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Behavioural dimorphism in male ruffs *Philomachus pugnax* (L.)

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many opportunities for copulating. For this reason the relative frequency of satellite genotypes will be increased in the next season. When the influx of new independent males is small, only the successful arenas of the previous year will be maintained. Because of the stable relations on these arenas satellite copulations will be rare. In this case the relative frequency of satellite genotypes will be diminished in the next season. So, the polymorphism in the Ruff may be due to selection of varying direction (cfr. HALDANE & JAYAKAR, 1963).

In fact this control mechanism only depends on the influx of new independent males. This implies that the proportion of satellite males in a population is not kept constant under all circumstances. In the case of a sudden increase or decrease in the numbers of independent males only, and in the case of a sudden increase in the numbers of satellites only, the ratio between both categories can be immediately corrected. However, in the case of a sudden increase or decrease in the numbers of both independent- and satellite males and in the case of a sudden decrease in the numbers of satellites only, the ratio between both categories will be thrown out of balance for a long period. An increase in the number of both categories will result in an increase in the relative frequency of satellite males (i); a decrease in the numbers of both categories in a decrease in the relative frequency of satellites (ii); and a decrease in the number of satellites only will result in a decrease in their relative frequency (iii). The first mentioned change (i) can be corrected in the next season after a small influx of new independent males (stable relations). The second (ii) and third (iii) deviations can only be corrected after a large influx of new independent males (also in the next season).

Thus, an important implication of this hypothesis is that independent males are favoured during periods with low numbers of male Ruffs (protection of mating places), and that satellites are favoured during periods with high numbers of males (protection of gathering of females). This favouring might enlarge the total reproductive output of the individuals in the population, since in small groups of males (females relatively common) the number of mating places might restrict the number of fertilized females, and in large groups (females relatively rare) the number of females might restrict the total number of copulations.

SUMMARY

In the Ruff two groups of males can be distinguished: independent males and satellite males. This classification is based upon differences in territoriality and behaviour, and is highly correlated with differences in the nuptial plumage. Independent

males are mostly dark coloured; their behaviour contains much fighting and related activities. They can be subdivided into resident males and marginal males. Resident males defend territories (residences), marginal males do not. Satellite males are mostly white. They behave peacefully and do not defend a territory. Satellite males have access to the residences on an arena (cfr. HOGAN-WARBURG, 1966).

In this study an attempt has been made to throw some more light upon the behavioural dimorphism (independent males *versus* satellites). On the one hand I tried to analyse the causation of this phenomenon, on the other hand I was interested in its biological significance. I have tackled these problems by means of an examination of film material, and by a quantitative study of the behaviour on different arenas (leks) in the field.

The film supplied me with detailed data about the behaviour of resident males, satellite males, and females in different external situations. On the basis of these data it was possible to analyse the temporal associations between the various behavioural units, for this purpose divided into "postures", "locomotion sequences", "action sequences", and "actions". The observed relations were largely similar for the three categories of individuals.

For this reason I was able to compose one model for the hypothetical causal mechanism underlying the behaviour of resident males, satellite males, and females. The display of postures was supposed to be controlled by the values of two variables, the display of the other units by the value of the same variables and directly by the external situation. The values of both variables depended on external stimuli and on the internal situation (partly determined by previous external stimulation). I could not obtain evidence for the existence of different mechanisms underlying the different groups of behavioural units serving one function, such as aggression, flight, and sex. These groups of behavioural units were fully integrated in the entire causal system. They each appeared at distinctive combinations of values of both variables. Aggressive and sexual behaviour appeared each at only one cluster of combinations, however, protective behaviour appeared at three clusters. The suitability of the drive concept for both variables has been discussed.

Normal behaviour of the three categories distinguished seemed to correspond to category-specific ranges of both variables. Female behaviour represented the one extreme, resident male behaviour the other one, and satellite behaviour was mainly intermediate. This intermediate behaviour has been ultimately ascribed to the light plumages of satellites and the genetical factors connected with that; the lack of a territory and distinct components in the behaviour of resident males towards satellites have also been emphasized as causal factors.

I presented arguments for the hypothesis that the status (independent or satellite) of an individual depends on genetical and environmental factors. The importance of genetical factors appears from the correlation between behaviour and plumage colour. The influence of the environment follows from (a) the inconstancy of the status of some individuals (particularly young ones), and (b) the relation between status of an individual and plumages of the other individuals present on the same arena.

It has been emphasized that some of the plumage colours occur exclusively in satellite males (satellite plumages), and others exclusively in independent males (independent plumages). Males with untypical plumages (intermediate colours) do not necessarily belong to one and the same category. They generally belong to the independent category when there are many males with satellite plumages on the arena, and relatively often to the satellite category when independent plumages are common. This phenomenon could not be ascribed to differential reproduction in previous seasons; it seemed to be connected with migration and changes of status, probably caused by low copulation frequencies.

It is argued that males with independent plumages are homozygotes with respect to a particular gene, that males with satellite plumages represent the same condition but with alternative alleles, and that males with untypical plumages are heterozygotes. This implies that both the behaviour and the plumage are influenced by one pair of genes (pleiotropy).

Resident males can enlarge their reproductive output when tolerating satellite males on their residences in particular situations. The presence of satellite males on residences promotes the attraction of females. However, the presence of satellites has no influence on the duration of female visits, moreover, it has a negative effect on the copulation frequency of resident males. It could be demonstrated that the behaviour of resident males towards satellites is either tolerant or intolerant. Intolerant behaviour occurs when the resident male acquires a high density of female visits on his residence; it also occurs during and after high copulation frequencies of the male concerned. In all other circumstances tolerant behaviour will be shown. Both kinds of behaviour regularly alternate with a period of some days up to some weeks. This causes a large fluctuation in the density of satellite visits to the residence. The density of female visits also fluctuates, but less extremely.

The other factors influencing female and satellite visits to residences have been analysed. This enabled me to formulate a model by which the oscillations in the densities of female and satellite visits could be simulated. Furthermore the effects of satellites on copulating of resident males could be studied. Satellite males appeared to play a very important role. A resident male cannot attract enough females for copulating without co-operation with satellites. The copulation success also depends on the tactics of the resident male, particularly on the adjustment of the tolerant-intolerant transition. Furthermore the degree of intolerance plays an important role.

In the Ruff we are probably concerned with a balanced polymorphism. The genetical diversity may be a consequence of superiority of heterozygotes (males with untypical plumage colours). Another explanation is provided by the mutual dependence between independent males and satellites. It is likely that the fitness of individuals of either category changes during oscillations of their relative frequencies, because of the change in the effectiveness of the co-operation with the other category.

It is suggested that the success of satellite males on an arena is negatively correlated with the number of stable relations between resident males. In the early part of the season, on recently established arenas, and after changes in the occupation of residences the copulation frequency of satellite males is high. This phenomenon is probably caused by the low number of attacks on non-territorial males in such situations. The high number of attacks on marginal males in the other situations implies that arenas seldom grow when stable relations are common. Hence the relative frequencies of independent males and satellites are supposed to be controlled by the influx of new independent males, and thus by the establishment of new arenas. This hypothesis implies that independent males are favoured during periods with low numbers of males, and that satellites have the advantage when there are many males.

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