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SECONDARY SEXUAL CHARACTERS AND ECOLOGICAL COMPETITION

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Secondary sexual characters are usually considered to be beneficial to the species by bringing the sexes together and by inhibiting mismating. However, there is the possibility that some sexual dimorphism may be adaptive in intra-specific feeding. Lack (1944) particularly, in recent years, has elaborated the thesis that two species with identical feeding habits cannot occupy the same area and habitat. If they do breed in the same area there must be some difference in feeding habits. Somewhat earlier, Steere (1894, p. 419) summed up the idea very well from his Philippine studies: "No two species structurally adapted to the same conditions will occupy the same area."

If individuals of closely related species can live in the same region and habitat only if they reduce ecological competition by eating mainly different foods, the question arises as to how this rule applies to individuals of one species. Especially important is nesting time, when, in some species, the male and female are restricted to a relatively small area during the period of building the nest, incubation, and raising the young. Here ecological competition would be at its highest. Sexual dimorphism is very common and is probably mostly concerned with mating, but with the high potential of dimorphism one might expect it to reduce competition for food.

There are numerous ways in which competition for food between the sexes is limited.

Outside the breeding season, in many birds in northern latitudes, the migration of the male and that of the female may be slightly different. The males tend to remain farther north throughout the winter, the females farther south. Thus, some intra-specific competition for food is eliminated, and for a part of the year most of each sex are living in a different environment, with different selection.
factors acting on them. These differences in themselves could initiate a sexual dimorphism.

There may be some sexual segregation during the period of reproduction. There are some species, such as the old squaw duck (Clangula hyemalis), in which, after egg-laying, the males desert the females, and while the latter incubate and raise their broods on fresh-water tundra ponds, the males live on salt water.

In the white-tailed ptarmigan (Lagopus leucurus) of the Rocky Mountains, the males are said to frequent the lofty peaks near the upper limit of vegetation, while the female is leading her brood of young among the more luxuriant alpine meadows in the valleys below, nearer tree line. In both these cases we have different environmental conditions for the two sexes for part of the year.

According to McIlhenny (1937), the boat-tailed grackle (Cassidix mexicanus) of Louisiana segregates into flocks according to sex during part of the year. The food habits vary somewhat according to sex. The crayfish (Cambarus), he writes, is a favorite food of the male.

In many species that are territorial, the resulting spacing out of the pairs may have an effect in lessening intra-specific food competition, though the importance of this aspect of the holding of territory by a pair has been questioned (Nice, 1941). Another result might be intensified intra-specific food competition for the two members of the pair. Within a territory, however, there may be specialization as to feeding areas, as in the St. Kilda’s wren (Troglodytes troglodytes), in which each parent tends to feed in exclusive food patches not used by the other (Harrisson and Buchan, 1934).

Structural differences between the sexes are common. Perhaps the commonest one is the frequent average difference in size, the female being usually smaller although occasionally she is larger (as hawks and owls). It assumes more interest when taken in connection with Lack’s conclusion (1944, p. 279) that when two closely related species occupy the same habitat in the same region they nearly always differ markedly in feeding habits and/or size. Here perhaps we have a factor in the evolution of size differences between the sexes. Storer (1952, p. 284), in discussing this aspect of the problem in hawks, writes: “A sexual difference in size in raptors has a selective advantage in permitting the existence of a denser population by increasing the size range and hence the available numbers of the prey.” The difference in size of the sexes in other groups,
too, may correlate with a difference in food preference and a lessening of ecological competition for food.

In the boat-tailed grackle, there is some difference in food preference between the sexes, as stated above, and one method of feeding, used by the female only, that McIlhenny records (1937) is as follows: In feeding, the female may hover close over the water to snatch food from it. “This method of feeding is carried on only by the females, as the long, heavy tails of the males prevent any attempt at flight feeding that entails hovering close to the water’s surface.”

Difference in bill shape is shown by the western grebe (*Aechmophorus occidentalis*). The male has a straight, the female an uptilted bill. This difference (apparently little known) has not been correlated with feeding or mating. But it is interesting when compared with the condition in two other diving species, the common and the yellow-billed loon. The male western grebe has a straight bill like that of the common loon (*Gavia immer*); the female’s is uptilted like that of the yellow-billed loon (*G. adamsi*). These two loons are geographical representatives, and where their ranges meet they are mutually exclusive, in different habitats. What may be adaptive in two forms occupying different habitats in the loons,
may be adaptive in the western grebes, in reducing intra-specific food competition.

The classical case of structural difference between the sexes, correlated with a difference in food habits, is that of the huia (*Heteralocha acutirostris*). The male has a straight, short beak, the female, a long, curved beak. The birds are largely insectivorous, eating many wood-boring grubs which the sexes may get in different ways. The male with his stout, straight bill may dig into rotten wood for hidden insects; the female probes into existing crevices and crannies. Buller (1888, p. 7) records that he had a pair in captivity. Sometimes the male, after removing the decayed part of a log, was unable to reach the grub, when the female “would at once come to his aid, and accomplish with her long, slender bill what he had failed to do. I noticed, however, that the female always appropriated to her own use the morsels thus obtained.”

**SUMMARY AND DISCUSSION**

The thesis that two closely related species of bird can occupy the same habitat in the same area only if they differ markedly in feeding habits or in size has two aspects: a short-term, every-day one that reduces ecological competition for food, and a long-term,
evolutionary one, that forces apart two closely related species and causes them to differ more and compete less.

Within a species, during at least part of the reproduction period, two individuals of the same species live and feed in a more or less limited area. The ecological competition for food would be as great as if two individuals of different species, but with the same habits, occupied the habitat in the same area. Some adjustment could be expected. I have shown that differences between the behavior of the sexes that reduce intra-specific competition for food do exist in some cases. Sexual dimorphism is common, and though usually considered as aiding the sexes in finding each other, and in avoiding mismating, some dimorphism, such as the difference in size between the sexes, may also serve as adaptation for slightly different foods. In a few cases sexual dimorphism is known to be correlated with a difference in feeding habits. This seems to correlate with, and be an extension of, the forces that promote reduction of inter-specific, ecological competition for food. This is the short-term effect.

The long-term, evolutionary aspect would seem to call for factors at work forcing the two sections of the dimorphic species (male and female) apart. In those cases in which the two sexes live under different environmental conditions part of the year, ordinary natural selection could be at work during this period. However, other factors, notably the necessity for coming together at least periodically, would seem to set limits as to how far these two forms could drift apart. While many elaborate secondary sexual characters may be concerned solely with mating, many less conspicuous ones may actually be concerned with the reduction of ecological competition for food between the sexes.

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