In the Fochteloo Black Grouse population, copulation success of adult males which had territories on an arena tended to increase in the course of their life; on arenas, copulations occurred most frequently on the centre where the oldest territorial males tended to occupy a territory. As mentioned before, the latter two phenomena have also been reported for other arena grouse populations (this section, and section 7.7.2). Thus, it is likely that in these populations also, the oldest territorial males tend to be most successful in mating. However, as far as I know, this has only been demonstrated directly by Robel (1967) for a Prairie Chicken population in Kansas. Robel studied arenas where juvenile as well as adult males were territorial. He observed 97 copulations there; none of these were carried out by juvenile males and most were carried out by 3rd year or older males, which were of an age probably reached by only about 15% of the Prairie Chicken males.

For arena males in the Fochteloo Black Grouse population, evidence exists that location of territory is not the only factor promoting copulation success of older territorial males. This probably applies to other arena grouse populations also: several authors report that copulations on grouse arenas are often highly unequally divided among the males with territories there, even among males occupying similar positions on the same arena. An example of this is presented by Johnstone (1969) for a Black Grouse arena in Scotland. This arena was attended by 8 territorial males, only 3 of these copulated and one of them obtained 26(90%) of the 29 copulations observed on the arena. Another example is given by Wiley (1973) for 3 Sage Grouse arenas in the U.S.A.: the number of territorial males per arena ranged from 30 to 60, the number of copulations from 42 to 112; on each arena only 2 or 3 males performed over 75% of all copulations observed. It is not yet understood which factors, in addition to location of territory, are responsible for copulation distributions like the ones mentioned.

Summarizing, it can be concluded that in arena grouse populations a relation exists between age and copulation success of males. Juvenile males have little chance of copulating. On arenas, older territorial males tend to be most successful in mating. Possession and location of territory influence copulation success of males, but other factors must also play a role.

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9. SUMMARY

This study deals with social behaviour of Black Grouse in a population in the northern Netherlands. Most attention is paid to behaviour of males. Social organization and life history of males are described and factors underlying the social behaviour of individuals are identified. Social behaviour in the study population is compared with that in other arena grouse populations.

Spacing pattern of individuals is an important aspect of social organization within a population. In studies on social organization of animals it is often supposed that spacing patterns arise as a result of attractive and repulsive forces between individuals (*e.g.* McBride 1966, Kummer 1970, Brown 1975). This study shows that these forces are not the only ones determing spacing patterns; in addition site attachments of individuals play an important role, at least in our Black Grouse population.

All marked individuals in our Black Grouse population tended to restrict their activities to a particular portion of the population distribution range. This indicates that site attachments were present in all individuals, but these were clearly strongest in territorial males. The latter males appeared to be strongly attracted to particular locations within

their territory, which are called display sites because the males spent much time displaying there. Home ranges of territorial males were smaller on average than those of non-territorial males and females and varied in size and location between individuals. Factors which probably influenced size of home range of a territorial male are 1. strength of the bond between the male and his display sites, 2. size of the male's territory, and 3. location of the male's display sites and his territory relative to the location of ecological resources. The location of the home ranges of different territorial males relative to each other appeared to be heavily dependent upon the location of the males' display sites. Several territorial males had display sites which were located close to those of other territorial males: on the same arena. Other territorial males had display sites which were located far away from those of other territorial males; these males displayed solitarily, away from arenas. Display sites of different territorial males could thus be located far apart or close to each other. When the display sites of two different territorial males were located closely together, their home ranges tended to be coincident. The farther apart the display sites of territorial males were, the less their home ranges tended to overlap.

Black Grouse individuals appeared to be strongly attracted to conspecifics, they were often in a flock, but site attachments of individuals could interfere with their gregariousness. Strength of site attachments of individuals tended to be negatively correlated with their gregariousness, *e.g.* individuals tended to be more gregarious in winter than in spring when their site attachments were strongest, and adult males, which were often territorial, tended to be less gregarious than juvenile males, which seldom defended a territory. The association frequency between individuals was heavily dependent upon correspondence in their site attachments: the more individuals differed in site attachments, the smaller was the chance that they met each other and the greater was the chance that each would go its own way again when leaving the meeting place. Males possessing a central territory on the same arena strongly corresponded with each other with respect to site attachments and often associated with each other in a flock, even when away from their territories on the arena. As a result central arena males were very gregarious; site attachments of these males did not interfere with their gregariousness. In contrast, site attachments of other territorial males (marginal arena males and solitarily displaying males) tended to interfere with their gregariousness.

Site attachments thus influenced flocking behaviour of individuals. On the other hand, it seems reasonable to suppose that the flocking tendency of individuals influenced time spent by them on the places to which they were attached. Probably, individuals spent less time on these places than they would have done if they had not been attracted to conspecifics elsewhere.

Establishment of display sites by males occurred on places where they had obtained certain kinds of experience in interactions with conspecifics; especially experience obtained in courtship interactions with females appeared to play an important role. Attachment to a certain display site weakened in males when it was not reinforced frequently; the same kinds of experience which triggered display site attachment played a role in maintenance of the attachment.

Display site attachment and territory defence appeared to be closely linked. Display site attachment played a role in establishment, maintenance, and enlargement of territories. Strength of the males' tendency to behave aggressively towards conspecific males was site dependent and highest in the neighbourhood of their display sites. After having established a display site on a certain place, non-territorial males often suddenly tried to resist the male possessing a territory there. This could lead to establishment of a new territory. The attractive value of display sites on their territory influenced time spent on territory by territorial males and thus influenced their chances of maintaining their territory. Territorial males could also become attached to sites located outside their own territory; this could lead to enlargement of territories.

Generally speaking, aggression tends to act as a repulsive force between individuals, which interferes with flocking and promotes dispersion of individuals. However, in our Black Grouse population aggression between two individuals in a flock seldom directly resulted in separation of the individuals. Dispersion of males over the population distribution range was primarily the result of differences between them with respect to site attachments. Aggression undoubtedly played a role in the development of these differences. By means of aggressive behaviour territorial males often prevented males intruding on their territory from obtaining experience there which could make them attached to that place. This promoted dispersion of the display sites of different males over the population distribution range.

Life span of individuals in our Black Grouse population appeared to be maximally 8 years. Average life span of males was about 4 years.

Some males established a territory for the first time in spring of their first year of life but most males became territorial for the first time in their second year of life. Sometimes a male did not become territorial until his 3rd or 4th year. After having established a territory, males usually continued to be territorial on the same display ground until the end of their life. Sometimes males lost their territory in summer but in these cases, if surviving, they always re-established a territory in the following season.

Males which established a territory on an arena usually obtained a marginal position first; some of these males obtained a central territory later. As a result of this, central males tended to be older than marginal ones.

Males which did not possess a territory had little chance of copulating. On arenas, older territorial males tended to be more successful in copulating than younger ones. Probably, this is partly a result of the preference of females to copulate on the centre, but there must be other factors promoting copulation success of older males on arenas. What these factors are, is not yet known. Another intriguing question which remains to be answered is why some arena males become very successful in copulating in the course of their life whereas others do not.

A comparison of data from our and other arena grouse populations indicated that differences between populations exist with respect to 1. maximum number of males territorial on the same arena (which is very high in Sage Grouse compared to other arena grouse species), 2. usual size of territories on arenas (which is very large in our Black Grouse population compared to other Black Grouse populations studied and populations of other arena grouse species), and 3. territory defence and copulation success of juvenile males (the

latter apparently may vary considerably between arena grouse populations; usually however, juvenile males seldom copulate). Although differences exist, the available evidence indicates that social organization is essentially the same in all arena grouse populations. Most or all what has been said hitherto in this summary about social behaviour in our Black Grouse population is probably also true for other arena grouse populations.

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11. SAMENVATTING

Dit artikel handelt over resultaten van een onderzoek naar het sociale gedrag van korhoenders in een populatie nabij Fochteloo in Zuidoost Friesland. De meeste aandacht wordt besteed aan het gedrag van hanen. Het sociale gedrag en de levensgeschiedenis van afzonderlijke individuen worden beschreven, en omgevingsfactoren die hierop invloed uitoefenen worden besproken. Tenslotte wordt het sociale gedrag van hanen in de bestudeerde korhoenderpopulatie vergeleken met dat in andere populaties van ruigpoothoendersoorten die arenagedrag vertonen.

De wijze waarop individuen over het woongebied van populaties verspreid zijn is een belangrijk aspect van hun sociale organisatie. Vaak wordt verondersteld dat spreidingspatronen het resultaat zijn van aantrekkende en afstotende krachten die individuen op elkaar uitoefenen (bijv. McBride 1966, Kummer 1970, Brown 1975). Uit dit onderzoek blijkt