

# The Functions of Communal Displays

By

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(Med et dansk resumé: Om funktionen af fælles-, „spil“)

The following remarks on communal gatherings in general, and 'leks' and roosts in particular, are prompted by the recent book by V. C. WYNNE-EDWARDS (1962) and were originally intended for inclusion in a review of that book (BRAESTRUP 1963). It was with the object of going a little deeper into this particular matter than would have been possible, even in a rather extended review, that separate publication was finally decided upon.

It would, of course, be inappropriate here to repeat in detail my impressions of the book. WYNNE-EDWARDS has chosen a topic full of interest, and he starts from certain basic assumptions which I consider to be generally sound. It may now, however, after a more painstaking study of the book, be possible to formulate clearly, in a few words, what I think is wrong with it. It could be said for example that in spite of its bulk, it contains far too few relevant facts. G. G. SIMPSON (1963) has recently given a very good definition of the word relevant in this context: Relevant observations with respect to a hypothesis are those that could *disprove* the hypothesis ("for disproof is often possible even if absolute proof is not").

Cautious theorists have always recognized this point, or at least they have acted accordingly. It is well known, for instance, that it was one of DARWIN's stated principles to pay special attention to facts which seemed to oppose his views. WYNNE-EDWARDS has, I think, been too concerned with producing evidence which

could conceivably support his hypotheses — and too little concerned with really testing them.

It is WYNNE-EDWARDS' opinion that communal gatherings of various kinds (associated usually with special displays) are for regulation of fecundity and dispersion. In birds with which we are here principally, if not exclusively concerned, he discussed communal prenuptial displays and the like, roosting behaviour, 'leks' (arena displays), and even the song of territorial birds, insofar as such vocal activities tend to be concentrated mainly at particular times (dawn and evening chorus).

He considers that by gatherings and displays of this type individuals receive information of the population density, that in some way they become conditioned by this information acting in a feed-back fashion in regulating the density, either by movements or by influencing the reproductive output. He therefore designated these phenomena by the self-invented term 'epideictic displays', "signifying literally 'meant for display', but connoting in its original Greek form the presenting of a sample". I hope that most biologists, even though they may be inclined to accept WYNNE-EDWARDS' theories, will agree that it is better to use uncommittal terms.

Insofar as these gatherings have a function, in addition to obvious purposes, such as roosting or mating, they serve, in my opinion, as a means for subdividing the species into more or less discrete

groups. This may have survival value in several respects, e.g. intergroup-selection is made possible.

However, with regard to a function

which regulates the density in the way maintained by WYNN-EDWARDS, I am of the opinion that grave objections may be pointed out.

### COMMUNAL ROOSTS

To begin with, let us consider how such a system is presumed to operate. This is explained most clearly with respect to the roosting habits of, e.g., the Starling in winter.

"During the day, when the individual bird is out feeding, it must be fully aware of — and presumably conditioned by — the prevailing level of subsistence available. At the end of the day it flies to the roost to take part in exciting social activities, and there is no difficulty in postulating that these reveal the other side of the picture, and condition the bird to the stress of competition that has to be faced within its present neighbourhood. These two essential indices — the availability of food relative to the number of mouths to be fed — supply all the information essential to elicit a response, either to be satisfied with the existing economy and remain, or to make a break and venture elsewhere." (W.-E.'s book p. 284). He goes on to say that this is, no doubt, a somewhat over-simplified picture, but if it is in the main correct, it offers a very simple explanation.

It seems to me that the information the bird receives is not at all exhaustive, and that the explanation is far from simple. The moot point is that even if the individual bird is able to sense in some way whether there are for instance 160,000 or 200,000 birds present at the roost, this number is significant merely in relation to the size of the area from which the birds derive. The flocks usually come in to roost from all directions, and it is stated (from personal investigations) that, "the majority of the birds are

constant not only to their roost but to the particular feeding ground they frequent by day" (W.-E. p. 284). How then is the individual bird to know the size of the area from which the total number derives? How is the bird to know whether a change of number is due to a change of area (which may occur, even in normally stable systems)? And is it probable that conditions in the feeding ground of a particular flock are a reliable index of the conditions in the area as a whole?

Instead of putting forward such far-fetched and highly unlikely explanations, it would surely be more feasible to assume that territorial behaviour and tension between flocks at the feeding grounds is a possible mechanism for regulating the numbers.

In contrast to the usual explanation that roosting assemblages have survival value in reduced mortality, e.g. from predatory attack, W.-E. argues that, "it quite commonly happens that predators are drawn to roosts and take a toll which they would find it difficult to equal in a scattered population." (W.-E. p. 299). The question one asks is, of course, whether the loss through predation (e.g., for 1,000 birds per week) is greater or larger in a communal roost than it would have been in a scattered population. It is obvious that in the case of large roosts comprising hundreds of thousands or even millions of birds, there would need to be a very heavy concentration of predators in order to cause any significant mortality rate, and there seems to be very slight evidence that this is actually the case.

Communal roosts are generally situated in very protected places, not only in respect to predators, but also with regard to climatic conditions (cf. e.g. GUÉNIAT 1948, p. 87 concerning the Brambling).

The Brambling (*Fringilla montifringilla*) is interesting in this connection because the habit of communal roosting is exceptionally spectacular here. One roost may contain several million birds. Nevertheless, it is not difficult to see that a regulation of dispersion in the way advocated by WYNNE-EDWARDS is out of the question. In birds such as the Starling and the Rook, from which W.-E. mainly derives his arguments, there is at least a certain stability in the location of the roosts and the extension of the area from which the birds come. The Brambling, on the contrary, is extremely irregular in its occurrence in winter quarters. This irregularity, which is partly due to the varying amount of beech-mast present in

the various regions, and partly to fluctuation in the numbers of winter visitors, makes it impossible to maintain traditional roosting places. In fact, we know from the admirable investigations by Swiss ornithologists (see e.g. SCHIFFERLI 1953, LANZ 1953, p. 14) that the roosting places are not the same ones during different "invasion years", and that, furthermore, there is a great deal of change during each particular winter.

Even if it is reasonably certain that the chief survival value of communal roosts consists in reduced mortality during the night, and even though we must refute WYNNE-EDWARDS' hypothesis of a function of density regulation, this does not necessarily mean that communal roosts have no social significance. It is quite probable, for instance, that these gatherings and the accompanying display may help to synchronize various activities, such as migration.

## ARENA DISPLAYS

We may now proceed to the discussion of arena displays ('leks'), another category of communal gatherings which, according to WYNNE-EDWARDS, have a function in regulating numbers. This time it is a question of regulating the reproductive output instead of merely regulating dispersion. The ideas involved are rather strange, and it is with some trepidation that I start to criticise them. The fact is that the mere mention of them at a recent meeting in our Natural History Society caused so much merriment that a friend of mine (who had not read the book), almost accused me of making fun for fun's sake, which, if true, would certainly have been a very serious matter.

I shall, therefore, pass very lightly over the impossibility (for physiological and psychological reasons) for the males to be able to "withhold coition once a suf-

ficient quota of hens has been fertilised" as a means of regulating the reproductive output (as WYNNE-EDWARDS maintains), and stress instead the utter impossibility of such a mechanism on other grounds altogether.

In the first place, it is necessary to remember that even if we were inclined to accept that "a constant number of males will undertake a fairly constant number of matings before their interest and willingness declines, and further matings are refused" (W.-E. p. 216), this would not at all insure any regulation of the reproductive output. The fact is that precisely in those birds with which we are here concerned (various gallinaceous birds, the Ruff, etc.), relaying is very frequent. Thus, if in a certain year there are more matings than usual this is either because there are more fertile hens than

usual, or because — owing to an exceptional amount of predation — more hens than usual have lost their clutches and are in need of being fertilised again. How are the males to distinguish between these situations? They are necessarily ignorant of conditions at the nesting sites. It is probable that the survival value of arena displays consists primarily of this non-appearance of the males at the nest. No mating or territorial manifestations (which may reveal the site to predators) are taking place here.

Unnecessary though it may seem to waste more time and paper on these absurdities, we may, in order to further the argument, point out a few more relevant facts (BANCKE & MEESENBURG 1952, 1958, 1960):

The same population of Reeves may visit different arenas, and the same is the case with Ruffs that have a more or less white colouration. While the remaining, dominant Ruffs have a special "standing place", each on a particular "hill", the "whites" have access to all the hills in the district.<sup>1)</sup>

Some of the dominant Ruffs are superseded on the hills by other Ruffs in the

course of the season. This withdrawal of the most successful males after some time, is no doubt due to exhaustion, and may be a feature common to all birds and mammals with arena display. In the face of this, W.-E.'s following surmise of the function of polygyny becomes merely incongruous, "the handful of participating males, being fully informed either of their own personal total or, where there is a communal lek, of the group total of matings performed to date, could be conditioned to respond when the appropriate complement had been reached by becoming sexually inert" — (W.-E. p. 515). A necessary pre-supposition would be that the same males were present all the time.

WYNNE-EDWARDS (p. 215) cites instances from the investigations of SCOTT (1942, p. 495) where, in the Sage-grouse a few hens may sometimes, on account of the temporary incapacity of the master cock on busy mornings, fly away unsatisfied. He apparently thinks that this may support his ideas. It is clear, however, from SCOTT's paper that if this happens, it is simply because of the late hour of the morning, otherwise the hens would be served by other males. He writes, "As the morning sun rises higher in the sky, the instinct to leave the area transcends all others, and some of these hens fly away unsatisfied" — and he continues, "Others may walk through the area and fall temporarily under the spell of an outside cock whereupon nature's chief act is accomplished". SCOTT's paper contains several definite observations on hens that, unsuccessful in being mated at the regular mating spot, go elsewhere to mate (p. 493-494). It is a mystery how anybody could imagine a regulation of reproductive output behind all this.

<sup>1)</sup> We have here, apparently, a very good instance of a trait which is upheld by special devices in the face of individual contra-selection (by predators). The "whites" are of value to the group in being eminently suited for making the hill conspicuous. But this very conspicuousness makes them so vulnerable to predation that they would be kept down to a minimum but for their favourable chances of success in breeding. This is accomplished by an instinct in the other Ruffs whereby they refrain from attacking the "whites" when the latter place themselves in their territories. Apparently this instinct could only be explained by intergroup-selection.

## OTHER TYPES OF COMMUNAL DISPLAYS

— WYNNE-EDWARDS states that it is typical for such gatherings and demonstrations, which he considers to have an "epideictic" function, to occur at special times and at a traditional meeting-place. This is generally the case (for obvious reasons) with roosts and leks. However, he is also of the opinion that "while it is the general rule, these two conditions are not entirely indispensable" (p. 326). In fact, the many other kinds of communal gatherings, prenuptial displays, etc., which will be discussed further on, very seldom fulfil these expectations. This is a field where, no doubt, much remains to be discovered, and there is also a need to accumulate facts which are widely scattered in the literature and often hard to find.

The important task of collecting and analysing all these facts will not be attempted here, but in order to illustrate the point mentioned above, a few data concerning the Corvidae (one of the best studied groups), may be cited.

Concerning the noisy gatherings of Jays (*Garrulus glandarius*) in the spring, GOODWIN (1951, p. 425) says that they "may involve anything from three or four to thirty or more birds. They seem essentially very similar to those of 'lek' birds except that there appears to be no set time or place for them to materialise, and the birds taking part seldom stay long in one group of trees but move about, one bird flying off and the rest following at intervals".

In the case of the Magpie (*Pica pica*), there seem to be several types of gatherings (LINSDALE 1957, 1946). One of them appears to correspond to the above mentioned gathering of the Jay, and another is connected with roosts. We have RASPAIL's (1901) very interesting observations on the function of the former type (in both Magpies and Jays) in cases where one of a pair has lost its mate in the breeding

season. When this occurs, all the birds in the neighbourhood congregate noisily at the scene of the incident. By the next day, the bird has found a new mate and nesting activities are again continued from the stage where they were interrupted. This form of behaviour has been seen in several instances where one bird of a pair has been shot while in the nest.

There is some uncertainty concerning a possible third type of Magpie-congregation, but W. STEWART (1928, p. 57) has claimed that in Lanarkshire, (Scotland) there are traditional Magpie-playgrounds with large gatherings during the latter half of winter. He states that "they are entirely different from the usual roosting parties seen at certain places in the autumn and early winter. They might rather be described as sportive and ceremonial occasions...". Further observations would appear to be necessary, but if the gatherings really are independent of roosting grounds, we may here have a case that strictly conforms to WYNNE-EDWARDS' definition. However, in this the Magpie would evidently be exceptional rather than normal.

The same combination of separate territoriality and gregariousness that characterises Magpies and Jays is also found in Ravens. Indications of traditional meeting-places (apart from roosts) are meagre, insofar as I am aware. With regard to the Northern American Raven, F. ZIRNER (in BENT 1946, p. 198) writes, "From the middle of August to about the end of September, and as a rule in the afternoons only, they congregate in a secluded spot of heavy timber and hold their daily concerts. For this purpose they select one or two of the tallest trees, sit facing one another and sing, mostly solo, but sometimes more at once". They are, however, not particularly addicted to a special locality for "when frightened once [they]

will not return to the same spot again, but otherwise they will return daily”.

COOMBES (1948) is of the opinion that in the English Lake District one or more flocks of Ravens are in existence throughout the year. He holds the view that these flocks consist of “birds that for a period of years do not breed, although a

proportion of them are seen to be paired”. There are even contacts between pairs during the breeding season. RYVES (cited in BANNERMAN 1953, p. 4), saw a pair of Ravens perform aerobatics in which they were joined by another pair. Later, the two pairs parted company again.

### VISITING BEHAVIOUR

This brings us to a point I am particularly anxious to stress in connection with purely social displays. These may be either in the nature of congregations or of visiting behaviour. Moreover, there may well be all manner of transitions between the two types.

The classical case, so to speak, of visiting behaviour is the one described by HUDSON (1892, p. 269) in the Spur-winged Lapwing of the Argentine Pampa. Unfortunately, this does not appear to have been re-investigated, but since HUDSON, apart from being a great writer, was certainly a keen and gifted observer, we may be sure that the account is, at least in the main, true. He says, “If a person watches any two birds — for they live in pairs — he will see another lapwing, one of a neighbouring couple, rise up and fly to them, leaving his own mate to guard their chosen ground, and instead of resenting this visit as an unwarranted intrusion on their domain, as they would certainly resent the approach of almost any other bird, they welcome it with notes and signs of pleasure”. The three birds then perform a sort of dance, uttering resonant drumming notes in time with their movements. Afterwards the visitor goes back to his own ground and his own mate, to receive a visitor himself later on.

In the Roedeer, the one animal with which I am really familiar, a kind of “chasing” is observed during the rutting season in midsummer. Rather surpris-

ingly, I found (BRAESTRUP 1952, p. 43) that this behaviour performs a function of a similar nature to the above.

The chases are of two kinds, a slow pushing movement (which may occur on a special mating spot, the “ring”) and longer excursions during which the pair run at full speed, the buck following the doe. That this “running” is actually a sort of play rather than a form of real pursuit, is seen from the fact that the doe may often take the initiative herself. She starts to run, glancing behind to see if the buck is following.

It is seldom possible in the forest to get more than brief glimpses of the chase. There are, however, a few localities in Denmark, situated in large estates, where the roe deer lives in the open fields. There it is sometimes possible to get a good and much more prolonged view of the running deer, and to watch the reaction when they intrude on the territories of other bucks. Normally, any violations of private territory are furiously resented, and the “foreigner” has an instinctive respect for the “owner”. As an example, the following incident is very revealing: The observer disturbs a buck at close quarters. The buck jumps over a fence, but on seeing a rival standing in his own ground on the other side, comes back again immediately.

The “running” pair, however, are received in a totally different manner. If the chase leads through fields with a heavy concentration of roedeer, each buck stand-

ing (usually accompanied by a doe) on his own territory, one may see, as it were, a wave of elation and joy spreading in the whole neighbourhood. If anyone considers this description too anthropomorphic, let him see for himself the difference between the violent reactions of a buck on encountering a rival too close to his territory under ordinary circumstances (his rage is often manifested afterwards by an 'attack' on a tree), and on the other hand, the playful and relaxed attitude towards the "running pair". The "owner" may run after them for a little while (the doe then being followed by two bucks), but the 'owner's' movements throughout testify that this is mere play.

One very essential point concerning these "chasings" is that they seem to occur within the common territorial bounds of a discrete community of roe deer. I have myself kept watch at a boundary which the local game-keeper pointed out to me as being the delimiting point between two populations with pronounced average differences in the shape of their horns. The game-keeper remarked that this boundary was respected even in winter, when roe-deer live in small flocks. I was able to observe that pairs approaching this boundary from either side turned round and went back again.

Sexual chases are also common in birds, and they may sometimes have a social function similar to those of the roedeer (BRAESTRUP 1953, p. 66). Thus, when a pair of yellow Buntings pass a foreign territory the male "owner" of the territory may follow them (HUXLEY 1930). A communal display in the House-Sparrow may start with a chase which attracts other males (SUMMERS-SMITH 1954). "There is a tendency for dual ceremonies to become social... and some of them merge into corporate activities so subtly that no rigid distinction is possible" (ARMSTRONG 1947, p. 164). The ceremonial piping parties of the Oystercatcher

are mentioned by ARMSTRONG (1947, pp. 166-171) as an example of displays akin to visiting behaviour as well as to typical communal displays. Typical visiting behaviour is described by OWEN (1951) in the Red-backed Shrike. ARMSTRONG (1947, p. 168) gives other examples of birds calling upon one another.

Knowledge of social displays is not yet as complete as we would wish, but the picture that emerges does depict several kinds of contact between members of discrete communities. Orderly congregations in special places and at fixed times (apart from roosts and leks) seem to be the exception rather than the rule.

Whatever their exact nature, all these various types of display are excellently suited for establishing ties between the various members of a community. There is no doubt about the evolutionary importance of a species being partitioned into discrete entities, and this more or less effective partitioning seems to be the rule in higher vertebrates. By this means group selection is made possible, and this again is a pre-requisite for the evolution of social traits which make the species as a whole more fit, although they may be detrimental to the breeding of the individual (cf. e.g. WRIGHT 1959, pp. 143, 148). In this sense (indirectly via the evolution of the yet little known regulatory mechanisms which they make possible), the social displays may be said to influence the reproductive output. But there seems to be no reason for assuming the existence of a direct regulatory function such as WYNNE-EDWARDS maintains.

The fact that there is always an element of gregariousness, even in species with pronounced individual territories, is no doubt also of great importance in making it easy for a population to change from one mode of life to another. Thus, a change from territorial behaviour in summer to flock-life in winter very often occurs. There may also be local differ-

ences within a species which consist of circumstances leading to colonial breeding in some localities, and the spacing out of pairs in separate territories in other regions. The fact that we often find closely allied species with pronounced dif-

ferences as to sociality also testifies that a change has occurred during evolution (KALELA 1954, pp. 6-10).

Finally, communal displays are, of course, important in synchronizing various activities (breeding, migration, etc.).

## SUMMARY

In a recent book by V. C. WYNNE-EDWARDS a function of regulation of numbers is ascribed to various kinds of communal displays, including arena displays (leks) and those going on in connection with communal roosting.

These claims are examined and categorically

refuted with respect to leks and roosts. With regard to other types of communal displays, the more orthodox view is held that they are primarily for tying together discrete groups, between which inter-group selection is thus made possible.

## DANSK RESUMÉ

### *Om funktionen af fælles-, spil<sup>4</sup>*

Den skotske biolog V. C. WYNNE-EDWARDS har sidste år udgivet en stor bog om visse af dyrenes sociale adfærdsmønstre, som han mener har en funktion ved at regulere forplantningen og fordelingen i terrænet, således at de pågældende dyr ikke overbeskatter deres hjælpeklider (fødedyr eller de planter de lever af). Vi ved jo fra menneskets fiskeri og hvalfangst, at en for intensiv efterstræbelse ("overfiskning") medfører stærkt nedsat udbytte, ja der kan endog være fare for uddøen af de pågældende dyr (bardehvalerne).

Det må anses for sikkert, at der kan finde en sådan regulation sted. Især kan man betragte territorieinstinkterne fra denne synsvinkel. Men hvad angår de forskellige former for fællesspil, som denne afhandling beskæftiger sig med, mener jeg at W.-E. med urette betragter dem som direkte antalsregulerende. Især kan man fremføre afgørende indvendinger mod at tilskrive overnatningsforsamlinger og parringsspillene (arenaspil) hos polygame fugle en antalsregulerende funktion.

Massekoncentrationer på bestemte overnatningspladser finder vi jo hos mange fuglearter om vinteren. Det er W.-E.'s opfattelse at disse forsamlinger (og de flyvespil der ofte ses i forbindelse med dem) regulerer fordelingen i terrænet på den måde, at fuglene derunder gør sig bekendt med den mængde, som er til stede på egnen, og sammenligner denne mængde med fødebetingelserne (det må naturligvis forudsættes at være en ubevidst proces i fuglens hjerne). Et ugunstigt billede skulle kunne bevæge en del af individerne til at søge andetsteds hen.

Indvendinger: — Selv om vi tænker os at fuglen skulle kunne sansse om der f. eks. er 160,000 eller 200,000 artsfæller til stede på overnatningspladsen, ville dette tal kun have en mening i relation til størrelsen af det område, hvorfra de kommer. Overnatningspladserne kan ganske vist hos nogle fugle normalt være de samme fra år til år, og området, hvorfra fuglene stammer, vides for Rågens vedkommende at kunne være nogenlunde konstant. Men selv her kan der indtræffe forandringer, og hvordan skulle da den enkelte fugl vide, om en tiltag af antallet skyldes tilskud af fugle fra fjernere liggende egne eller en stor tæthed i forhold til fødemængden, som den for øvrigt kun har kendskab til på det begrænsede område, hvor den selv har fourageret?

I stedet for en så kunstig forklaring er det dog lettere at forestille sig, at det er individtætheden og territoriale spændinger (eventuelt mellem flokke indbyrdes) ude på fourageringspladserne, der virker regulerende.

W.-E. mener endog, at antalsregulering er masseovernatningspladsernes primære funktion, og han vil drage deres hensigtsmæssighed i tvivl, når det gælder undgåelse af fjenders efterstræbelse. Et meget vægtigt modargument kan hentes fra Kvækerfinken, der netop har de mest storslåede overnatningsforsamlinger på ofte adskillige millioner fugle, og hvor W.-E.'s forklaring i al fald umuligt kan passe. Kvækerfinkens opræden om vinteren i et givet område er jo nemlig uhyre varierende fra år til år, således at det er umuligt, at denne fuglearart kan få et system af traditionsbestemte overnatnings-



steder, hvortil fugle fra et bestemt område søger — hvilket som nævnt er den første betingelse for en antalsregulation ad denne vej. Vi ved da også fra grundige undersøgelser i Schweiz, at de store invasioner, som med års mellemrum finder sted, har forskellige sovepladser hver gang, og at de store masseforsamlingspladser først bygges op i vinterens løb under stadige forandringer.

— Endnu mere absurd er forestillingen om en antalsregulation gennem de forsamlinger som kendetegner forskellige polygame fugle i parringstiden. Der skulle her være tale om en regulation af forplantningen på den måde, at de få dominerende hanner, som er næsten ene om at effektuere parringen, skulle kunne holde sig a jour med antallet af parringer og eventuelt indstille dem på et passende tidspunkt. Dette stemmer for det første yderst dårligt med fysiologiske og psykologiske forhold. Den stakkels Brushøne, som kommer forgæves til parringspladsen, fordi de tilstedeværende Brushaner er blevet enige om at nu kan det være nok for i dag (eller for i år?) giver ligesom ikke noget sandsynligt billede. Men rent bortset fra det, er der andre og helt afgørende grunde til, at man totalt må forkaste en sådan mulighed. De pågældende polygame fuglehanner kan ikke have noget kendskab til, hvad der foregår på redepladserne. Det er så at sige arenaspillets 'idé', at de ikke har det. Redestedets beliggenhed kan bedre holdes skjult, fordi der ingen parrings- eller territorie-manifestationer finder sted her. Derfor kan hannerne ikke vide om et større antal parringslystne hunner betyder flere forplantningsdygtige individer — eller om det skyldes mange omlægninger, fordi reder er ødelagt. Endvidere er det et vistnok gennemgående træk ved arenaspil (hjorte, Brushaner), at de dominerende hanner ikke kan holde en sæson ud, men erstattes af andre mod slutningen.

I al fald Brushøns kan besøge forskellige spillepladser og er således uafhængige af dominerende hanners eventuelle 'altruistiske' tilbageholdenhed.

— For de mange andre slags fællesspil er det karakteristisk, at der er alle overgange fra masseforsamlinger, der kan minde om arenaspil, til visitadfærd, hvor f.eks. en han besøger et fremmed par på deres territorium, ofte under jagttagelse af bestemte ceremonier.

Fælles for dem er, at de er egnede til at knytte en bestemt gruppe nærmere sammen til en enhed, der er til en vis grad avlsmæssigt adskilt fra andre grupper. Dette har bl. a. den betydning, at der ved naturlig udvælgelse grupperne imellem kan opstå sociale instinkter, der er til gavn for gruppen og arten — uanset at det ville være en fordel for det enkelte individs forplantningschancer at sætte sig ud over dem. Til disse træk hører især sådanne, som regulerer forplantning og fordeling i terrænet. I denne indirekte betydning kan da de pågældende 'spil' siges at virke antalsregulerende, men kan næppe tænkes at gøre det direkte, således som WYNNE-EDWARDS forestiller sig det.

Fællesspil må også virke til at samordne forskellige cykliske foreteelser (forplantning, træk) i tid (synkronisere dem), og også masseovernatninger og areaspil kan (ud over deres iøjnefaldende funktion) have denne betydning.

Det er karakteristisk for WYNNE-EDWARDS' bog, at han har været alt for ivrig for at finde tilsyneladende plausible støttegrunde for sine hypoteser — og i alt for ringe grad har interesseret sig for, hvad der kunne tale imod. Videnskabelig metode består i en sådan stadig prøvelse, for — som den bekendte amerikanske biolog G. G. SIMPSON har udtrykt det — direkte bevis for en hypotese kan være umuligt at føre, men modbevis er ofte muligt. Gennem forkastelse af det forkerte, kan man nærme sig sandheden.

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