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Arena behaviour of the Black Grouse (Lyrurus t. tetrix)

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A summary account is given here of some of the most characteristic behaviour-patterns illustrated in my film from southern Sweden, which was shown at the Symposium.

Figure 1 gives a survey of the main postures of the cocks on the arena. The non-displaying cock (1) has a spool-shaped body and the feathers lie close together over it. The hissing posture (2) is one of the most common attitudes of displaying cocks, in which the head is stretched forward, the neck is thin, and from the open bill the hissing call, rendering 'choo-icht', is uttered. While doing this, the cock usually flaps his wings; often he makes a short jump into the air, alighting with his head in another direction. The flutter-jump (3) is a conspicuous action. The cocks jump about 5 feet up into the air, often alighting 50 to 60 feet away, fluttering their wings violently, and uttering hoarse hissings.

It seems highly probable that the hissing and the flutter-jumping behaviour are closely related. The first few movements of the jump are nearly the same as those of the hissing attitude. The latter is commonly observed, while the former is performed only in certain situations and especially in the high season. I interpret the hissing behaviour as an incomplete flutter-jump being ritualized. In fact, the number of hissings per unit of time gives one of the most practical measurements of the degree of activation of the lek motivation. The more hissings, the higher the intensity of the display behaviour.

The flutter-jump is released, partly by visual and partly by auditory stimuli. Normally, the cocks react to other cocks, or to hens flying away from or towards the arena. But they are poor recognizers of their own species, since every bird that has about the same wingbeat rate as the grouse may stimulate jumping. During my 7 years of Black Grouse studies, I have observed that on arenas with Golden Plovers in the vicinity, the activity of the cocks is higher than on those without them. Other cocks jumping, jumping sounds or hen calls from a loudspeaker also have the releasing effect.

Sexually motivated general behaviour in the Black Grouse I tentatively term the normal display posture (4). In this attitude the cocks are 'rookooing', probably a behaviour corresponding in the main with the singing of the song birds. It should be noted that this posture constitutes the basis of the courtship posture and is an often used behaviour in hostile situations. In fact, the purpose of the normal display posture is very difficult to define; it has many functions, none of which can as yet be said to be the most significant.

The 'rookooing' is a complicated sound. The strophe of fully motivated cocks lasts about 2.5 seconds, on an average, with little range of variation (figure 2 (2)). The sound spectrogram shows that 'rookooing' is composed of three phases. In the first, the neck swells continuously, in the second it pulsates vigorously (causing even the tail feathers to vibrate) and in the third the bill is opened and air is expelled. No anatomical research has yet

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been performed on this subject, but close-up studies of displaying cocks render possible the following interpretation of the method of sound production. During the first second, air is inhaled till the cervical air-sacs are maximally filled. This air is then 'manipulated' in some way into the air-spaces of the throat. At the very end of the strophe, the cock exhales

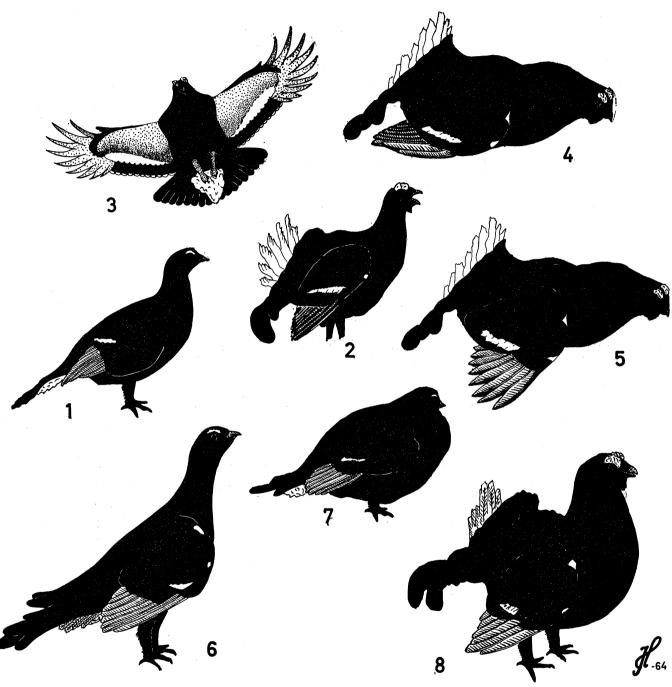


FIGURE 1. Postures of Black Grouse on the arena:

- (1) Non-displaying posture
- (2) Hissing posture
- (3) Flutter-jumping (or alighting)
- (4) Normal display posture ('rookooing' attitude)
- (5) Courtship posture
- (6) Alarm posture
- (7) Resting posture
- (8) Threat posture

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air through its open bill: at temperatures below zero a cloud of condensed vapour is formed in front of the cock, a phenomenon easily seen in backlit performances.

In low intensity activation the normal 'rookooing' display strophe is introduced by a number of openings of the strophe. I call these abortive introductions intention utterances by analogy with intention movements. Excellent information may be obtained concerning the state of the performing cock by studying the number of intention utterances: the greater the number, the weaker the motivation.

When hens are on the arena, male activity normally increases. Cocks not occupied in fighting behaviour are vigorously 'rookooing', and those with a hen in their territory or its vicinity adopt the *courtship posture* (5). The only difference between this and the former attitude (4) is in the wing carriage. In the normal display posture they usually do not touch the ground but in the courtship posture *both* wings are lowered, and the extended primaries stiffly scrape the ground.

In this attitude, and intensively 'rookooing', the cock circles around hens within his territory (or outside the arena!). Mobile hens elicit more circling than immobile. In the latter case, the cock stops obliquely behind the hen, sometimes in a squatting posture. Copulation will ensue if the hen crouches before the cock and does not withdraw when he approaches. A more thorough treatment of courtship behaviour will be published in a forthcoming paper.

The first reaction of the cocks to frightening situations is the alarm posture (6). I suggest this term not only because it indicates that the cock is alarmed, but also because every male seeing another in this posture will also take alarm and adopt the same attitude. Certainly this behaviour is a somewhat stereotyped introduction to the flying-away patterns. Besides the normal preparation for flight, the alarmed cock extends his neck as high as possible and anxiously turns his head around. Tentatively I would interpret this behaviour as intention movements that have become ritualized during the evolution of sociability in order to promote the maintenance of the population.

During arena activity, the cocks are often engaged in challenging, threatening, or fighting. In fact, the behaviour patterns described earlier intermingle with those of hostility to such an extent, that it is often impossible to identify whether some postures are chiefly manifestations of the courting drive or of the fighting drive. A more complete analysis of these problems is beyond the scope of this report. Here, only some of the observations of interest to the ritualization and related phenomena will be discussed.

The threat posture (8) of the Black Grouse is characterized by a swollen neck and a somewhat withdrawn head. The bill is partly opened, and the wings slightly extended from the body.

It may perhaps, in accordance with Tinbergen, be contended that the threat posture is comparable to the upright threat posture of Herring Gulls, being a result of conflicting attack and escape drive. Still, such a supposition will certainly not elucidate all the features of threat behaviour of Black Grouse. First, this posture is often adopted in the middle of the territory, where the attack drive might be expected to be stronger than that of escape. Secondly, the swollen neck is not a feature of actual fighting. Thus, the threat possesses an element beyond that of the fighting patterns. This element will be found only in normal display and courtship postures. Evidently, threat is a composite of elements

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from incipient fight and normal display. At the territorial boundary, however, the neck often becomes narrower, and the head is more lowered to facilitate an attack.

During the first years of my Black Grouse studies, I thought that the raised tail of displaying cocks served to stimulate the hens. Now, I am less convinced of the accuracy of this interpretation, owing, *inter alia*, to the following observations. Fighting hens often raise their tails as cocks do, but in courting situations they never do so. Weakly motivated cocks often display in the 'rookooing' posture with unraised tail, especially when the wind is blowing hard, but in fighting it is always tilted upward. Moreover, I have often seen hens prefer a cock with damaged tail-feathers to one with a perfect tail when both males were courting side by side.

All I can say with conviction is that the threat posture is a result of ambivalence. As mentioned above, the normal display posture is used also in boundary disputes, especially when hens are in the vicinity. This psychological claim of territory is the display fighting (figure 3, to the left).

There is another interesting connexion between threat and normal display posture. In the former the cock nearly always utters a plaintive nasal call, which I term the conflict call. This is closely related to the 'rookooing' sound, as illustrated in figure 2. At the top left of this figure, and at the bottom right, a typical conflict call is recorded: the varying pitch gives the tone a nasal timbre. When a threatening cock changes to 'rookooing', or vice versa, the voice changes too. 'Proper rookooing' is possible only if the neck is nearly horizontal. When the neck is raised the 'rookooing' sounds gradually become more nasal. In the most upright position, i.e. the threat posture, the cock exhales air with (opened bill) and the true conflict call is produced.

Many authors claim that the conflict call is a combat call. It is true that the call is always heard from fighting or challenging cocks. Actually, the sounds are most obvious in ritualized fighting (see below) and during intention movements of attack. On the other hand, the call is frequently heard from cocks near the arena in the morning before the first display, from cocks left alone on the arena after their neighbours have flown away, and from cocks foraging in the fields or frightened in the forests, etc. As the call is always uttered in situations of conflicting motivations, I prefer the term conflict call. It must, however, be pointed out that the call can be produced even in postures without swollen neck, raised tail, etc: the neck is, however, always upright.

The question is whether the conflict call acts as a releaser. All I can say at present is that no such function has been determined, and that 'artificial' calls from a loudspeaker on the arena do not seem to affect the cocks.

In 'duels' or tournaments, not including actual fights, the Black Grouse makes two types of head movement. In one, the beak is directed at the opponent, in the other towards the ground. The former represents intention movements of attack, the latter is a displacement activity (figure 3). The duels may be called 'bowing-duels'; bowing movements often play a very conspicuous part in their performance. While the food-seeking movements (the 'example' of the activity) are slow and executed from an initial position of forward-stretched neck, the displacement-bowings begin from a nearly upright position and are very rapid. Thus, the behaviour is probably ritualized and therefore slightly modified. Many observations lead to the supposition that the opponent reacts to the bowings. In

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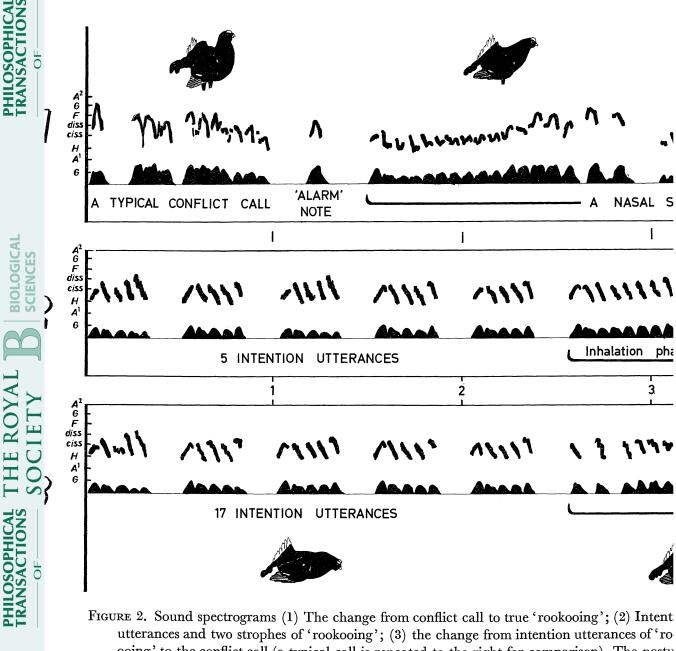
other words, the displacement activity inhibits the opponent's attack drive and this effect is to the advantage of the species. Experimental studies could reveal the significance of the bowings more convincingly.

Lastly some words may be said about the territorialism of the Black Grouse. Intensive research on the subject has been carried out on three arenas. During two years, every change of position on the arena grounds has been recorded on maps for each cock present. The result of these investigations can be only summarized here. It should be mentioned that the populations studied were either stable or decreasing.

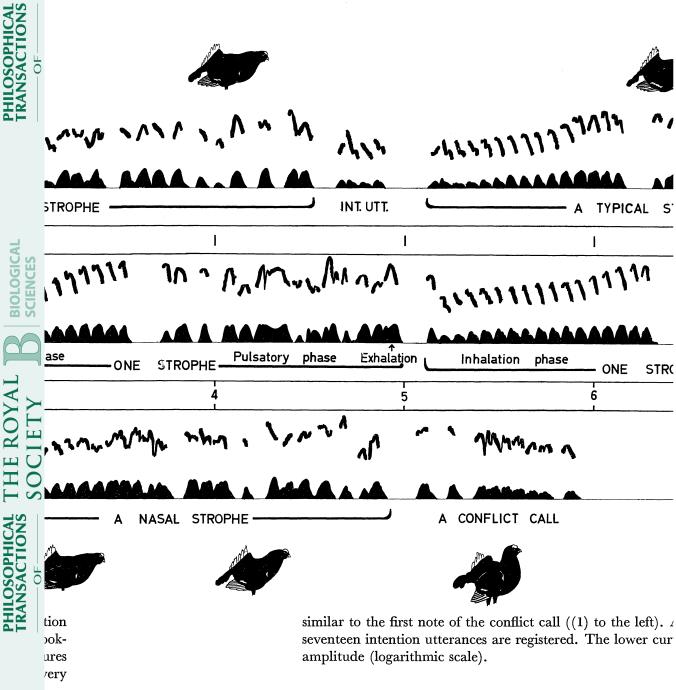
The territorial cock walks from rival to rival. After a hostile confrontation at one end of the territory, the opponent's impulses to attack diminish and those of other immediate neighbours become increasingly stronger. In consequence the cock walks or runs to and fro within his territory between different rivals (as shown in the film). Certain spots on the boundary line are usually preferred for hostile confrontation. When two aggressive cocks meet at a non-preferred part of it, they walk side by side to the nearest confrontation spot.

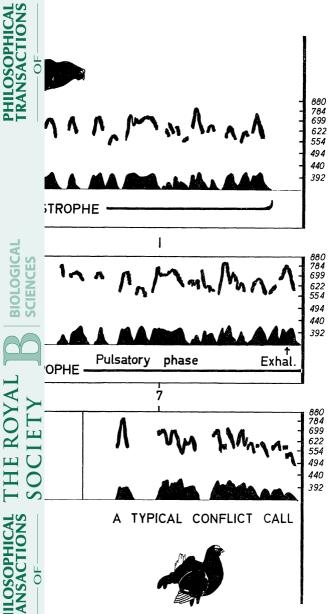
These studies have made it possible to determine the exact position of the boundaries for each cock. As seen in figure 4, these run between features of the ground configuration, e.g. tufts, hollows, bare spots, trees, etc. The territorial cock knows his boundaries well, but in winter the snow covers his landmarks and the territory picture changes. After the melting of the snow, however, most of the old cocks recognize their old territories. In the arena most thoroughly studied, I knew each cock by his appearance from one year to the other and had some of them ringed. There I discovered that most of the boundaries were older than the cocks defending them. This is due to the fact that a territorial cock will fight every cock close to or approaching his territory, but always at the boundary. If, for instance, the $\operatorname{cock}\,N$ in figure 4 is absent one morning, L can trespass to N's territory. If G then catches sight of L, he may fight him, but only at the G-N boundary. If, on the other hand, G is the first one to enter the empty N territory, L will meet him at the N-L line. Non-territorial cocks seeking for ground to establish a territory may enter earlier defended, but temporarily or permanently unclaimed territories. Within these they are not chased by the other cocks, but at the boundaries they are restricted in displaying. In this way, the older cocks fix the territories of the young newly established ones and, consequently, the boundaries often remain the same as earlier.

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At the bottom left only five of the rve in each spectrogram shows the

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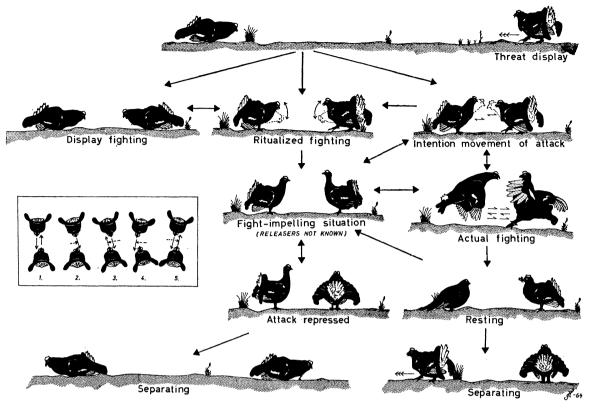


FIGURE 3. An outline of hostile behaviour of Black Grouse at territory boundaries.

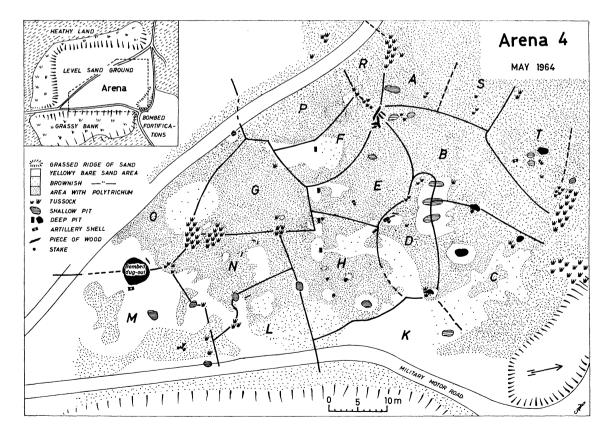


FIGURE 4. Territories of sixteen old Black Grouse on one of the arenas studied in 1964.



FIGURE 2. Sound spectrograms (1) The change from conflict call to true 'rooknoing'; (2) Intention utterances and two stroplies of 'rooknoing'; (3) the change from intention utterances of 'rooknoing' to the conflict call (a typical call is repeated to the right for comparison). The postures shown at the top and bottom illustrate the variations of neck position. The 'alarm' note is very

similar to the first note of the conflict call ((1) to the left). As the bottom left only five of the seventeen intention atterances are registered. The lower curve in each spectrogram shows the amplitude (logarithmic scale).