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Phil. Trans. R. Soc. Lond. B 1966 **251**, 375-386
doi: 10.1098/rstb.1966.0023

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Social and communal display

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[Plates 12 and 13]

At all stages of the preparation of this paper I have been given the benefit of Sir Julian Huxley's very effective help and guidance. In addition, many biologists have advised on various points, notably Professor Ernst Mayr, Dr A. J. Hogan-Warburg, Dr J. P. Kruijt, and Dr H. Lind.

The discussion is restricted to birds in which communal and social displays are comparatively well studied and constitute unique examples of extreme ritualization. We can see various stages of their evolution. Following the pioneer work of Selous (1901, notably pp. 68–95), and especially that of Huxley (1914, 1923), evidence has accumulated to indicate that threat and courtship display—with which we are here concerned—derive originally from movements and postures which are the expression of conflict situations. Ritualization then takes place under the influence of natural selection towards realizing greater adaptive (biological) value of the expressive actions, both as a means of unambiguous communication and as 'releasers' of appropriate conspecific behaviour (for more detail see contributions by Huxley, Lorenz, Hinde, and Cullen, in this volume).

In the case of ritualized leks and other forms of social display, there is to begin with, a general stimulative function which is also found in individual courtship display. But this effect is greatly exaggerated when several individuals display together. In the case of social displays the stimulation may also promote other activities than reproduction, for example, migration. The transmittance of instinctual 'moods' by this means may have pronounced physiological effects and tends to synchronize the activities in question ('Fraser Darling effect' with respect to breeding activity; cf., for example, Crook 1965, p. 190).

Secondly, as in other ritualized displays, the signalling function is perfected, which means greater formalization and uniformity of motor behaviour, together with exaggeration of the conspicuous structures and colours involved. A third, very important point—well illustrated here—is that ritualization of hostile behaviour reduces actual combat with its ensuing possible damage to the species.

Finally, these displays demonstrate the decisive influence of the ecological background and general mode of life of the species in question. Thus, a prerequisite for the specialized communal displays by males for mating purposes—arena displays—is the male's abandonment of parental duties.

In the majority of birds the male's share in rearing the young acts as a counter-selective brake against the exaggeration of striking structures and colours shown off in display. For various reasons, briefly discussed later, male cooperation in reproductive duties has in a small percentage of birds been easily dispensable or even disadvantageous, and has therefore been dispensed with. The evolution of bizarre display characters may then advance

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further, and this tendency is enormously enhanced by the fact that, when a pair-bond is no longer necessary, polygamy, or rather promiscuity, ensues. This, in turn, means that intra-sexual selection is greatly intensified because one male may secure a large number of matings and others few or none (Darwin 1871; Huxley 1942, pp. 427, 484). Such promiscous males may either display singly (e.g. numerous Pheasants and Birds of Paradise) or on a communal display ground, an arena or lek. In the latter case, which concerns us here, female choice is decisive. On the other hand, the previous acquisition of a mating stance, a small territory (a court) in the arena is normally a prerequisite for a male's chances of successful mating. Furthermore, the courts are not of equal value. It seems to be a general rule that most matings go to males in the centre of the lek (cf., for example, Kruijt & Hogan 1966, on Black Cock).

Naturally, the close proximity of several males, each in his own court, makes strong demands on the ritualization of sexual and aggressive tendencies in order to avoid interruptions of matings. In various grouse species with arena displays and in ruffs, the stabilizing factors consist in each male being tied to his own territory, in that the sexual urge is diverted by ritualized territorial strife, and by immobile postures as part of courting behaviour. The system may work in a more or less effective way as exemplified by a comparison between the two best studied species: the North American Prairie Chicken and the European Black Cock (Hamerstrom & Hamerstrom 1960; Kruijt & Hogan 1966).

In the Prairie Chicken (*Tympanuchus cupido* subsp.) the general plumage of the male is less specialized (much less different from that of the female) than in the related Black Cock (*Lyrurus tetrix*) presumably owing to the greater need for crypticity. However, when the 'feather horns' and the naked, coloured air-sacs on the neck are shown off in display the male Prairie Chicken's appearance is striking, but in the event of danger these ornaments disappear, and the bird becomes inconspicuous. The air-sacs are formed by the anterior, modified portion of the oesophagus. In addition to their visual effect, they are also important for the production of the special loud sound which is the reason for the arenas of these birds being called 'booming grounds'.

In the Black Grouse—except in sound-producing apparatus—sexual dimorphism has advanced much further. The male, even when not displaying, is strikingly different from the female. Accordingly, the Hamerstroms (1960), who have studied both species, were struck by the greater perfection of the Black Cock mating system: the 'Black Cock tend to respect each others' territories, when hens are present, more than Prairie Chicken do' (p. 278). Kruijt & Hogan (1966) confirm this by comparing the Hamerstroms' statistics concerning the number of mating interferences in the Prairie Chicken with their own findings for the Black Cock: 17·5% of the matings were disrupted by neighbours in the former compared to 4·2% in the latter.

Black Cock are notable for visiting the lek at almost all seasons. This may certainly have survival value in stabilizing the territorial system, but lek display (autumnal display in particular), may also have some sort of imprinting function. The attraction shown by Black Cock females for conspecific males must have a genetic basis, but in order to develop this attraction properly it may be important for young females to be able to watch displaying males early on in their first year. Autumnal display can in fact attract hens (Höhn 1953, p. 57). (See also contribution by I. Hjorth to this Discussion.)

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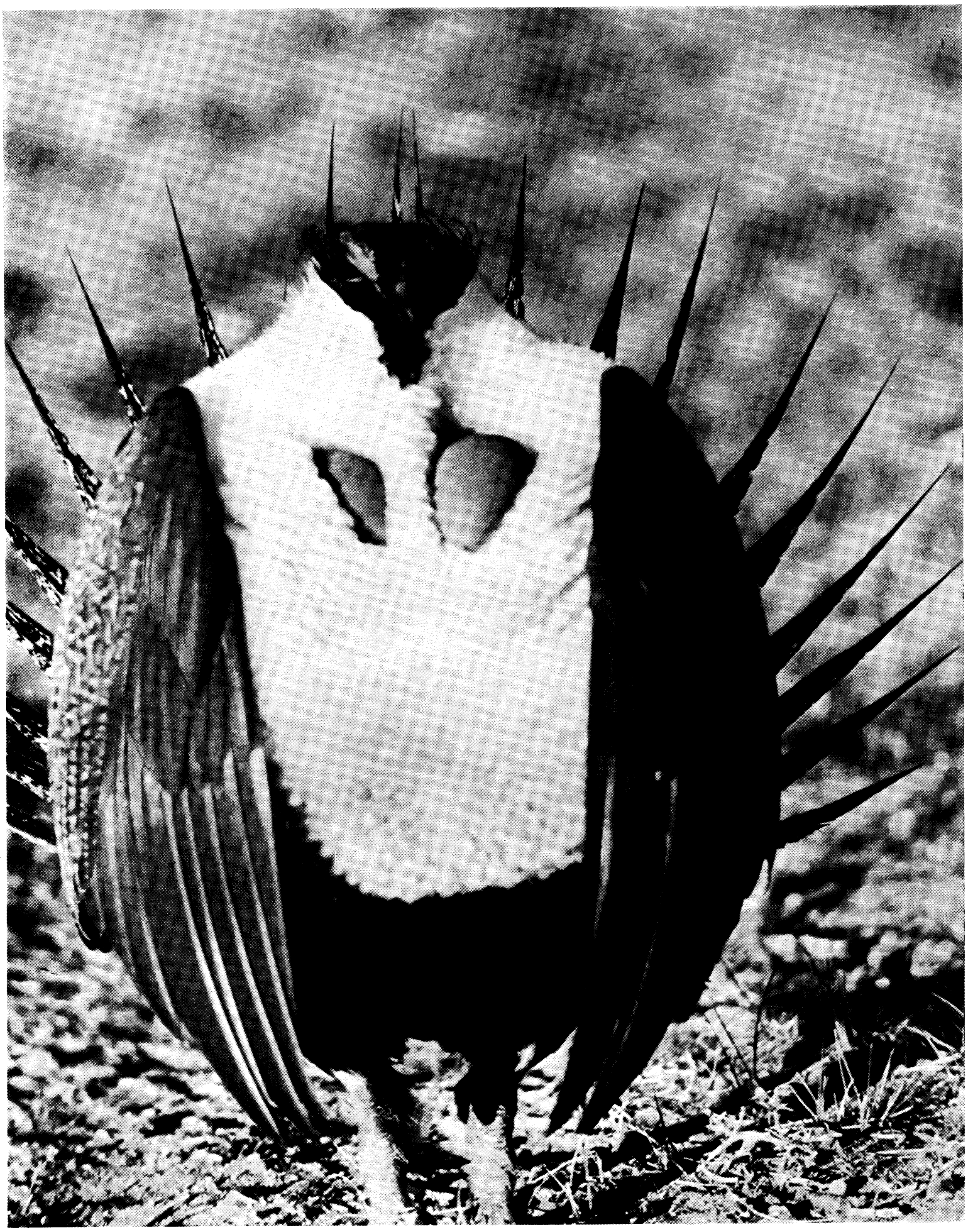

Sage Grouse male in display. (Photo by Charles W. Schwartz.)

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Ruffs on the 'hill'. Four of the five males are in 'pairs'. The two light-coloured birds are 'satellites' (cf. text, p. 378). They show the squatting, ecstatic posture in the presence of a female (left bird). (Photographed in North Jutland by C. C. Doncaster.)

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The Sage Grouse *Centrocercus urophasianus* (plate 12), an American bird related to the Prairie Chicken, has very large arenas with up to 400 cocks. The concentration of matings among a few cocks is here carried to an extreme. Scott (1942, p. 483) estimated that 87% of the matings are achieved by less than 3 % of the cocks present in the arena, while in the Black Cock, Kruijt & Hogan (1966) found that about the same proportion is achieved by approximately one third of the cocks. It further appears from Scott's account that the gregarious tendency of the hens is an important contributory reason for their concentration in a few mating areas.

As space prohibits discussion of the less well-known lek displays in Sharptailed Grouse, (*Pedioecetes phasianellus*) (cf. Roberts 1932, p. 397) and Capercaillie (*Tetrao urogallus*) (cf. Lumsden 1961), we may pass on to the Ruff (*Philomachus pugnax*), a wader related to the sandpipers, perhaps particularly the Pectoral Sandpiper (*Calidris melanotos*), the behaviour of which in the breeding season shows certain resemblances to that of lek birds (Pitelka 1959).

Male Ruffs are unique among arena birds—indeed among all birds—in being highly polymorphic in their breeding plumage: no two males are alike in coloration. When in close proximity on their assemblages they produce a sort of flower-bed effect that may greatly enhance the stimulatory efficacy of the lek (Christoleit 1924; Ford 1940). No sounds are emitted. Absence of polymorphism in other lek species may be partly due to selection for specific distinctiveness to avoid hybridization. The ruff has no close relatives with lek display: it can therefore do without the 'information' derived from distinctive colours.

Some male ruffs have their own mating territories (courts) close together in the central part of the lek while others are as a rule kept out of this area. An interesting point, first discovered by Bancke & Meesenburg (1952, 1958), is that some males with white, or largely white, nuptial plumage, both general but notably in ruff and ear-tufts, are allowed to enter the central part of the 'hill' and stay together with the territory owners without having a 'run' (display territory) of their own. These authors also noticed that the 'white' individuals took no part in the fights and that they visited different hills. Hogan-Warburg (1964, 1965) confirmed and extended these observations by prolonged and careful study in Holland.

She found a pronounced dimorphism of behaviour as between non-white independent males and white satellite males. The former are either residents, with their own 'run' on the hill, or marginal males which are kept at a distance from the central residence area. Resident males start their career as marginal males, and may also lose status, later as a result of a fight. They then behave again as marginal males. The 'white' satellites' behaviour is strikingly different from that of independent males: aggressive elements are predominantly absent and they never acquire a 'run' (residence) of their own. This peaceful disposition appears to be the main reason for their being permitted access to the territories of resident males. However, an inborn inhibition in non-white males against attacking white individuals may also be involved. This is indicated by the fact that a few individuals are met with which in spite of their typical satellite behaviour have a somewhat darker plumage, and these are relatively unsuccessful in achieving copulation—not because females discriminate against them, but because they are less able to maintain themselves on an occupied 'run' than normal satellites.

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Independent males with anomalous plumage (i.e. dark but with much white in the ruff and ear-tufts) are also unsuccessful. They often fail to acquire resident status on the lek (Hogan-Warburg 1965, pp. 41–42). Thus there seems to be strong selection against 'wrong' combinations of colour and behaviour.

Presumably, the conspicuous white plumage of the satellite males makes them especially effective in attracting and stimulating females. They are, therefore, of value to the community as a whole, and possibly even to the individual male with whom they share a territory, in spite of the fact that they compete with him with respect to matings. However, Hogan-Warburg found a difference here between large and small leks. On large leks (with up to a score of residents), most residences appeared to be almost inaccessible to satellite males owing to the greater intolerance of the resident males: residences which did harbour satellites were seldom chosen by the females. On small leks (with three to eight residences) the resident males showed great tolerance towards satellites, and the females generally selected those which at that particular moment were multiply occupied. The study of this interesting species is being continued in Holland and in Denmark with the object of further elucidating the selective pressures involved.

The photograph (plate 13) shows two satellite males, each side by side with a resident, in the squatting, ecstatic posture in which the male 'freeze' in the presence of females.

Still more striking instances of cooperation between males for attracting and stimulating females are found in a totally different bird family, the Manakins (Pipridae) from south and middle America. They are relatives of the Tyrant Flycatchers (Tyrannidae) and the Cotingas (Cotingidae). The latter contain the famous Cock of the Rock (*Rupicola*) (Gilliard 1962) and at least one other species with arena display (Sick 1959, p. 274). Many others have singly displaying but promiscuous males.

As an extreme example of a Manakin's social display one may mention *Chiroxiphia caudata* from Brazil. The males are beautifully coloured, large for a Manakin (25 g), the general colour light blue (the same shade as that of the famous Morpho butterfly from the same region), the head black with a red crown, the wings and tail predominantly black. Up to three or four males may take part in the display (Sick 1959, pp. 284–85). The sketches (figure 1) show three males 'dancing' before a female. The males sit close together quivering in a single vibrating and strikingly coloured mass, and their voices blend in chorus (*a*). The one farthest away from the female then hovers a moment in the air facing the others (*b*) and lands close to the female, where the others have made room for him by moving a little sideways (*c*). He quickly turns round (*a*). The male now farthest away starts to hover, and the performance is repeated with clockwork precision. An immature male often takes the role of the female. No matings were observed (see below).

In other species of *Chiroxiphia* two males cooperate by emitting synchronized, far-carrying calls and by combining in a regular cartwheel dance. In one of these species (*C. pareola*) in Tobago Island, it is known that copulation is preceded by a quite different, mainly silent, display (Snow 1963 *a*, *b*) involving only one male, except that even in this case the role of the female may be acted, to some extent, by a young male (no actual attempts at mating with the young male is mentioned). Snow suggests that one dominant male 'owns' each display perch, and that the male joining him for the synchronized calling

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and dancing probably has his own display perch in the vicinity. Snow (1963 *b*, pp. 174–175) points out difficulties in accounting for the evolution of this behaviour, which seems disadvantageous to the individual 'helpers'. (Perhaps the helpers are younger birds ready to take over the display perch when the owner dies?)

Snow's and Sick's observations seem to indicate that in all species of *Chiroxiphia* there are two different kinds of display—one involving two or more males (and apparently never leading directly to mating), the other male and female only. This is slightly reminiscent of conditions in the Dabbling Ducks (*Anatini*) recently discussed by Wall (1965). Here, of course, a pair-bond is formed. An interesting point concerning the ducks is that, whereas the social display is highly ritualized and shows clear-cut differences between species, the precopulatory display is simple and less ritualized. The former has a function in affording opportunity for pairing up and as isolating mechanism, i.e. as a barrier to hybridization, through its specificity.

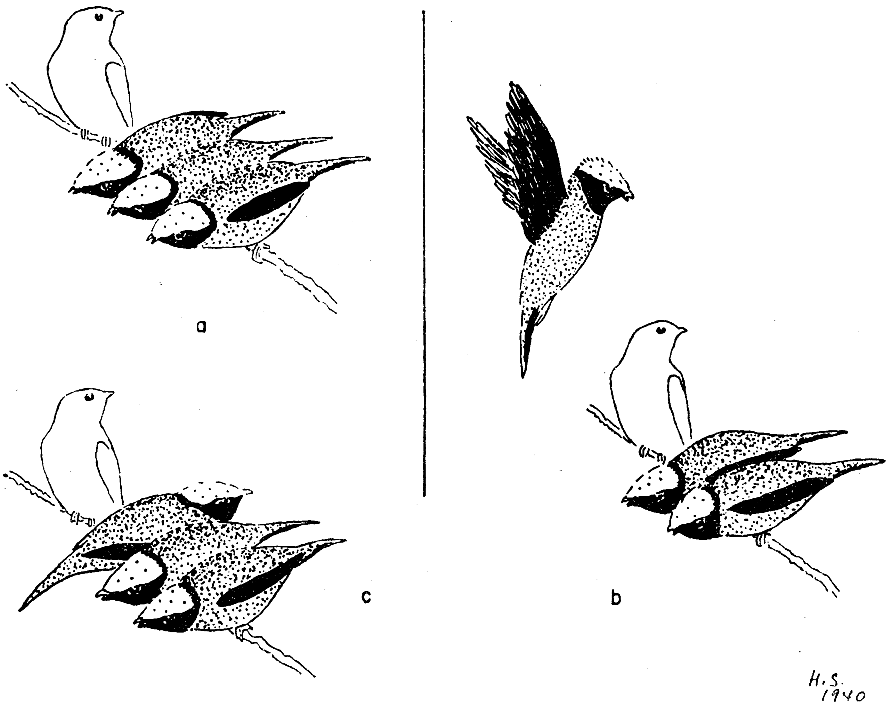

Figure 1. A case of cooperation between males for the attraction and stimulation of females. Three males of *Chiroxiphia caudata* (a Manakin) dancing before a female (or a young male). See text. (After Sick 1959.)

These ducks are similar to the lek birds in that the male takes no part in brooding and caring for the young, but differ from them in having a prolonged pair-bond, lasting normally from some time during the winter until brooding is well under way. This arrangement helps to avoid hybridization, as Wall points out. However, the main reason why an early pair-bond is established (often far away from the breeding quarters) is probably the frequent instability (dependent on rainfall, etc.) of the breeding habitats: accordingly, nomadic tendencies are favoured.

At this stage, we may briefly touch upon the reason for male withdrawal from parental

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duties. The first prerequisite, as already mentioned, is that the task of caring for the young, which in most birds is shared to some extent by both parents, should be comparatively easy. Accordingly, it occurs especially in nidifugous birds (Huxley 1923, p. 283) and in tropical, frugivorous or nectar-feeding birds with few young (Snow 1962, p. 98–99, 1963 *a*). We may assume that direct selection operates against the males sharing in nesting duties. The probable basis for such selection is, of course, the danger of having gaudily coloured males near nests which must remain hidden. This argument is slightly weakened by the fact that striking male differentiation is usually evolved subsequent to the abandonment of parental duties: however, even in species with male parental cooperation and slight sexual dimorphism a tendency to avoid display near the nest may be clearly seen (Huxley 1923, p. 282).

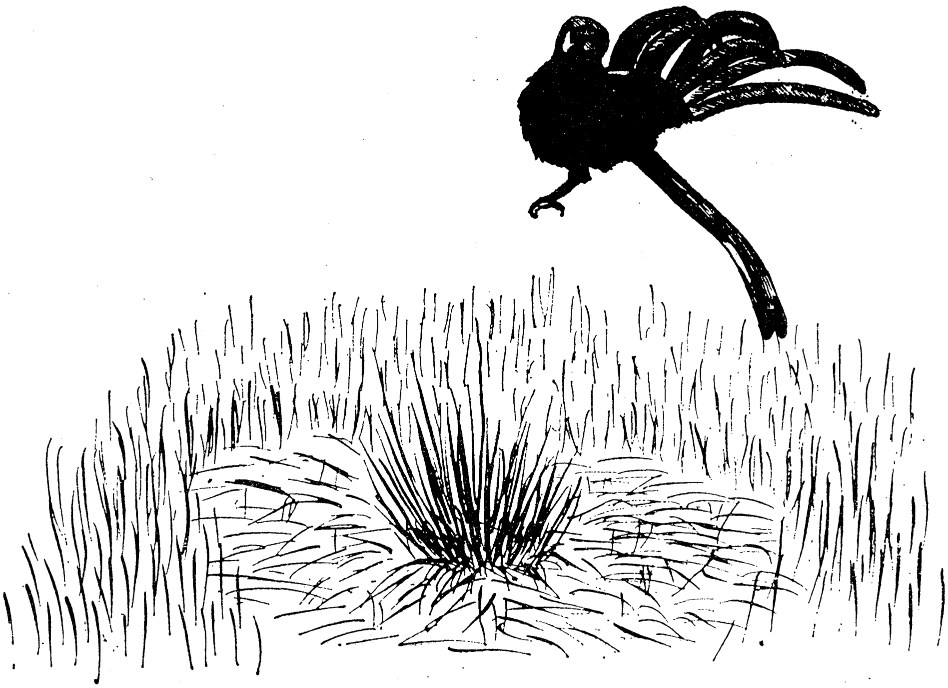

FIGURE 2. A male of Jackson's Widow-bird dancing in his court. The central tussock functions as a nest substitute. (After Etkin 1964—based on photographs by V. D. van Someren.)

A revealing instance of the operation of this factor is found in African Weaver Birds (Ploceidae), in which the male breeding plumage is extremely specialized. In most species of Euplectes (the Bishop Birds) the male is polygamous. He constructs well-hidden nests among grass to which he attracts females, but once the female has started egg-laying he avoids the nests (figure 2). However, in Jackson's Widow-bird (*E.* (*Drepanoplectes*) *jacksoni*) the male displays, usually in close proximity to other males, in a court consisting of a ring of beaten down grass. In the middle of the ring a tuft of grass is left, and this serves as a nest-substitute to which he attracts females. He apparently never approaches the true nests (van Someren 1946; cf. Crook 1964).

In nidifugous birds especially, food-competition is no doubt an important factor, the lessening of which (by concentrating the care of the young on one parent) has survival

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value: notably this tendency is very apparent and widespread among shore birds on arctic tundras (Pitelka 1959). Further discussion of the role of this factor in the evolution of lek displays must be reserved for a special paper in which some evolutionary problems with a possible wider significance will be discussed.

Briefly, I am of the opinion that Gilliard (1962, 1963) was right in suggesting that a main biological advantage of lek behaviour may be that it accelerates the speed of evolution—though only that of specific male display characters. This in turn implies the possibility of comparatively rapid speciation (i.e. formation of new species by 'splitting') by setting up barriers to hybridization between geographically isolated populations of a species (relevant facts and arguments may be found in an important paper by Sibley (1957) who is, however, mainly concerned with the taxonomic aspects). Such tendencies must have selective value in cases where adaptive radiation becomes possible. This happens when new ecological niches become available, either because the ancestors of the group in question have arrived in a region with fewer feeble competitors or because the group has acquired new general adaptations. As a probable instance of the first case one may mention the birds of paradise, a group of highly evolved passerines in the 'primitive' New Guinea region (for morphological evidence of an adaptive radiation in this group, cf. Bock 1963). Instances of the second case are, I think, the South American Cotingas and Manakins which are apparently derived from insectivorous Tyrant Flycatchers and have become especially adapted to a frugivorous diet. According to Snow (1962, p. 92) some Manakins, at least, take fruits in flight in Flycatcher fashion.

Birds of Paradise, Cotingas and Manakins are among the groups in which court display by males with no share in parental duties is preponderant. This preponderance could be the result either of a selective pressure for bizarre male display characters, which in turn could force the males away from the nests with ensuing promiscuity and lek display; or the lek displays could have originated more 'fortuitously' in one species owing to the special opportunities and selection pressures mentioned above. In such a case the species in question may have given rise to a successful multiform group owing to the comparative ease with which it could have split up and invaded the various niches available. A combination of both processes has probably been operating.

Especially among the birds of paradise a large number of 'generic hybrids' are known (partly owing to the opportunities for their detection afforded by the plume trade). Thus in spite of the specialized display characters involving male structure, coloration and posture which make the males easily recognizable, the females do sometimes make mistakes. As this is wasteful biologically there will be a strong selection for distinctiveness, a high degree of which is necessary (1) owing to the very brief period during which the females have anything to do with males, and (2) because the females have no occasion to become conditioned to adult males of their own species during the nesting period. Concerning the first point, it has been stated that the females only visit the display area when ready for copulation. This is an exaggeration for it seems to be a general rule that the females visit arenas or single courts at least a few days before copulation occurs. Thus the stimulation afforded by watching displaying males does play a role in the sexual maturation of the female, as in other birds, even though this period is greatly shortened. Most species of the group have, as already mentioned, singly displaying males, but some of the

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true Birds of Paradise (*Paradisaea*) form an exception in that several males display in close proximity in a tree-top area.

Male birds of paradise afford extreme examples of bizarre structural peculiarities which, owing to the strong selection for distinctiveness and attraction in promiscuous birds, may evolve so far that the future of the species may become precarious. Even though excessive mortality among males is brought about by these handicaps there will still be enough males left for fertilization, but spread to new areas may be much impeded, and the entire species may become vulnerable if conditions change.

However, there are means by which this tendency may be kept within bounds. A recent Finnish investigation on Black Cock (Koivisto 1965) has provided good evidence that the social system on the arena ensures that, in spite of the fact that males are practically in full mating plumage at 1 year of age, they have only very slight chances of mating until they are at least 3 years old. This means, of course, that the cocks that manage to father progeny are strongly selected for general vigour and survival ability.

This finding may well be of general application. A main survival value of arena displays in general may well be that they make possible an elaborate social system allowing the females to select the oldest and most vigorous males. Of course, the validity of this view can only be tested by further research, but it opens up possibilities for solving many problems.

Among promiscuous birds, species with lek display in the strict sense—i.e. with several males in close proximity, each in his own court, are in the minority as against the many species with court display by isolated males. There are all sorts of transitions between the two conditions, and even in such a manifest arena-species as the Black Cock, singly displaying males are now and then found as an anomaly.

At first sight it seems most natural to suppose that the primitive condition is that of singly displaying males. It may be argued (E. Mayr, *in litt.*) that there is only a slight difference between the song-post of, say, a Chaffinch and the display perch of one of the many species of Birds of Paradise displaying singly at a great distance from other males. Starting from this condition communal displays could be brought about by the advantage, and consequent selective value, of several males displaying in close proximity. It is certainly obvious that the stimulatory effect is greatly enhanced by this means (Snow 1962, p. 99; 1963*a*).

However, a good case could also be made for the opposite supposition. The communal arena displays may be initial, and the scattered courts may represent 'exploded arenas' (Gilliard 1963, p. 43). This view takes as a starting-point the frequent tendency to social gatherings even in territorial monogamous species. Prenuptial gatherings in particular are widespread and may occur in special areas. For instance, the Sheld Ducks congregate at definite localities for mating (Holstein 1932) even if they have staked out their breeding and feeding territories elsewhere. They also have prenuptial gatherings, sometimes on land (Huxley 1951).

The so-called Magpie marriages are also of special interest in this connexion. Raspail (1901) observed that when one of a pair of Magpies loses its mate in the breeding season, all the birds of the neighbourhood congregate noisily at the scene of the incident. By the next day the bird will have found a new mate, and nesting activities are continued from the stage where they were interrupted.

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In the Birds of Paradise the preponderance of singly displaying males may tempt us to assume that group display is the derived condition. But even here we may find an argument for the opposite view. Rand (1940) states that one of the primitive forms with a pair-bond and male participation in nesting—*Macgregoria*—is highly gregarious, with ritualized communal aerial-chasing displays.

Among the promiscuous species of Grouse, social display occurs mainly in open country habitats and solitary display in forests (Hamerstrom & Hamerstrom 1964, p. 344). This seems to apply to lek birds in general. Exceptions mostly involve cases where the display is vocal. For instance, in Hummingbirds the male (with one or two exceptions) has no share in nesting duties. In most species the males have isolated aerial displays, but certain modestly coloured forest species of the genus *Phaethornis* (cf. Sibley 1957, p. 175) display in groups, each male emitting the insect-like sounds distinctive for each species.

The Great Snipe (*Capella media*) (cf. Armstrong 1947, p. 220; Ferdinand 1966; Ferdinand & Gensbøl 1966), is unique among arena birds in displaying mainly at night. Accordingly, sound is predominant and sexual dimorphism is slight.

We may assume then that male organization in lek birds (in the wide sense), whether displaying singly or in groups, is largely governed by ecological conditions and general mode of life. If so, it may be suggested that the two modes of origin or arena display outlined above are equally possible and have both occurred, and that at every stage transitions are practicable in both directions. This accords with the general flexibility characteristic of avian social systems. We see it annually in many species which are territorial in the breeding seasons and gregarious in the off season, and similar changes seem often to take place phylogenetically.

Social displays may help to facilitate transitions of this kind. Such displays not directly concerned with mating are widespread among birds, though knowledge is fragmentary and serious studies are much needed. Various instances from South America are given by Hudson (1892, ch. XIX). Turner (1924, p. 9) has seen Bitterns congregate, in groups of four to six birds, during May and early June, 'playing together in the air over a given spot': they may come from a distance of three miles.

The aerial displays of Swifts ('screaming parties') round the nesting colony are known by all inhabitants of European towns. 'They occur throughout the breeding season, indeed they are most intense shortly before the birds leave in late summer, and play a definite part in the start of migration' (Lack 1956, p. 46). Lack (1941, p. 438) also thinks it almost certain that the remarkable social evening display of the Stone-Curlew in autumn, described by Selous (1901, pp. 9–15), is a preliminary to migration. He has seen similar social excitement in many other 'shore birds' (Charadrii) often resulting in a party rising high in the air and proceeding on their migration.

A performance which as, Huxley pointed out (Huxley & Montague 1925; Huxley 1938, p. 444; cf. also Makkink 1942; Lind 1965), has a special interest in this connexion is the piping parties of the Oystercatcher (figure 3). Up, to a dozen birds may be involved. It occurs in many kinds of situations: courtship, territorial strife, etc. It is infectious, and assemblies of this kind no doubt have a social and stimulatory function. It seems that the piping activity is the only outlet by which the bird can express various emotions.

In territorial non-colonial species social gatherings, even in the middle of the breeding

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season must tend to bind the populations together into groups. Such species may also exhibit a number of other traits pointing in the same direction. It has often been noted that they are not dispersed solely according to suitable habitats, but they tend to occur in patches ('neighbourhoods', cf. Fisher 1954, p. 73), within which habitats may be occupied that are inferior to unoccupied habitats lying between them. Proximity to other occupied territories is thus among the factors influencing habitat selection. Manifestations of territorial aggression and courtship, even if they occur within the private territories, no doubt have a stimulating effect on neighbouring pairs. Bird song can also be regarded to some extent as a communal activity. This is manifested by the frequent simultaneous outburst of song, as in the 'dawn chorus'.

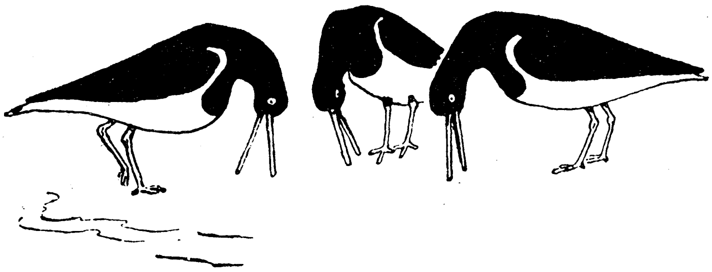

FIGURE 3. A small piping party of Oystercatchers. (After Makkink 1942.)

These social tendencies may pave the way to congregations for mating purposes, while pair-bonds and separate breeding territories are still maintained. At this stage more specialized social 'institutions' may also be evolved—like the creche system in the Sheld Duck, where a few adults (presumably birds which have lost their brood) may take care of the young while the parents migrate for moulting (Hori 1964; Boase 1965).

It seems inevitable that the tying together of populations into groups has certain evolutionary consequences (cf. Braestrup 1963, and in preparation). To discuss this would lead us into the highly complex problem of group selection which has purposely been avoided here.

REFERENCES (Braestrup)

Further references may be found in the publications cited—especially in the more recent ones.

Armstrong, E. A. 1947 *Bird display and behaviour*. London: Lindsay Drummond.

Bancke, P. & Meesenburg, H. 1952 A study of the display of the Ruff. I. *Dansk Ornith. Foren. Tidsskr.* **46**, 98–109.

Bancke, P. & Meesenburg, H. 1958 A study of the display of the Ruff. II. *Dansk Ornith. Foren. Tidsskr.* **52**, 118–141.

Boase, H. 1965 Shelduck broods in the Tay Estuary. *Brit. Birds* **58**, 175–179.

Bock, Walter, J. 1963 Relationships between the Birds of Paradise and the Bower Birds. *Condor* **65**, 91–125.

Braestrup, F. W. 1963 The functions of communal displays. *Dansk Ornith. Foren. Tidsskr.* **57**, 133–142.

Christoleit, F. 1924 Zum Balzspiel des Kampfläufers. *Pallasia* **1**, 181–197.

Crook, J. H. 1964 The evolution of social organization and visual communication in the Weaver Birds. *Behaviour* (Suppl.), no. 10.

Crook J. H. 1965 The adaptive significance of avian social organizations. *Symp. Zool. Soc. Lond.* **14**, 181–218.

Darwin, C. 1871 *The descent of man and selection in relation to sex*. London: John Murray.

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Etkin, W. 1964 Reproductive behaviours. In *Social behaviour and organization among vertebrates* (ed. Etkin, W.), pp. 75–116. Chicago: University of Chicago Press.

Ferdinand, L. 1966 Display of Great Snipe. *Dansk Ornith. Foren. Tidsskr.* **60**, 14–34.

Ferdinand, L. & Gensbøl, G. 1966 Maintenance of territory in the Great Snipe on the display ground. *Dansk Ornith. Foren. Tidsskr.* **60**, 35–43.

Fisher, James 1954 Evolution and bird sociality. In *Evolution as a process* (ed. Huxley, J. *et al.*), pp. 71–83. London: George Allen & Unwin.

Ford, E. B. 1940 Polymorphism and taxonomy. In *The new systematics* (ed. Huxley, J.), pp. 493–513. Oxford: Clarendon Press.

Gilliard, E. T. 1962 On the breeding behaviour of the Cock-of-the-rock. *Bull. Amer. Mus. Nat. Hist.* **124**, 31–68.

Gilliard, E. T. 1963 The evolution of Bowerbirds. *Sci. Amer.* **209**, 38–46.

Hamerstrom, F. & Hamerstrom, F. 1960 Comparability of some social display of Grouse. *Proc. XII Int. Orn. Congr. Helsinki* 1958, pp. 274–293.

Hamerstrom, F. & Hamerstrom, F. 1964 Article 'Grouse'. In (ed. Thomoson, A. L.) *New dict. birds.* London: Nelson.

Hogan-Warburg, A. J. 1964 The courtship of the Ruff. *Arch. néerl. Zool.* **16**, 154–155.

Hogan-Warburg, A. J. 1965 Social behaviour of the Ruff. (Thesis.) Groningen.

Höhn, E. O. 1953 Display and mating behaviour of the Black Grouse. *Brit. J. Anim. Behav.* **1**, 48–58.

Holstein, V. 1932 Lidt om Gravændernes Biologi. *Dansk Ornith. Foren. Tidsskr.* **26**, 102–107.

Hori, J. 1964 Parental care in the Shelduck. *Wildfowl Trust. 15th Annual Rep.* 1962–63, pp. 100–103.

Hudson, W. H. 1892 *The naturalist in La Plata.* London: Chapman Hall.

Huxley, J. S. 1914 The courtship-habits of the Great Crested Grebe; with an addition to the theory of natural selection. *Proc. Zool. Soc. Lond.* pp. 491–562.

Huxley, J. S. 1923 Courtship activities in the Red-throated Diver; together with a discussion on the evolution of courtship in birds. *J. Linn. Soc.* (*Zool.*) **35**, 253–292.

Huxley, J. S. 1938 Threat and warning coloration in birds, with a general discussion of the biological functions of colour. *Proc. 8th Int. Orn. Congr. Oxford* 1934, pp. 430–455.

Huxley, J. S. 1942 *Evolution the modern synthesis.* London: George Allen & Unwin.

Huxley, J. S. 1951 Communal display in the Sheld-Duck. *Brit. Birds* **44**, 102–103.

Huxley, J. S. & Montague, F. A. 1925 Studies on the courtship and sexual life of birds. V. The Oystercatcher. *Ibis* (12), **1**, 868–897.

Koivisto, I. 1965 Behaviour of the Black Grouse during the spring display. *Finnish Game Res.* no. 26, 1–60.

Kruijt, J. P. & Hogan, J. A. 1965 Social behaviour on the lek in Black Grouse. (In the Press.)

Lack, D. 1941 Some aspects of instinctive behaviour and display in birds. *Ibis* (14), **5**, 407–441.

Lack, D. 1956 *Swifts in a tower.* London: Methuen.

Lind, H. 1965 Parental feeding in the Oystercatcher. *Dansk Ornith. Foren. Tidsskr.* **59**, 1–31.

Lumsden, H. G. 1961 The display of the Capercaillie. *Brit. Birds* **54**, 257–272.

Makkink, G. F. 1942 Contribution to knowledge of the behaviour of the Oyster-catcher. *Ardea* **31**, 23–74.

Pitelka, F. A. 1959 Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of Northern Alaska. *Condor* **61**, 233–264.

Rand, A. L. 1940 Breeding habits of the Birds of Paradise: *Macgregoria* and *Diphyllodes. Amer. Mus. Novitates*, no. 1073.

Raspail, X. 1901 Cérémonie de second noces chez les Garruliens. *Bul. Soc. Zool. Fr.* **26**, 104–109.

Roberts, T. S. 1932 *The birds of Minnesota*, Vol. I. Minneapolis: University of Minnesota Press.

Scott, J. W. 1942 Mating behavior of the Sage Grouse. *Auk* **59**, 477–498.

Selous, E. 1901 *Bird watching.* London: L. J. M. Dent.

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Sibley, C. G. 1957 The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. *Condor* **59**, 166–191.

Sick, H. 1959 Die Balz der Schmuckvögel. *J. Orn.* **100**, 269–302.

Snow, D. W. 1962 A field study of the Black and White Manakin, *Manacus manacus*, in Trinidad. *Zoologica, N.Y.* **47**, 65–104.

Snow, D. W. 1963*a* The evolution of Manakin displays. *Proc. XIII Ornithol. Congr.* pp. 553–561.

Snow, D. W. 1963*b* The display of the Blue-backed Manakin, *Chiroxiphia pareola*, in Tobago, W. I. *Zoologica, N.Y.* **48**, 167–176.

Someren, V. D. van 1946 The dancing display and courtship of Jackson's Whydah. *J. East African Nat. Hist. Soc.* **18**, 131–141.

Turner, E. L. 1924 *Broadland birds.* London: Country Life Ltd.

Wall, W. von de 1965 'Gesellschaftsspiel' und Balz der Anatini. *J. Orn.* **106**, 65–80.

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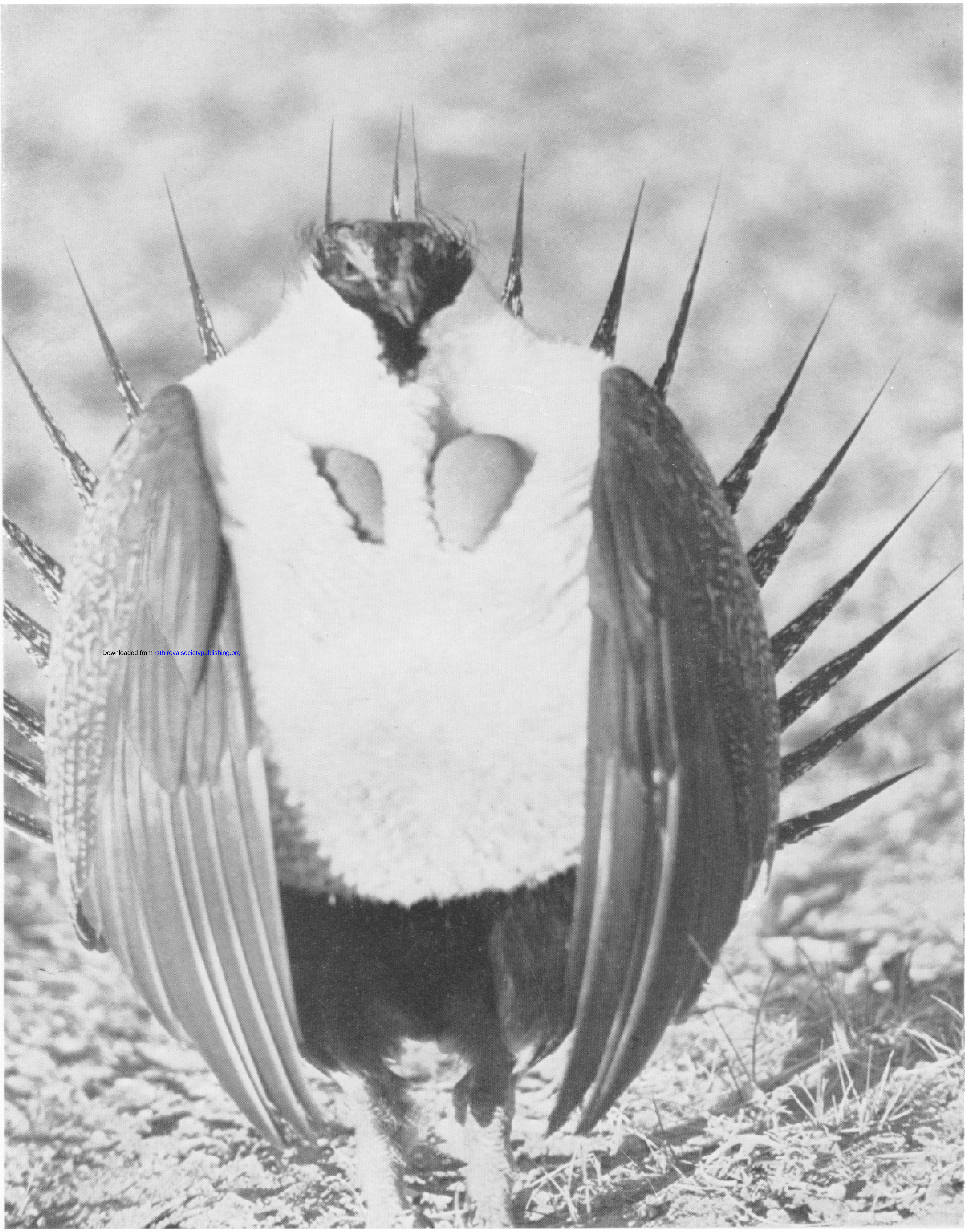

Sage Grouse male in display. (Photo by Charles W. Schwartz.)

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Ruffs on the 'hill'. Four of the five males are in 'pairs'. The two light-coloured birds are 'satellites' (cf. text, p. 378). They show the squatting, ecstatic posture in the presence of a female (left bird). (Photographed in North Jutland by C. C. Doncaster.)

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