AGGRESSIVE NEGLECT AS A FACTOR IN INTERSPECIFIC COMPETITION IN BIRDS

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In their comments on an earlier paper of mine (1959), on the subject of competition between species in the Moluccan Islands, Hutchinson and MacArthur (1959) coined the phrase *aggressive neglect* to describe the tendency of one species to neglect its nest or young owing to the release of excessive aggressive behavior in the presence of a second species. This aggressive behavior with consequent limiting of the reproductive rate has been suggested by myself *(t.c.)* as possibly having survival value in cases of interspecific competition.

According to the Volterra-Gause principle, two species may not occupy identical niches. And yet under certain circumstances, such as the case of the Asian-derived sunbirds and the Australian-derived honeyeaters in the Moluccan and New Guinea islands, it appears as if these species were in competition, not complete, in the absolute sense, but to a degree where the presence of one appears to affect the other. One evidence of this is the fact that on small islands throughout the area one species or the other may occur but not both. Thus in such confined situations where the total available biotope is highly compressed, competition has gone in favor of *Nectarinia,* the sunbirds, or *Myzomela,* the honeyeaters (see Figure 1).

On larger islands such as on Batjan in the Moluccas where I made my study,[1] small habitat preferences in addition to behavioral differences may then allow these species to co-occur. In this connection additional observations may be of interest. Both on Batjan and on Halmahera Island I observed an Asian-derived species, a moderate-sized, olive-yellow-colored bulbul, *Hypsipetes affinis.* This bulbul, which seems closely allied to species found in Sanghir and the southern Philippine Islands to the northwest, was found by us in small parties in a variety of habitats varying from cut-over scrub and garden patches to heavy evergreen forest, ranging from sea level up to at least 3,300 meters. In our experience the species showed no special habitat preference, being found indiscriminately on the edges of human habitation or in undisturbed forest. Birds in breeding condition tended to be in pairs and presumably held territories, although I was unable to determine the size or composition of these. Out of the breeding season, groups or small flocks, perhaps family parties, numbering up to eight individuals or more, were found in the forest, occasionally attracting other species such as

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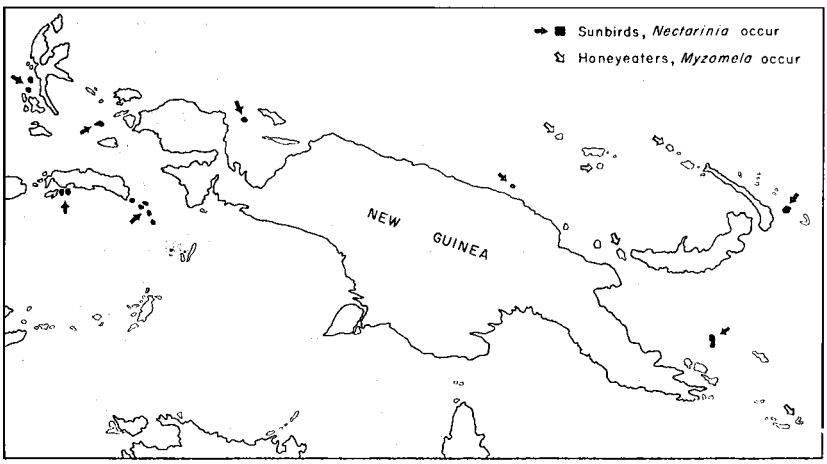

Figure 1. Small islands in the New Guinea area on which, so far as is known, only sunbirds or honeyeaters occur.

monarch flycatchers into the group in one of those typical mixed feeding flock associations. These birds primarily feed on insects, often visiting the corollas of flowers in bloom in the trees. Small fruits on vines or trees in the forest are also eaten. *Hypsipetes* has a fairly long history in the Moluccas, having been divided into several recognized local populations or subspecies.

A large honeyeater, *Melitograis gilolensis,* also occurs on Halmahera and Batjan and is closely comparable in size to the bulbul. This honeyeater occurs from sea level up to at least 1,600 meters altitude. As far as could be observed, the honeyeater also primarily feeds on insects, usually those attracted to flowering or fruiting trees, but also feeds on nectar as well as small fruits. Thus both species tend to feed on similar types of food, with the honeyeater having a greater predilection for nectar, and the bulbul a greater predilection for small fruits. The bulbul, however, will take nectar of flowers that are accessible in size, thus indicating that the mode of life of these two very divergent species is closely similar. *Melitograis* is presumably of considerable age, being an endemic genus of the archipelago.

From the observations made on Halmahera and Batjan, it would appear that in this case, as in that of the sunbirds and the smaller honeyeater referred to earlier *(t.c.),* the species are to a very considerable extent in competition, and that whereas the bulbul is numerous, the large honeyeater, *Melitograis,* is uncommonly encountered. Although we saw the bulbuls frequently, usually in pairs or small parties, we observed

Melitograis infrequently and then always single individuals only even during the breeding season. Presumably *Melitograis* ranges widely and has a scattered population. Furthermore, it appears to be highly aggressive. On one occasion, on Halmahera, I observed a single honeyeater fly assertively at a small flock of bulbuls, chasing them vigorously and dispersing the group in every direction. On another occasion, on Batjan, a single large honeyeater was in a flowering tree, *Erythrina* sp., near the shore. It continually darted actively out at other birds when they attempted to come into the tree to feed. This tree, which was in full flower, had a rather small canopy not more than 6 meters across. Perhaps the area was sufficiently constricted to be incompressible in the eyes of the honeyeater, so that it quickly attained a threshold of intolerance. In other cases smaller species like the small honeyeater, *Meliphaga,* flower-peckers, *Dicaeum,* sunbirds, *Nectarinia* and even leaf-warblers, *Phylloscopus,* had all been observed in the crown of the flowering *Albizzia* trees, albeit there was much "chasing" going on. But, of course, the crown of these trees is very large indeed, 25 or 30 meters across.

These observations, however, would indicate that the wide-ranging, larger honeyeater, which appears to be to a considerable extent in competition with the common and widespread bulbul, is aggressive and is locally dominant. Here again perhaps is a case of aggression playing a part in interspecific relations that may serve as a type of density-dependent phenomenon effective in regulating abundance and thus reducing competition.

OTHER POSSIBLE EXAMPLES

Another island group in which species of widely differing origin have come into contact is the Hawaiian Archipelago, where both the Drepanidae of New World origin and the Meliphagidae of the Australian region occur. Scott Wilson (1890-1899) speaks of the large honeyeater, *Moho nobilis,* the "O-O" of the Hawaiians, as being noted for its pugnacity toward its "arch rival," *Vestiaria coccinea,* the "Iiwi," a New World honey-sucker. So noted was this antagonism that bird trappers for the old royal family would snare an "Iiwi," place it on a branch with bird lime all about, and thus catch the "O-O" as it dove down to the attack. Both genera fed on the flowers of the lobelias native to the Islands, such as the ohia or the tree-lobelia. *Moho* appears always to have been a bird of some rarity in the Hawaiian Islands, aside from the fact that its feathers were used in feather cloaks. In any case it is perhaps significant that the scarlet Iiwi, *Vestiaria,* was also in demand and under human predation, and yet is still relatively common today, while

Moho has become extinct on Hawaii, Oahu, and Molokai. That interspecific competition has played a part in the unequal population ratio of these species and their subsequent histories is perhaps confirmed by the additional statement of Perkins (1903) that on Kauai the local species of *Moho, braccatus,* had somewhat changed its feeding habits and was eating insects as well as wild bananas, and had adopted more creeperlike habits. Kauai is, of course, a relatively small island with a considerably compressed biotope compared with the larger island, and thus species of similar habit might tend to evolve new feeding adaptations under conditions of enhanced competition.

I have already mentioned other examples of possible aggressive neglect as described in the literature (Hagen, 1947; Pitelka, 1951). It is possible that detailed observations of the interrelationships between *Neodrepanis,* the wattled "sunbird" [a member of the *Philepittidae,* as pointed out by Amadon (1951)], and *Nectarinia notata,* the green sunbird on Madagascar, would prove of interest in this connection. Rand (1936) notes that both species fed in certain forest trees in the humid forest zone, whose flowers had very long corollas. Observations indicate that *Neodrepanis* is local and uncommon, while *Nectarinia* is prevalent.

INTERSPECIFIC TERRITORIALISM

An interesting recent paper by Simmons (1951) shows that interspecific territorialism is common among closely related species of chats, chatlike thrushes, and shrikes on their winter quarters and appears to have obvious adaptive significance. Among woodpeckers, Selander and Giller (1959) have shown that two closely allied species, *Centurus carolinus* and *C. aurifrons,* show marked interspecific territorialism in their narrow zone of sympatric occurrence in central Texas. A third species, *Melanerpes erythrocephalus,* of similar size, while differing widely in appearance and to a noticeable extent in food foraging habits, still demonstrated aggressive behavior to a marked degree when presented with dummy mounts of *C. carolinus.* It seems conceivable that, should the nesting territories of these species in a zone of overlap become accidentally compressed, the phenomenon of aggressive neglect might come into play.

AGGRESSION IN WATERFOWL SPECIES

Aggression is very marked in certain species of waterfowl, particularly among shelducks and certain geese placed in the tribe *Tadornini* by Delacour and Mayr (1945). Many of these species occur in what might be described as marginal habitats, close to the snow line in the moun-

tains, or in xeric zones, or on barren islands. Species such as the Egyptian and Blue-winged geese, the Cereopsis and Andean geese, the Paradise and other Shelduck, and the Crested Duck are occupants of widely spaced territories in the breeding season and will fight savagely among their own kind, or with other waterfowl species.

A notable example under semiwild conditions is that of the population of Trumpeter Swan, *Olor buccinator,* in the Red Rocks Federal Refuge in Montana. There is a specific carrying capacity of the lake. A certain number of pairs of swans occur that can nest. The rest are said to be nonbreeders, which, in fact, would seem to mean birds that for one reason or another have been prevented from breeding by the constant territorial fighting. It is a fact as shown by annual censuses that the reproductive rate of the successful breeding pairs is materially cut down as the total population increases. Perhaps this is directly correlated with the need for constant aggressive defense of territory, as there is no diminution of food supply.

On my waterfowl preserve I attempted for several years to keep Blue-winged Geese, *Cyanochen cyanopterus,* at liberty in the large pond that contained other species of geese. During the spring breeding season the Blue-winged pair spent a large part of their time attacking other species such as the Barnacle Geese, *Branta leucopsis,* even while the latter were nesting. The Barnacles and other species nested successfully, while no attempt was made by the Blue-wings to nest, although pairing was noted. Later, placed in a small enclosure by themselves, the Blue-wings nested successfully.

In the case of waterfowl living in a marginal habitat such as the wind-swept, exposed islands off the coasts of southwestern Australia and Tasmania where the Cereopsis Geese, *Cereopsis n. hollandiae,* occur, it is conceivable that a behavior pattern such as aggressive neglect could be of adaptive significance if for any reason the habitat should become constricted so that the population resulting from a normal reproductive rate could not be supported. Thus the factor of aggressive neglect could vary between species, serving as a useful mechanism to a lesser degree, as clutch size has been shown to be adaptively significant by Lack in his many publications.

SUMMARY

Field observations in the Moluccan Islands of eastern Indonesia indicate that interspecific competition may involve a phenomenon in which the dominant, more aggressive species maintains a reduced numerical ratio to a partially competing species with which it is sympatric by its

very aggression and consequent reduction in brood size or nesting success. Other possible examples are sought, and it is suggested that this phenomenon could occur in cases of interspecific territorialism under constricted conditions. Possible cases among aggressive species of waterfowl are considered.

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