact if one goes near a roost tree in the evening, one is confronted with a cacophony of sounds as the squabbling birds settle in and prepare for the night. This is another type of group-behaviour with costs and benefits associated in a manner that is similar to group-nesting. However, it is different from colonial-nesting in a very fundamental way. Nesting colonies are what have been described as 'central place systems' i.e. an individual belonging to the colony has to perforce return to it every day during the breeding season because it may have chicks or eggs in the nest. On the other hand, a roosting site is not a central place system in that an individual is not bound to return to it every day and can change its roost site every now and then.

Concluding Remarks

Many of the ideas with respect to coloniality and territory size, discussed in this article, have been developed further by later workers and the interested reader may find the literature suggested towards the end useful. Secondly, the reader may appreciate that, in India, with the wealth of biodiversity that we have at our doorstep, it is possible to address interesting problems, often without any sophisticated equipment or major expenditure. A case in point is heronries, a study of which would be useful from the viewpoint of both basic ecological research as well as conservation.

Suggested Reading

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