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PAIR-FORMATION IN BIRDS

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There is probably more ignorance concerning pair-formation than there is of any other aspect of bird behavior. This paper attempts to summarize existing knowledge on this subject in order to stimulate further work. I am greatly indebted to Dr. Ernst Mayr and Dr. G. Kingsley Noble for their stimulating discussions with me, and to Dr. Alden H. Miller for seeing the paper through the press, an undertaking which was rendered necessary by the international situation.

A review such as the present one involves a large number of references. Papers contributing to the general discussion are cited in the standard way, but if those dealing primarily with a particular species were treated in the same manner, the text would be heavily encumbered with authors' names and years of publication. Hence papers of the latter type are listed at the end of the paper (p. 284) under the species concerned and are not referred to elsewhere. While this means a little extra trouble for the reader, it saves considerable space. Further, where one recent paper summarizes previous work on a species, I have usually thought it unnecessary to give the earlier references as well. The references are not a complete bibliography of bird courtship; only papers dealing explicitly with pair-formation are included, and in this field I have omitted many articles on typically territorial species of passerine birds, as these are now too well known to need detailed reference. In such a wide field, some references to pair-formation have almost certainly been overlooked, but in other instances omission has been deliberate where, as with the Ostrich (*Struthio camelus*), Great Bustard (*Otis tarda*) and others, the descriptions are too vague to be of value.

LENGTH OF THE PAIRING BOND

This section owes much to the sound classification by Heinroth (1928). Birds fall into five main groups: those in which the sexes (1) meet solely for copulation, (2) have a bond simply for a few days at the time of copulation, (3) form into pairs some time before copulation but separate shortly afterward (ducks), (4) remain paired for the raising of the brood or for the breeding season, or (5) pair for life. (The few species which breed in groups, and do not form pairs at all, are discussed later.)

1. *Sexes meeting solely for copulation.*—(a) All species which meet at communal display grounds or "leks"; among gallinaceous birds, Blackcock (*Lyrurus tetrix*), prairie chickens (*Tympanuchus*), Sharp-tailed Grouse (*Pedioecetes phasianellus*), and Sage Hen (*Centrocercus urophasianus*); among wading birds the Ruff (*Philomachus pugnax*) and Great Snipe (*Capella media*); among passerine birds, two genera of birds of paradise, *Paradisaea* and *Parotia* (information from Mayr), one of the bower-birds (*Priondura newtoni*), the Cock-of-the-rock (*Rupicola*), Gould Manakin (*Manacus vitellinus*); and among hummingbirds, *Phaethornis superciliosus* and *P. guyi*, and *Pygmornis longuemareus*. The birds in this group form a striking example of convergent evolution in behavior.

(b) Various species in which the male is isolated and displays conspicuously, and in which the female comes to him: among gallinaceous birds, the Ruffed Grouse (*Bonasa umbellus*), the Spruce Grouse (*Canachites canadensis*), and *Dendragapus*; among birds of paradise, *Diphyllodes magnificus* and probably other species; also probably most bower-birds (Ptilinorhynchidae) but too little is known of these to be certain. Steinfatt claims that the European Woodcock (*Scolopax rusticola*) comes in this category, but the evidence seems inadequate. In the species of this group it is not known if the female always returns to the same male.

(c) The Boat-tailed Grackle (*Cassidix mexicanus*), in which the females visit the flocks of males; this bird might almost be classed with the lek birds, but the males have no definite stations.

(d) The Cowbird (*Molothrus ater*) and European Cuckoo (*Cuculus canorus*) at times, but both these sometimes seem to form a more definite attachment.

2. *Sexes having a bond for a few days at time of copulation.*—In North American hummingbirds the male and female seem to remain together for a few days, but the male does not take any part in nesting activities and is then, perhaps, driven away by the female. Whether he takes a new female is not known. In the Wagler Oropendola (*Zarhynchus wagleri*) the members of the pair are also associated for only a few days, this ceasing at incubation. This also applies to the Penduline Tit (*Remiz pendulinus*) and to the weaver *Ploceus philippinus*, in which, unlike *Zarhynchus*, it is the male which builds the nest; once the female is incubating, the male *P. philippinus* builds a new nest and acquires another female; this sometimes occurs in *R. pendulinus*. It also occurs in the bishop-birds *Euplectes hordeacea* and *E. nigroventris*, but here, although the male takes no part in the rearing of the brood, the females nest in his territory, and he usually gives calls when they enter or leave, hence the bond is rather more lasting.

Among wading birds, the female Red-necked Phalarope (*Phalaropus lobatus*) leaves the male at the beginning of incubation, as do the tinamous (*Calopezus elegans*; *Crypturus*) and button quails (*Turnix*). At least at times, male and female Cowbirds (*Molothrus ater*) and European Cuckoos (*Cuculus canorus*) form temporary attachments.

3. *Ducks.*—Among many species of ducks the male normally leaves the female soon after she has laid, but the situation differs from that in the species mentioned in group 2 in that pair-formation often occurs in late autumn, winter or early spring, so that members of a pair remain together for several weeks before laying. Occasionally a male Mallard (*Anas platyrhynchos*) remains with the nesting female and attends the ducklings, and this also happens occasionally in other species. Thus there is gradation into the next group.

4. *Sexes remaining together for raising of the brood or for the breeding season.*—In this category fall the great majority of passerine and near-passerine birds, together with herons, nearly all wading birds, most of the different groups of sea birds, the birds of prey if they do not pair for life, and many other groups too numerous to list completely. Of special interest is the fact that a few gallinaceous birds are included, such as Bob-white (*Colinus virginianus*) and the American quail of the genus *Lophortyx*, and also a few birds of paradise, such as *Manucodia ater*, *Macgregoria pulchra*, and *Phonygammus*.

As regards the length of the pairing bond, most migrant passerine species, as for example New World warblers, pair up only shortly before nesting. But many resident species pair up several weeks or even months before nesting. The British Robin (*Erithacus rubecula*) pairs in mid-December but nests about the end of March; the

Loggerhead Shrike (*Lanius ludovicanus*) pairs up from November onward, and the Jackdaw (*Coloeus monedula*) forms pairs in the autumn. Regarding the other end of the breeding cycle, in species which have more than one brood, some normally retain the same mate for a second brood, although changing exceptionally, while in others, like the House Wren (*Troglodytes aëdon*), the mate is regularly changed between broods. The data on this last point are too well known to need specification; Tinbergen (1939, pp. 45-46) gives a valuable summary.

5. *Birds which pair for life.*—It seems to be commonly believed that most large birds pair for life, but positive evidence is extremely scanty. Three errors must be avoided. First, migrant species of loons and grebes have been said to pair for life because they arrive on the breeding grounds already paired, but they may well have paired in their winter quarters. Second, observations on captives are not reliable, since the birds are kept unusually close together. Third, cases of re-mating must be distinguished from true life-pairing where the pair remain together all the time. Thus, White Storks (*Ciconia ciconia*) frequently re-mate, but since the males usually arrive before the females, Schüz considers re-mating due to a tendency for the birds to return to the nest used in the previous year. In the British Robin, re-mating has been observed a number of times when it was certain that the sexes separated in autumn. Other instances where passerine birds have re-mated in a second year will not be summarized here except in cases when there is evidence that they remained paired outside the breeding season.

Among passerine birds, the most convincing evidence for life-pairing is in the Wren-tit (*Chamaea fasciata*), where the pair keep their territory for life. Pairs of Cardinals (*Richmondena cardinalis*) and California Thrashers (*Toxostoma redivivum*) will remain at least loosely associated in winter and so may be said to pair for life. The Marsh Tit (*Parus palustris*) stays in pairs, which wander in winter, and the same is stated to be true for the Willow Tit (*P. atricapillus*), Crested Tit (*P. cristatus*) and at times the Blue Tit (*P. caeruleus*), although I have not read of certain evidence for these latter species. Pairs of Great Tits (*P. major*) have bred together five years in succession, which certainly suggests that they remained together outside the breeding season, although this was not investigated. Other passerine species suspected of life-pairing are Crested Lark (*Galerida cristata*), European Nuthatch (*Sitta europaea*), White-breasted Nuthatch (*S. carolinensis*), Brown Creeper (*Certhia familiaris*), Black Redstart (*Phoenicurus gibraltariensis*) and Stonechat (*Saxicola torquata*), although the evidence is not complete, so far as I know. The cowbird *Molothrus rufo-axillaris* sometimes occurs in pairs throughout the year. Exceptionally, pairs of British Robins and of Mockingbirds (*Mimus polyglottos*) have shared a territory in autumn and bred together next spring, but normally the members of the pairs separate. Corvids are commonly supposed to pair for life. They are frequently seen in pairs at any season, but this alone is insufficient evidence, for Lorenz found that his Jackdaws (*Coloeus monedula*) changed mates at times. A pair of Carrion Crows (*Corvus corone*) certainly nested together for ten successive years, which indicates that life pairing occurs at times in this family. Of course even if the corvids change mates occasionally, their habit of associating in pairs at any season (which also seems true of Magpies, *Pica pica*, and of various kinds of jays) puts them in a different class from species in which the sexes have no pairing relation outside the breeding season.

Pairs of Great Spotted Woodpeckers (*Dryobates major*) are thought by Steinfatt to remain together, but by Tracy to separate, after the breeding season. In captivity, parrots (Psittacidae) pair for life, and since Tavistock found this true of platycercine parrots under semi-wild conditions, this may well be true in the wild. I have found no reliable evidence that any falconiforms or owls pair for life in spite of repeated statements that they do so; this should not be taken to mean they do not pair for life. Swans (*Cygnus*) and geese (*Anser*) pair for life in captivity, as does the Mute Swan (*C. olor*) under semi-wild conditions, and the general opinion is that this is true of wild birds.

Mr. H. Eliot Howard informs me that the Moorhens (*Gallinula chloropus*) on his pond have remained permanently paired except when an accident has befallen one of them. In amplification of his published papers on the Little Grebe (*Podiceps ruficollis*), Mr. P. H. T. Hartley writes that some of these birds remained permanently paired throughout the winters of 1932-33 and 1933-34. Birds breeding for the first time, and birds which have lost their mates, form pairs in February and early March; the reason that there was so much new pair-formation in the spring of 1935 was that the drought of 1934 had driven the birds from the inland pond where he observed. Mr. Hartley also adds that he has never seen sexual manifestations among the individuals forming winter flocks on the estuaries; so, unlike the individuals on the inland pond, those in the estuaries may not remain permanently paired.

It is thought that the barbet *Trachyphonus d'arnaudii*, the hornbill *Bycanistes cristatus*, and the Mallee Fowl (*Leipoa ocellata*) may pair for life, as pairs usually are seen together. Spur-wing Plovers (*Belonopterus chilensis*) are said to keep to the same mate and territory for life.

In gulls, the evidence is incomplete. Herring Gulls (*Larus argentatus*) have been recorded nesting together in four successive seasons, but whether they remained paired in winter is not known. Black-headed Gulls (*Larus ridibundus*) arrive paired at the gulleries (personal observation) and Miss M. Rothschild informs me that some of her abnormally crowded captive Black-headed Gulls retained a loose pairing in winter, and re-mated in spring, but this is not certain evidence for the wild state. Manx Shearwaters (*Puffinus puffinus*) and Wilson Petrels (*Oceanites oceanicus*) have re-mated in a second year, but there is no evidence as to whether these birds remain paired outside the breeding season. It is evident that far more data are needed on this subject.

Shortly after completing the manuscript for this paper, I read the interesting account by Skutch (1940), who states that in various tropical American passerine birds members of pairs remain associated outside the breeding season, keeping in touch with each other by special calls or song. This is common in wrens, including *Pheugopedius hyperythrus* and *Thryophilus modestus*, and also occurs in the Northern Tody Flycatcher (*Todirostrum cinereum*), the Tyrannine Antbird (*Cercomacra tyrannina*), the Buff-throated Saltator (*Saltator intermedius*) and the Prevost Cacique (*Amblycercus holosericus*).

MANNER OF MEETING OF THE SEXES

With regard to the way in which the sexes meet, birds may be divided into two main categories, those in which one sex maintains a territory with conspicuous display, and those which form into pairs while in flocks.

Birds with one sex isolated.—The isolated displaying sex is normally the male, but in a few species, as for example the tinamous (*Crypturus*) and Red-necked Phalarope (*Phalaropus lobatus*), it is the female. The size and nature of the territory varies considerably, as discussed later. Birds in this group with large territories (in some cases later used for feeding, in others not) include the great majority of passerine and near-passerine groups, which are far too numerous and well known to need specific mention, also some birds of prey, of which the Peregrine Falcon (*Falco peregrinus*) has been studied best, the Bittern (*Botaurus stellaris*), and some gallinaceous birds (*Bonasa umbellus*, *Canachites canadensis*, and *Dendragapus*). Among the wading birds there are the Little Ringed Plover (*Charadrius dubius*), Red-necked Phalarope (*Phalaropus lobatus*), Woodcock (*Scolopax rusticola*), some individual Lapwings (*Vanellus vanellus*), Oyster-catcher (*Haematopus ostralegus*), Golden Plover (*Pluvialis apricaria*), and Redshank (*Tringa totanus*). Also there are some individual Great Crested Grebes (*Podiceps cristatus*) and at least some individual Moorhens (*Gallinula chloropus*).

This group includes in addition a large number of colonial nesting birds with extremely small territories, such as herons (*Ardea cinerea* and *Nycticorax nycticorax*), and many sea birds (cormorants, gannets, frigates, and some penguins). In some of these birds, especially the frigates and certain cormorants, the visual and vocal display is just as spectacular as that of any territorial passerine species. Colonial passerine species with isolated males include the Tricolored Red-winged Blackbird (*Agelaius tricolor*) and the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) among the Icteridae, *Ploceus philippinus* and presumably other colonial weaver-finches, and probably colonial-breeding swallows. The gap between the extremely colonial species and those with large territories is fairly marked, but is bridged by such species as the bishop-bird *Euplectes nigroventris*, the Barn Swallow (*Hirundo erythrogaster*) and the Starling (*Sturnus vulgaris*), which breed in groups but in which the males are rather too far apart to be described as colonial.

A third group of birds with isolated males are the lek species, already listed. It is possible that individual *Phaethornis* exchange song perches at their meeting grounds, but in *Manacus vitellinus* and *Lyrurus tetrix* each male has a fixed territory.

Birds which form pairs when in flocks.—This category includes many fringillid genera, notably *Coccothraustes, Loxia, Spinus, Leucosticte, Carduelis,* etc. Other passerine species include the Bush-tit (*Psaltriparus minimus*) and perhaps other tits, the waxwings (*Bombycilla*), the Brewer Blackbird (*Euphagus cyanocephalus*), Bay-winged Cowbird (*Agelaioides badius*), and perhaps the Fieldfare (*Turdus pilaris*) and Redwing (*Turdus musicus*). Also included are many migratory wading birds, such as Willet (*Catoptrophorus semipalmatus*), Avocet (*Recurvirostra avosetta*), Wilson Phalarope (*Steganopus tricolor*) (personal observation with J. T. Emlen of a migrating flock in pairs) and some individual Oyster-catchers (*Haematopus ostralegus*), Lapwing (*Vanellus vanellus*), Golden Plover (*Pluvialis apricaria*), and Redshank (*Tringa totanus*); all terns (*Sterna*) and gulls (*Larus*) so far studied fall in this category as do some grebes (*Colymbus*), loons (*Gavia*), all the ducks (Anatidae), platycercine parrots, some gallinaceous birds such as the European Partridge (*Perdix perdix*), the American quails of the genera *Lophortyx* and *Colinus* and probably the pigeons and doves.

For completeness, some rather special cases already described elsewhere must be mentioned under those where the sexes pair in flocks, namely, the Boat-tailed Grackle (*Cassidix mexicanus*), the Cowbird (*Molothrus ater*), the Wagler Oropendola (*Zarhynchus wagleri*) and Smooth-billed Ani (*Crotophaga ani*).

Whereas pair-formation has been studied in detail in a number of species where the male is isolated, no similar investigation has been made of how pair-formation occurs in a flock. This is one of the biggest gaps in the subject under review.

Variation in manner of pair-formation.—Often the members of a family of birds all show the same general type of pair formation, but in a few groups there is a remarkable diversity. Thus the birds of paradise and the gallinaceous birds both include (1) lek species, (2) birds with isolated males and sexes meeting solely for copulation, and (3) birds which pair for the breeding season; Stoddard suspects that some Bobwhite (*Colinus virginianus*) may remain paired during the winter. Again, the Icteridae include (1) species with isolated males holding large territories in which most of the food is later obtained, such as the Western Meadowlark (*Sturnella neglecta*) and probably the North American orioles (*Icterus*); (2) birds with isolated but smaller territories which are not feeding areas, such as the Red-winged Blackbird (*Agelaius phoeniceus*); (3) colonial species with isolated males, such as the Tricolored Red-wing (*Agelaius tricolor*) which nests in large colonies, and the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) which nests in small colonies; (4) birds which form pairs when in flocks, such as the Brewer Blackbird (*Euphagus cyanocephalus*) which nests in groups and the Bay-winged Cowbird (*Agelaioides badius*) which nests solitarily; (5) birds which form only a very temporary pair-bond, such as the Wagler Oropendola (*Zarhynchus wagleri*); (6) birds which meet solely for copulation, like the Boat-tailed Grackle (*Cassidix mexicanus*); and finally (7), the cowbirds (*Molothrus* and a few other genera), some of which are parasitic, some not, and which present very diverse habits. The Icteridae would well repay a detailed behavior study, such as Friedmann has already made for the cowbirds. A similar, but perhaps not quite so diverse, series could be traced in the Ploceidae, which include extremely colonial species, moderately isolated polygamous territorial males, strictly monogamous forms, and parasitic species; but the Ploceidae have been comparatively little studied.

In some birds there is variation even between individuals of the same species. Thus, from the summaries in the "Handbook of British Birds" and other sources, it appears that some individual Oyster-catchers (*Haematopus ostralegus*), Lapwing (*Vanellus vanellus*), Golden Plover (*Pluvialis apricaria*) and Redshank (*Tringa totanus*) have paired up when in the flocks, in some cases before reaching the breeding grounds (have some of these remained paired during the winter?), whereas other individual males arrive at the breeding grounds unpaired and claim isolated territories. Further study of these species is needed. In the Great Crested Grebe (*Podiceps cristatus*) some individuals arrive on the breeding grounds paired and in other cases the unmated males take up territories. In the British Robin (*Erithacus rubecula*) and Mockingbird (*Mimus polyglottos*) another type of individual variation occurs; usually the members of a pair separate and hold isolated territories in the autumn, but occasionally they remain together.

Territory.—I do not propose to include a full discussion of the functions of territory. (For my more recent views, see papers of 1937, 1939.) It may be pointed out that a territory in which an isolated male displays and obtains a mate takes four main forms: (1) in a lek bird it has no function except in courtship; (2) in colonial birds, such as frigates, the nest is later placed there; (3) in birds such as some waders the territory is fairly large but food is obtained outside it; (4) in some passerine species most or all of the food is obtained within the territory. But these four do not exhaust the categories of territorial birds. (5) Many of those species which pair up when in flocks later defend territories around their nests (wading birds, gulls, terns, grebes, loons, *Lophortyx,* probably some of the fringillid genera cited, and possibly some ducks). The two main functions which have been ascribed to territory are pair-formation and food; but all these species pair up before taking up their territories, and many of them feed exclusively or mainly outside their territories. Hence, the significance of their territory remains unknown; possibly it originates through defense of the mate against rivals, but in many instances a definite, limited area is acquired and defended. Further study of this group is needed. (6) Autumn territories, found in the British Robin, Mockingbird and Loggerhead Shrike (*Lanius ludovicianus*) are discussed elsewhere

(Lack, 1939). (7) The territory defended by each female Cuckoo (*Cuculus canorus*) is a laying area, and does not necessarily have the same boundaries as the territory defended by the male. (8) Smooth-billed Anis (*Crotophaga ani*) defend a group territory.

Polygamy, polyandry and promiscuity.—Mayr (1939) has recently summarized the data on irregular sex relations in birds, and discusses polygamy and polyandry. Occasional cases of bigamy in normally monogamous species are now known from many species, and need not be detailed; Tinbergen (1939, p. 43) gives a good summary. Regular polygyny occurs in the Bittern (*Botaurus stellaris*), Corn Bunting (*Emberiza calandra*), several species of bishop-birds, of which *Euplectes hordeacea* and *E. nigroventris* have been best studied, in *Ploceus philippinus* and doubtless other ploceids, in the Red-winged Blackbird (*Agelaius phoeniceus*), the Tricolored Red-wing (*A. tricolor*), the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) and the Wagler Oropendola (*Zarhynchus wagleri*). In all these species except the last the male is territorial (though the size of territory varies considerably), and the females nest in the territory of the male. Other species for which regular polygyny has been claimed are Penduline Tit (*Remiz pendulinus*), Muscovy Duck (*Cairina moschata*), Ostrich (*Struthio camelus*), Great Bustard (*Otis tarda*), Wild Turkey (*Meleagris gallopavo*) and Rose-colored Pastor (*Pastor roseus*). The last has also been claimed to be polyandrous, and is therefore more probably promiscuous, but both this species and the others require further study, as do a number of species for which only rather vague evidence has been produced.

Regular polyandry is rarer than polygyny, but occurs in tinamous (*Crypturus*), button quails (*Turnix*) and the painted snipe (*Rostratula*), in all of which the female is the conspicuous displaying sex. In phalaropes the female displays, but regular polyandry has not been proved, although it is suspected by some workers (see Tinbergen, 1939).

In the above-listed polygynous species that have been adequately studied, there is a definite, though in some cases very temporary, bond between the two sexes; in some the male is occupied with only one female at a time, in others it retains contact with all its mates. The other main group of birds, popularly supposed to be polygamous, are the lek species, already listed, together with those other gallinaceous birds which have no regular pairing bond. But in these one should not speak of "polygamy" at all, since no true pair-bond is formed; promiscuity is the correct term.

There is great ignorance as to the sex ratio in species that are promiscuous. Thus, in the Blackcock (*Lyrurus tetrix*) some workers have claimed that the lek habit results from a surplus of males, others from a surplus of females; the actual sex ratio is unknown and may well be equal. In the Ruff (*Philomachus pugnax*) Selous proved that one male copulated with several females. He could not be certain that one female was mounted by more than one male, but thought this occurred and it seems probable since individual females will visit more than one lek. For the other species, the male apparently copulates with several females, but it is unknown whether the female always returns to the same male or not.

The Boat-tailed Grackle (*Cassidix mexicanus*) seems to be promiscuous and this is more probably the situation than polygyny or polyandry in the Rose-colored Pastor (*Pastor roseus*). Promiscuity holds at times for the parasitic Cowbird (*Molothrus ater*) and Cuckoo (*Cuculus canorus*), in the latter apparently because the female's territory is not coextensive with that of a male, and further some females do not have territories. Exceptionally, promiscuity occurs in many other species, for the paired males of normally monogamous species will occasionally copulate with a strange female, as observed by Howard in the Moorhen (*Gallinula chloropus*). Portielje (1938) summarizes other cases, which need not be detailed here.

An exception to the normal avian condition of monogamy takes a different form in the timeliine bird *Yuhina brunneiceps*. Groups of individuals of both sexes build a nest, in which several females lay, and both sexes help to raise the brood. Skutch (1935) summarizes numerous instances where odd individuals of various species attach themselves to a mated pair and help them to raise the brood. These examples help one to understand how the curious condition in *Yuhina* may have been evolved, in which there cannot be said to be pair formation at all. The same quite possibly applies to the California Woodpecker (*Balanosphyra formicivora*) and to a few other species. Group nesting also occurs in the Smooth-billed Ani (*Crotophaga ani*) and here there seems to be strict monogamy at times, polygyny or polyandry at others.

SEX RECOGNITION

Earlier work.—In recent years the manner of sex recognition and the detailed behavior at pair-formation have received considerable attention even though relatively few species have been studied in any detail. Craig (1909) and Whitman (1919) conclude that doves do not know the sex of a strange individual until they are at close quarters, when behavior differences occur. Allen (1934), working on the Ruffed Grouse (*Bonasa umbellus*) concluded that, in general, birds have no recognition of the sex of another bird, but that, in pair-formation, the dominant individual takes the male role, the subordinate bird the female role, irrespective of sex; normally, but not invariably, the male is dominant to the female. Independently, Hingston (1933) expressed rather similar views, more crudely and more generally applied. From experiments with mounted birds, Noble and Vogt (1935) discovered that in many species with pronounced sexual dimorphism the male can distinguish the female by plumage.

Lorenz' views.—Lorenz (1935) classifies pair-formation into three main types. In the first (lizard) type, the male pursues all others of its species; a strange male fights, but weak males and females are pursued and copulated with. This type, rare in birds, occurs in the Muscovy Duck (*Cairina moschata*). The second (labyrinth-fish) type is the commonest in birds, and includes the Ruffed Grouse. Lorenz accepts Allen's conclusions provided they are restricted to this group. Each sex possesses the potentialities of both sexes; an individual tends to react as a male unless subdued by the fighting or dominance display of another individual. For the formation of the pair, male dominance is essential. Homosexual pairs can occur. Specifically included in this category are various gallinaceous birds, ducks, pigeons, and the Jackdaw. In the third (cichlid-fish) type, there is display by both sexes and no dominance order. The birds are not sexually ambivalent, for, if they were, each would have to act as a male. The female is not made inferior; examples: herons, stork, swans, geese, Great Crested Grebe.

Lorenz put forward his classification tentatively and as a basis for further work. He does not claim that his categories are exhaustive, and he allows for great variation within each. Nevertheless, I find it impossible to use them, even as a basis for a revised classification. First, his system involves placing such birds as *Bonasa*, which do not form true pairs at all because the sexes meet simply for copulation, with types like the corvids which pair for the breeding season and perhaps longer. Second, as is clear from Heinroth (1911) and Phillips (1922), Muscovy Ducks do sometimes differentiate females ready to mate from other individuals, and the female at times waits for the male instead of fleeing. Hence this species must be placed in the second category. Indeed no species of bird seems to fall in Lorenz' first category. Then, Lorenz' second and third categories do not represent definable divisions of behavior. Females of at least most species in the second group show some display, so might be classed in the third, mutual display, category. Also, the Night Heron (*Nycticorax nycticorax*), put by Lorenz in the third category, would, from Noble, Wurm and Schmidt's work (1938), be placed in the second category, since it shows dominance reactions, and homosexual pairs may be formed; but it also has mutual courtship. Again, Allen (1934) for the Canada Goose (*Branta canadensis*), and others for the Mute Swan (*Cygnus olor*), have recorded homosexual pairs, although both species are placed in the third category.

Tinbergen (1939) points out that Lorenz' description of each main type includes a number of criteria of a different order, which cannot well be combined. Nevertheless, Lorenz relies mainly on one character, that is, the method of sex recognition, on which basis Tinbergen redefines the three groups as follows: (1) where only the male has releasers, hence, non-displaying males are treated like females; (2) where releasers are present in the female so that all individuals that do not show the female releasers are attacked (treated like the male); (3) where releasers are present in both sexes. Tinbergen considers that (1) the lizard type and (2) the labyrinth fish type are really the extremes in a series, perhaps not occurring in perfect form in any birds. All birds are therefore in the third, cichlid, group, in which both sexes possess releasers, but when those of one or the other sex are poorly developed they approach one or the other extreme. This seems very sound.

In conclusion, it should be pointed out that Lorenz ought not to be criticised too much, since his was the first constructive attempt to classify and coordinate our knowledge of an extremely complex subject; his paper has had a decidedly stimulating effect on many workers, including the writer. Further, the criticisms here offered are partly the result of facts which were not known when Lorenz wrote his paper.

Dominance.—The term dominance was first used in birds in the social hierarchy experiments of Schelderuppe-Ebbe (1935). But the meaning of dominance is quite different in the statement that the male dominates the female in pair-formation or copulation, as pointed out by Noble (1939). He rightly distinguishes between the former type of social dominance and the latter type of sexual dominance. Further, evidence for this distinction is found in Nice's observations. The male Song Sparrow (*Melospiza melodia*) courts the female by "pouncing." Nice (1938) writes: "The object of pouncing is domination"; and again (1939): "Although he dominated her by his pouncing, yet in many little everyday encounters, she dominated him." Nice evidently supposes that in the sexual sense the male dominates the female (as the theory requires), but in the social sense it seems as if the female is dominant to the male. Shoemaker (1939) finds that, in the canary (*Serinus canarius*), whereas males normally dominate (social sense) females, in the mated pair the female dominates (social sense) her mate, which would be contrary to theory if social and sexual dominance were the same.

But even when this distinction has been made, there are considerable difficulties, since dominance has been used in a vague and partly subjective sense. For example, it has been stated that "dominance and fear are the important principles . . . in controlling the mating cycle" (Allen, *loc. cit.*), and that "the object of pouncing is domination" (Nice, *loc. cit.*). Working on Night Herons (*Nycticorax nycticorax*), Noble (*loc. cit.*) is much more explicit, and at times simply means by dominance the relative positions of male and female, in particular, which has its head and neck higher. But he also states that at the beginning of pair-formation the male is in a subordinate position and his display "gradually restores his dominance." Noble refers to what is obviously an important relation between the pair, but it is extremely difficult for those who have not worked with similar species to know just what is meant.

The dominance theory was put forward partly to explain sexual ambivalence, whereby in homosexual pairs of birds one member may go through all the actions typical of the opposite sex. Since I have recently discussed sexual ambivalence elsewhere (Lack, 1940), I will only state that this behavior is extremely complex, and probably has a different basis in different cases, sometimes genetic, sometimes hormonal, and sometimes due to various types of external situation.

The dominance theory postulates that at pair-formation the male in some sense impresses or overpowers the female, sometimes through aggressive display. To prevent a possible misinterpretation, I should state that the aggressive behavior shown by English Robins at pair-formation (Lack, 1939) is not related to dominance in any way; it is sporadic, soon dies away and probably results from the maladjustment of the formerly isolated individuals to the new situation in which a second individual is tolerated. Verwey (1929) has a similar suggestion for parallel behavior in the Common Heron (*Ardea cinerea*).

To conclude, I would not deny the importance of sexual dominance, but it needs clearer definition, and it is not nearly so widespread in birds as Allen (1934) implies. I cannot say more since I have not studied at first hand any species in which it occurs.

First and later reactions.—Tinbergen (1935, 1939) working on sex discrimination in the Red-necked Phalarope (*Phalaropus lobatus*) and the Snow Bunting (*Plectrophenax nivalis*) stresses the difference between a first reaction released by a very general external situation, and later reactions with more particular releasers. Judged on its first reaction to a bird at a distance, a male Snow Bunting apparently cannot distinguish the two sexes, but its behavior when at closer quarters shows that it does so readily. Further, the simplicity of the releaser for the first reaction is not due to inadequate visual powers.

In general, Tinbergen (1939) thinks that (1) species with marked sexual dimorphism, such as some of those used in the experiments of Noble and Vogt (1935), may discriminate the sexes at the first reaction; (2) other species, like the Snow Bunting and the Red-necked Phalarope, do not do so at the first reaction but do so without difficulty at close quarters; and finally (3) species like the Common Tern (*Sterna hirundo*) and Ruffed Grouse have a much longer undifferentiated reaction of the sexes, since both sexes behave in the same way for a comparatively long time after first meeting. This general classification seems sound. Male Blackcock (*Lyrurus tetrix*) obviously recognize females at once; this was corroborated by experiments with mounted birds. I have not studied carefully any species like the Snow Bunting or the Red-necked Phalarope. The British Robin (*Erithacus rubecula*) has a long period of identical reaction of the sexes, so comes in the third group.

Observations on captives.—In the wild, each male Ruffed Grouse is isolated. Drumming, by which means the female normally locates the male, was, according to Allen (*loc. cit.*) greatly reduced in captivity. Consequently, Allen's conclusions on sex recognition do not necessarily apply to wild birds, which, I should guess, discriminate each other's sex much more readily. I would therefore not include the Ruffed Grouse in Tinbergen's third category without further evidence. In general, pair-formation, particularly when isolated territorial males are involved, is likely to be highly abnormal in captivity. This also is indicated by the much greater frequency of hybridization in captivity between species than occurs in the wild.

Sex recognition at the time of pair-formation.—I agree with Tinbergen (1939) that the terms "sex recognition" and "sex Kumpan" imply entities which do not exist. Lorenz (1935) has shown that for different phases of its behavior a bird's "recognition" of its own species is related to very different external signs or releasers; what releases one reaction does not necessarily serve for another. The external situation leading to pair-formation is markedly different from that leading to copulation, and it is different again for other sexual reactions. In particular, the experiments with mounted birds refer to copulation, and do not necessarily have any bearing on pair-formation.

In the British Robin (Lack, 1939) one cannot speak of sex recognition at any stage of the breeding cycle. In pair-formation, the unmated male treats intruding males and mated females alike, but reacts differently to an unmated female. How he differentiates an unmated from a mated female is unknown, but since pair-formation takes some time, discrimination is evidently difficult. The robin is perhaps exceptional. In other small passerine species, for example the Song Sparrow, *Melospiza melodia* (Nice, 1938), the male reacts similarly to all strange females, whether mated or unmated, hence the problem here is genuinely one of sex discrimination, which in the Song Sparrow, where the sexes are alike in plumage, depends primarily on a special call of the female. In other species, for example the Chaffinch, *Fringilla coelebs* (Lack, MS), it depends on plumage differences. In such species, the male does not normally form a pair with an already mated intruding female because (1) the latter rarely leaves her territory, and usually retreats to it at once when chased, whereas an unmated female, though she may be chased out, keeps returning to the same territory; (2) in some species, like the Song Sparrows, the mated male defends his female; (3) in others, like the Chaffinch, the mated female drives out other females from the territory.

Clearly far more facts are needed on behavior at pair-formation. Some species discriminate the sexes readily, some have a generalized first reaction but discriminate at close quarters, in others some kind of dominance relation is perhaps involved. There are yet others in which the behavior does not seem to fit into any simple pattern. The pair comes together gradually and with difficulty. Brian Roberts informs me that at the beginning of the season Gentoo Penguins (*Pygoscelis papua*) of both sexes have similar behavior (females as well as males may defend stations), but gradually the birds sort themselves out. (His account supersedes that by Levick on *P. adeliae*, who claimed that the isolated sex was normally the female.) In Common Terns (*Sterna hirundo*) both sexes behave alike at the beginning of pair-formation, and the problem is simpler in British Robins and Common Herons only to the extent that the males maintain territories which the females visit. When a careful study has been made of those species which pair up in flocks, a similar complexity will probably be revealed in many cases; the members of a pair gradually come together, using many small interrelated mutual actions, with intervals when they move apart again. I think it will prove exceptional to find pair-formation depending on a simple dominance mechanism or set of releasers.

Before closing this section, mention may be made of the present confusion concerning pair-formation in cormorants and shags (*Phalacrocorax*), in which some writers affirm that the male is the isolated displaying sex, others the female, and some that either may do it. Observations refer to different species, but it is unlikely, though possible, that the different species differ in this respect. Possibly the situation is similar to that in *Pygoscelis* and *Sterna*, but more data are needed for accurately sexed birds.

Individual recognition of mate.—After the pair has formed, "sex recognition" is a quite different problem; it is that of distinguishing the mate individually from all others of her species. Such individual recognition of the mate from others, often at considerable distances, by sight and in some cases also by sound, has now been proved for many species. Only in moments of unusual stress will a territorial bird attack its own mate, then usually very temporarily; such attacks were recorded several times in British

Robins which had been paired for weeks or months. The differences involved in distinguishing an individual bird are normally too fine for the human observer to detect and indicate the accuracy of which bird vision is capable. Whitman and Craig working with doves, and Nice with the Song Sparrow, show that in addition to its own mate, the male distinguishes the sex of neighboring birds through individual recognition, acquired by previous experience.

Sex recognition at copulation.—The external situation provided by the female leading up to copulation is different again, and the releasers are evidently much simpler than those involved in pair-formation. The major stimulus in most species is simply that the female keeps still. In some species (British Robin and Moorhen) the head is somewhat lowered, in other species (many fringillids and the Tricolored Red-wing, *Agelaius tricolor*) the beak is pointed upward. Again, in some species the tail is somewhat depressed or spread, and in some the wings may be slightly drooped. That the position of head, tail and wings are subsidiary is illustrated by the frequency with which a male bird will copulate with a mounted bird, in which the only feature of the inviting female provided is its stillness. (See Noble and Vogt, and many recent behavior studies.) In a few species (Song Sparrow, Nice, *loc. cit.*, and the flicker *Colaptes auratus*, Noble, 1936), the female also gives a special call. Noble thinks this is why, unlike most birds, a male flicker does not copulate with a female mount.

One must not argue too much from experiments with mounted birds. Because a male mounts an object, it is not safe to deduce that the male fails to distinguish this object from a living female of its own species. The point is illustrated by human sex perversions and by the record, quoted by Dobzhansky (1937), that a horse copulated with a stuffed cow. Probably the plumage and structural characters which differentiate related species of birds or the two sexes, and which are undoubtedly of importance in pair-formation, do not form an essential part of the external situation releasing copulatory behavior in the male bird. In nature, a strange species or a male of the same species would normally not assume the posture releasing copulation in the male. When Noble and Vogt (1935) find that a male House Wren (*Troglodytes aëdon*) will copulate with the mount of a Winter Wren (*Nannus hiemalis*), it does not, of course, follow that a House Wren cannot distinguish a live Winter Wren from its own species at the essential time of pair-formation. The same workers' experiments with various sexually dimorphic species are of great interest because they show that, although, through being motionless, a male mount provides the main (but probably not the sole) factor in the external situation releasing copulation, nevertheless the males of sexually dimorphic species did not copulate with mounted males; the male plumage counteracted the other influence. Experiments with the Galapagos finch *Geospiza fuliginosa* (Lack, MS), in which the males are black and the females gray-brown, showed that breeding males would sometimes copulate with black male mounts. But, it is shown that they can discriminate the sexes by plumage differences because courtship directed toward a male mount occurred in fewer individuals, and here tended to be less intense, than courtship of a female mount. All one can say is that in *Geospiza fuliginosa* the male plumage had a less inhibitory influence over the reaction to motionlessness of the mount than in the sexually dimorphic species investigated by Noble and Vogt.

In elicting copulation, the internal state of the male is extremely important. At the appropriate stage of the breeding cycle, the internal factors leading to his mounting the female are normally of such strength that copulatory behavior is released whenever the female assumes a particular attitude, but not otherwise (except when experimentally imitated). But, if the male's internal state is unusually strong, other external situations, normally inadequate, may release mounting; if unusually weak, the normal external situation may be inadequate; sometimes the female then assumes an exaggerated posture, which may or may not lead to the male being able to mount. (See Lack, 1939.)

That personal recognition of the mate is not a main factor in releasing copulatory behavior is shown by the mated males of many species which have copulated with mounted specimens, and is particularly well shown by a British Robin which copulated four times with a mount while its own female stood beside it posturing at the specimen. The latter situation is particularly striking since a male robin normally attacks at once any strange robin in its territory (the mate being recognized individually). In this experiment, the mount provides the external situations for two reactions: (1) motionlessness, releasing copulation; and (2) a strange robin, releasing attack. Since most male robins attack a mount, the second is usually predominant. In nature, of course, it does not normally happen that a strange individual provides the releaser for copulation, but Howard has observed this in a Moorhen, whereupon the previously aggressive male copulated.

SEXUAL SELECTION

Under sexual selection, Darwin discussed the female's selection of a mate and the secondary sexual characters which have been evolved by this means. Modern discussions usually include all secondary sexual differentiation, though much of it is not thought to have evolved through the female's selection of her mate in the narrower sense in which Darwin conceived it. Secondary sexual differentiation is associated with four distinct types of display in birds: (1) antaposematic display (Huxley, 1938), that is, threat display between rivals, especially rival males; (2) gamosematic display, or display which assists the pair to find each other; (3) epigamic display, or display between the sexes to promote copulation; and (4) post-nuptial display, or display between the sexes after copulation.

The first three types of display, antaposematic, gamosematic and epigamic, have all doubtless contributed to the evolution of brightly colored areas in male, and less commonly, female, birds, since one can find species in which a colored area is used exclusively in one or the other of these types of display. Gamosematic display involves sexual selection in the narrower Darwinian sense, since gamosematic characters are those which influence the female in selection of a mate at pair-formation. Antaposematic display can also be included in the Darwinian meaning, since such threat display results in the male's acquisition of a mate, even when the immediate object of such fighting is the acquisition and maintenance of a territory. But epigamic display is in a different category, since in monogamous territorial birds the female normally has no chance of seeing the epigamic display of any male except her mate, and the latter may have been selected some weeks or months earlier. There is direct evidence that epigamic display stimulates ovulation (Craig, 1911; Matthews, 1939) and indirect evidence (see especially Howard, 1929) that it helps to synchronize the two sexes in copulation, since most such display occurs when the other sex fails to respond adequately. Hence epigamic display and associated color patterns have survival value, though not at all on the same grounds as those postulated by Darwin. While epigamic display is often individual, Darling (1938) shows the influence of the group on its effectiveness, and I have shown that there may also be group selection of gamosematic display in lek species like the Blackcock (*Lyrurus tetrix*).

Postnuptial display sometimes takes the same form as epigamic display, as in the Great Crested Grebe (*Podiceps cristatus*), and sometimes that of the male feeding the female (Lack, 1940). It is commoner in birds than usually realized, and apparently serves to maintain the bond between the pair (Huxley, 1914; Lack, 1939). I know of no instance where any structure or colored area is used exclusively in postnuptial display, so that the latter has probably played no part in the evolution of such structures.

The only experimental investigation of sexual selection in birds is that on Budgerigars (*Melopsittacus undulatus*) by Cinat-Tomson (1928), who found that the females preferred the males with the larger number of throat spots. Before accepting this result it is essential to know how pair-formation is effected in wild Budgerigars (the method adopted in the experiments seemed highly artificial), and what types of display utilize the throat spots. This is not to deny the value of the experiment, especially since Noble (1938) has demonstrated similar sexual selection in fish.

It has often been assumed that sexual selection is unaffected by other species. But I have found that male secondary sexual plumage is commonly lost in land birds of oceanic islands. In such species, threat, pair-formation and epigamic display are presumably just as important as on the mainland. Nevertheless there is a further function for such plumage, namely, to enable the female to recognize and pair up with a male of her own, as distinct from some other, species, since hybridization is at a selective disadvantage. The few land birds which have colonized oceanic islands are normally removed from all related species which the female might confuse with her own, hence this function disappears. The opposite of this process is seen in such birds as the pheasants (Phasianidae) and some other gallinaceous birds (*Tetrao* and *Lyrurus*), the birds of paradise (Paradiseidae), and the hummingbirds (Trochilidae) in which, correlated with the absence of a definite pairing bond, hybridization is relatively common, and in turn correlated with this, there is a maximum development of male secondary sexual differentiation, each species being strikingly distinct from the rest. Here, gamosematic characters must not only be striking, but similar throughout the species, and distinctive from all those of all other related species in the same region. The Ruff (*Philomachus pugnax*) would seem to be one of the few species in which the secondary sexual plumage varies considerably. Molony (1937) naively attributes this to variations in female taste, which seems unlikely. Two points may be noted: (1) although variable, the plumage of each Ruff is quite unlike that of any other species; (2) the birds display in a group, hence may, to some extent, be selected as a group, so that individual variation is less important.

SUMMARY

1. In some species of birds, the sexes meet solely for copulation, in some they form a very temporary pair-bond, in most they pair for the brood or the breeding season, in some they pair for life.
2. In many species the male is isolated in a territory, which varies greatly in extent in different species, and the female comes to him there. In a few, the female is the isolated displaying sex. In many other species, pair-formation occurs in the flocks.
3. Throughout some families of birds the type of pair-formation is similar, but considerable variation is found within the Icteridae, Paradiseidae and some other groups.
4. Some individual *Podiceps cristatus* and *Haematopus ostralegus* form pairs when in the flocks, others through isolated territorial males.
5. In some species the territory is used neither for pair-formation nor feeding.
6. The data on polygyny, polyandry and promiscuity are summarized.
7. One should not speak of "sex recognition," but of the external situations leading to pair-formation, copulation, etc., situations which are often different for different phases of sexual behavior.
8. Sex recognition is discussed, particularly the views of Lorenz, Noble and Tinbergen, and the phenomena of dominance, first and second reactions, and copulation

with mounted specimens. The data are too few for a comprehensive classification and analysis.

9. Sexual selection is associated with four distinct types of display, of which (1) antaposematic and (2) gamosematic come within the Darwinian definition, whereas (3) epigamic display does not. (4) Postnuptial display, though common, may not have had much influence on the evolution of structures. The loss of male secondary sexual plumage in species inhabiting oceanic islands is discussed.

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