

4.—THE RÔLE OF DOMINANCE IN THE SOCIAL LIFE OF BIRDS

BY G. K. NOBLE

BIRD flocks are held together by mutual attractions which are often innate. Witness the flocks of Cowbirds (*Molothrus ater*) which gather from broods reared by a wide variety of foster parents. On the other hand, training may seriously modify these reactions. In extreme cases, such as the Graylag Goose (*Anser anser*) described by Heinroth and Heinroth (1928), mere exposure of the young to a foster parent for a short period at the time of hatching will bind these young to this foster parent for a long period (Lorenz, 1935). Again, there are forces tending to disrupt the flock and these of course vary with the age of the bird and with the conditions of the environment. It is a curious fact that one regulating mechanism of bird society, the dominance drive, has been credited with both centrifugal and centripetal powers. In recent years this drive has been studied experimentally in many groups of vertebrates and certain general conclusions have been reached which give us a better understanding of bird behavior.

It is now well known from the studies of Schjelderup-Ebbe (1924), Masure and Allee (1934), Murchison (1935, 1936) and Skard (1937) that no two hens, or roosters, can remain very long together in the barnyard without establishing which is superior or inferior to the other. In a flock, a dominant hen may peck a subordinate without fear of retaliation. The latter may be dominant over a third, and the third over a fourth. The 'pecking order' which results is not closely correlated with the relative weights of the birds. Schjelderup-Ebbe (1935) believes that the circumstances of the first meeting of the two hens and their relative courage are as important as strength in determining which will become dominant. A position in the pecking order is not, however, always determined at the first meeting but may be deferred for days. Masure and Allee (1934) found that the ranking birds tend to make more contacts than do those lower in the social scale. This suggests that an inherent aggressive disposition may favor a bird's securing a position high in the order.

Among Domestic Fowls the males early become dominant over the females. Schjelderup-Ebbe (1924) noted that the vigor of the attack of the rooster on the hen abates with the rise of sex interest but he insists that "only in those cases where the male absolutely dominates the female does she submit to copulation unresistingly." He further generalizes that in all animals, female dominancy has a detrimental effect on procreation. Murchison (1935) found that if a hen is released between two roosters she tends to move toward the more dominant of the two males. It would seem that roosters high in the order would have greater opportunities of mating. When, how-

ever, roosters were released with hens in a large yard each cock was found to have his 'favorites' which were not always high in the pecking order (Skard, 1937).

Dominance behavior has been reported in many groups of birds but the social hierarchies, where adequately studied, have been found less fixed than those of the Domestic Fowl (Allee, 1938). Tompkins (1933), working with three species of California birds in winter, found that the most solitary species, a towhee, *Pipilo maculatus falcifer*, had the most rigid social hierarchy. The dominance drive in some form or other appears widespread throughout the vertebrate series. In fishes, as for example in the common swordtail, *Xiphophorus helleri*, a 'straight line' system, as rigid as that of the fowl, occurs (Noble and Borne, 1938). In this species it is possible clearly to distinguish the sex from the dominance drive merely by cooling the water, for the sex drive disappears first. Similarly among infra-human primates, Maslow (1935, 1936) has been able to distinguish the two drives. These had been confused previously in primates chiefly because sexual behavior patterns form part of the dominance display.

The difference between social and sexual dominance may be readily observed in birds. If we release immature and adult Black-crowned Night Herons (*Nycticorax nycticorax hoactli*) together in a large cage, the latter will select the most suitable perches and drive the immatures out of these areas. This aversion for one another is a manifestation of the dominance drive but a peck order, similar to that of the domestic fowl, does not appear unless the birds are crowded together in a strange area. If the young herons driven from their perches have their sex drive hypertrophied by treatment with male hormone they are able to drive away the adults even if they are only thirty days old (Noble and Wurm, 1938). The latter aggressive behavior differs from the former not only in the vigor of the attack but in the incentives involved. The treated young are excited by sticks which they play with in a formalized manner. The sex drive makes the birds come near suitable nesting areas while the dominance drive determines merely a wide spacing of them in the cage.

The dominance drive in all vertebrates is continuous, not cyclic like the sex drive. Further, the latter drive has a well-known hormonal basis unlike the former. Schjelderup-Ebbe (1924, 1935) employed the word dominance to cover a wide variety of phenomena such as the driving of a crow by a kingbird, or the seizing of a sparrow by a bird of prey. Where the motivation is entirely different, as for example in the case of a hawk stimulated by hunger contractions of its stomach to seize prey, as contrasted with a heron aroused by sexual hormones to drive others from a nest area, it seems highly desirable to distinguish the phenomena with adequate terminology.

It has long been recognized that most male passerine birds when sexually

motivated seek first territories and not female partners. Since these territories may be large their value as a potential source of food for the young has been frequently stressed. Recent observations have tended to minimize the food value of territories (Lack, 1937). After five years' study of the Great Crested Grebe (*Podiceps cristatus*) Venables and Lack (1936) believe that territory "results from an aggressive disposition possessed by some individual Grebes only, and which is of no fundamental significance to species."

The word 'territory,' like that of dominance, has been employed to cover a variety of phenomena. Brooding and winter territories, recognized by ornithologists (Meise, 1936), may frequently be distinguished from sexual territories on a motivational basis. Recently Tinbergen (1936) has suggested that the term 'territory' be restricted to "an area which is defended by a fighting bird shortly before and during the formation of a sexual bond." Unfortunately this definition would rule out the area immediately surrounding a courting Ruff or Black Cock for the female merely comes to the *lek* for copulation purposes and no bond in the strict sense of the word, that is a pairing off, is formed. Nevertheless, these small mating areas have primarily the same function as the heron's territory; they make possible the male's recognition of a sexually-ready female. The Black-crowned Night Heron does not copulate the moment a female enters a male's territory. After her sex is identified, courtship takes place and it is during this period that bonds are formed which will hold the pair together during the breeding season.

Territory, like dominance, is by no means restricted to birds. Sexual territory is a direct consequence of the nest-building habit in vertebrates. Where both parents in either fish or birds are to share equally in the duties of rearing the eggs and young, the future parents engage in courtship activity which borrows and frequently formalizes some of the behavior patterns of nest construction or young-rearing. The modalities of a later stage of life history are merely projected forward and abbreviated until they are often merely 'symbolic' of the normal pattern. The biological value of this transposition seems clear. The future parents must associate together, react in common if bonds are to be formed which will hold them as a pair during the entire breeding season. There is no sudden 'imprinting' (Lorenz, 1935) of a sexual partner at this later stage of development but only gradual conditioning. The human keeper of birds who handles his charges too frequently may find a bird has attached itself to him in a bond of sexual affection. If pairs of birds or fishes are to form a bond between themselves they must develop behavior different from the feeding or locomotion of non-breeding members of the group. It is therefore not surprising that the rule for both fishes and birds is to project forward in the cycle modalities of

behavior which normally unfold later in a fuller form. Birds have gone beyond fishes in the greater variety of their courtship and also in borrowing behavior patterns, such as sexual preening, which are restricted to no phase of the life history. Further, females of many different species differ from fish in adopting the begging attitude of the young when inviting coition by means of distinctive cries.

It has not been adequately emphasized that every territory, largely as a result of this forward projection of nesting behavior, is itself more or less sexually stimulating. A young male dove breeding for the first time tilts forward while sounding the nest call. He shifts his position until he finds a corner which more or less fits his body while in the tilted attitude (Craig, 1918). Similarly a young night heron breeding for the first time not only plays with sticks in an excited manner but attempts to place them in such a position that they will form a rough platform. Female night herons are also excited by sticks but never to the extent of playing with them in a formalized manner. Nevertheless by treating a female with male hormone (testosterone propionate¹) it is possible gradually to increase this interest until the full male pattern develops. It then becomes clear that the difference between the masculine and feminine point of view on territory is not due to brain differences but merely to the amount of male hormone in their bodies (Noble and Wurm, 1938).

Species vary in the components of their courtship; similarly they differ in the relative importance territory plays in their pairing off. For example, Lehrman and I saw groups of Laughing Gulls (*Larus atricilla*) early in the season this year (1938) standing on drift weed at a distance from their later nesting territories. The females were begging indiscriminately among the males. By adopting the juvenile behavior they were trying to force males to regurgitate. Sexual readiness of the female of this species is indicated by begging and not by her entering an area which has become sexually stimulating to the male. After this initial pairing off the birds stand together in pairs and weld the marriage bond with mutual head-bobbing. It is only later that they secure a territory and this is a nesting, not a sex territory.

In a few vertebrates the female may become sexually interested in a territory before the male. The female salmon begins to dig her nest before the male arrives (Noble, 1938), female Oropendolas (*Zarhynchus wagleri*) start nest construction before the male becomes attracted to the activity (Chapman, 1928). Females of the European Cuckoo (*Cuculus canorus*) have their own territories and own sex call, a bubbling note, very different from the male's call which we hear from the familiar cuckoo-clock. There may be vigorous battles among females (Skinner, 1922) but not among

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males when they are attracted by the cry of the female (Nötel, 1921). The latter is peculiar in that she is stimulated not by the nesting behavior of her male but by that of her victims. This condition is apparently the result of early training for the females tend to victimize the particular species in whose nest they were reared. Just as pigeons, reared by parents of other species, prefer to associate with these species instead of with their own kind (Whitman, 1919), so the cuckoos reared by foster parents are attracted by nesting behavior of these birds later in life.

Mammals frequently breed within well-circumscribed home ranges which have been called territories (Burt, 1937; Darling, 1937) but these home ranges of non-egg-laying vertebrates differ from sexual territories of birds and fishes in that the terrain itself is not sexually stimulating to the mammal (unless contaminated by secretions of the opposite sex). They are merely occupied areas in which the owners resent trespassers in or out of the breeding season. Many non-breeding fish or birds resent intruders into their domains in exactly the same way. This aversion to newcomers is widespread in the vertebrate world and being an aversion it may increase the strength of a dominance drive. A non-breeding pigeon low in the pecking order, if allowed to remain in a small area, becomes dominant over a superior pigeon which is introduced into this area for the first time (Noble, Wurm, and Schmidt, 1938). Obviously a territory so useful to a subordinate bird has nothing to do with a sexual territory. It is merely a retreat, which, because of its strangeness to newcomers is avoided by them. In brief, while a territory is any defended area, sexual and nesting territories are characterized by sexual or nesting activity, in contrast to a retreat which is occupied because it is familiar and defended because any newcomer is irritating to the resident.

In a few birds, such as Gould's Manakin (*Manacus vitellinus*), the female may build her nest beyond the territory which is sexually stimulating to the male (Chapman, 1935). This nest area is undoubtedly stimulating to the female for it tends to satisfy her parental drive. A nesting territory may be, therefore, distinguished from a sexual territory or a mere retreat on a motivational basis. In most birds the distinction between a sexual and a nesting territory is less clear because the nest construction takes place in the male's sexual territory. In species such as the Robin (*Turdus migratorius*) where the female alone usually builds the nest in the male's sexual territory, the latter is stimulating to the male only in that it offers a place suitable for his song or display. Selous (1933) considered the nest of the Mute Swan (*Cygnus olor*) a "sexual maelstrom," and the same may be said of the nest of the night heron and that of other birds with courtship behavior involving nesting material. In species in which the female alone builds, special behavior patterns, such as 'sexual flight' (Howard, 1929) may be utilized

as a substitute for mutual courtship in assuring the formation of nuptial bonds. Sexual flight resembles mutual courtship of fishes and birds in that the pairs engage in a mutual ceremony which is highly stimulating to both partners. Mutual courtship is widespread in such primitive birds as swans, grebes and herons. It may be considered the primitive pattern from which other types of avian courtship have been derived.

Courtship movements of fish and birds usually include: (a) threat movements which serve to drive other males from the territory and to test the sexual readiness of the females; also, (b) 'symbolic' or mutual movements which aid in the formation of bonds. The female bird, when threatened by a territory-holding male, postures and this releases further sexual behavior in the male (Craig, 1909). This threat may take a wide variety of forms but when it resembles the normal threat of a socially dominant bird it tends to confuse the distinctness of the two drives. Allee and Collias (1938) have shown that hens injected with male hormone may rise in the pecking order. This is to be expected, however, since males dominate females and the treatment had merely partially reversed the sex of the hens. A more extended treatment would very probably have produced a complete sex reversal such as Noble and Wurm (1938) described in the night heron.

In birds such as the night herons, which do not threaten the sex partner during courtship, the male frequently endeavors to secure a more erect position of head before copulating. In this sense the male may be said to be dominant over the female. Nevertheless, in the night heron there is no dominating challenge of the male which releases sexual behavior in the female. Still, male night herons which fail to secure the dominant position of the head fail to copulate. Crested Grebes and Moorhens (*Gallinula chloropus*) which fail to show a difference in head posture, practice 'reversed coition' (Huxley, 1938). The absence of reversed coition in the night heron is not due to head-posture alone. At the beginning of courtship the male holds the head lower than that of the female and yet no reversed coition occurs. Dominant head-posture in the night heron is merely a position necessary for coition. Incidentally, it makes the male bird dominant over the female with the result that she gestures first when they practice mutual courtship ceremonies. If a male will adopt a similar subordinate position, he may remain in another male's territory and if they practice mutual ceremonies, a bond may form between them.

In many birds the dominance threat to the sex partner is done vocally. In these cases, as for example in many passerine birds, the males usually have little sexual adornment. Compare two such polygamous species as the Corn Bunting (*Emberiza calandra*) and the Ring-necked Pheasant (*Phasianus colchicus torquatus*). Voice of the former takes the place of the impressive livery of the latter. The Song Sparrow (*Melospiza melodia beata*) "pounces"

on the female after she has revealed her sex by special notes. Nice (1933) considers this analogous to the sexual flight of the Yellow Bunting (*Emberiza citrinella*) and, since copulation comes later, it may be a method of securing a bond of attachment between two birds of a pair. Further, many birds, such as the Starling (*Sturnus vulgaris*) described by Kluijver (1933), apparently induce posturing in the female by song alone, although here again the importance of the posture of the male has not been determined. Impressive behavior, whether postural or vocal, differs from a true attack which would only serve to call forth defensive behavior in the female. Impressive behavior alone does not result in the formation of a nuptial bond. Other behavior patterns are necessary for this, among both birds and fishes.

In correlation with the different courtship patterns of birds, mounted specimens placed in the sexual territories of different species produce different results. A mounted female night heron calls forth no response from either sex. In the same way mounted Flickers (*Colaptes auratus luteus*) are ineffective in producing copulatory behavior, for the male waits for a sexual cry or motion from the female to release his response. A mounted female pheasant or wren will induce this behavior in the male even when the female is a differently marked species. The quiet figure of the mounted bird deceives the male. The latter reacts as if the mounted bird had postured to his vocal or feather display.

In birds with marked sexual dimorphism, such as the rooster, merely caponizing has sometimes been found to call forth sexual behavior in other males (Pézard, 1926). To what extent posturing of the capon or merely lack of male carriage is responsible for these cases is not clear. The rooster differs from the hen in the greater amount of male hormone in his tissues as indicated externally by the larger comb. Apparently the different carriage in the two sexes is a function of the amount of the male hormone present. This may be true also of sexually homomorphic birds such as the night heron. It does not follow from this that within one sex the relative position of a bird in its social hierarchy is correlated with the amount of male hormone present in its tissues, because these hierarchies may form long before sexual maturity.

Sexual dominance may or may not make use of the same threat employed in social dominance but there is a wide difference between them. Social dominance is directed toward objects with an uncanny eye for detail. The social position of the newcomer is learned by experience and a bird second or third in a pecking order is distinguished at once even though we can see no difference between them. In striking contrast, the more emotional behavior, namely, that activated by the sex drive, tends to ignore detail although sex differences in color may be recognized. The evidence at present at hand indicates that this recognition is also a matter of training. Young

Red-winged Blackbirds (*Agelaius phoeniceus*) at first mating will copulate with mounted birds of either sex, but older individuals captured in the field copulate only with female mounts (Noble and Vogt, 1935). A badly mounted or posed bird is usually avoided socially but it will often produce a sexual reaction provided that the courtship is one in which a threat releases posturing in the live sexually ready female.

Sexual dominance has precedence over social dominance apparently in most vertebrates, although Lorenz (1931) did not seem to find it so in the case of his Jackdaws (*Coleus monedula*). In night herons on breeding territory, social dominance becomes reduced as evidenced by the frequent approximation of nests. In canaries, even subordinate birds are dominant in their own territories (Allee, 1938). In Jackdaws (Lorenz, 1931) and monkeys (Maslow, 1934-1936), pairing with a male high in the social order raises a female in her social order. Such females, out of their social position, so to speak, may become very mean to their former superiors. Where females have little sexual aversion for one another, as for example in the Corn Bunting described by Ryves and Ryves (1934), polygamy tends to arise. This type of diminution of aversion merely means that the female is less aggressive in the defense of her nest area and may or may not be correlated with a weak dominance drive outside of the breeding season when sexual attractions and aversions are not in operation. Nevertheless, there is some evidence that a socially subordinate male may not defend as large a sexual territory as a more dominant male. Chapman (1935) found this to be true of Gould's Manakin and the same would be expected in any group with crowded territories.

Reproduction of mammals is believed to differ from that of birds in that "it is more related to emotional states and more under the control of higher nervous centres, with the result that stimulative display is rare in the former, common in the latter" (Huxley, 1938). Birds differ from most mammals (except rabbit, ferret, etc.) in rarely ovulating without external stimulation. Craig (1913) has shown that caressing a virgin dove by hand and Bartelmez (1912) that merely keeping a pigeon in a cage adjacent to a courting male would induce ovulation. From such data as these Marshall (1936) concludes that the biological value of sexual display and adornment is "to bring about ovulation and the related processes at the most appropriate time." Courtship does aid synchronization of male and female sexual behavior even in fish (Noble and Kumpf, 1936). There are, however, other facts to consider. The elaborate courtship of nest-building fish differs from the simple display of most viviparous species, roughly, in the same degree that the courtship of birds differs from that of mammals. It is the nest-building habit of birds and the need for the formation of bonds in species which rely chiefly on visual and auditory cues that have been responsible

for the elaborate courtships of birds. Where the courtship is short but brilliant, the display may be a threat, essential to induce female posturing, but not producing a marriage bond. Where the courtship is long and with many 'symbolic' components, bonds are formed which will hold the pair together for the season.

In conclusion, therefore, it may be repeated that display, i.e., sexual dominance behavior, has exactly the same function in fish and bird. Social dominance is found not only in these groups but throughout the vertebrate series and is readily distinguished from sexual dominance. Territory should also be sharply divided into different categories. Sexual territory, which is so characteristic of most birds, is, however, found in most egg-laying and nest-building vertebrates. It arises from the sexual interest of the animal in an area suitable for nesting and it functions primarily to test sexual readiness of the opposite sex and to make possible the formation of sexual bonds. Sexual territory is not to be confused with a nesting territory which has a different motivational basis, nor with an isolated retreat which is defended by many vertebrates against intruders at any season.

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