

Territoriality, breeding ranges  
and relationship between the  
sexes in a Danish wild phea-  
sant (*Phasianus colchicus*)  
population

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## Data sheet

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## Summary

Territoriality, breeding range, harem size and stability, and faithfulness of females to territory-holding males, were studied in a Danish pheasant *Phasianus colchicus* population in the period 1975-83. The 367 ha study area was situated at the Kalø estate in Eastern Jutland, Denmark and consisted of forest and agricultural areas (Fig. 1).

Trapped birds were sexed and divided into two age classes: yearlings and adults. A total of 751 pheasants (296 males, 455 females, Table 1) was marked with leg bands and neck collars (Fig. 4). Visual observations of pheasants were made throughout the year, primarily during the breeding season, March to June (Table 2).

Data on size and composition of the Kalø population are summarised in Table 3. Mean population size per 100 ha was 27.3 birds, varying between 19.9 and 33.8 (Fig. 5). The mean number of males and females was 12.5 and 14.8, respectively.

Of 173 marked adult males, 136 were territorial, 4 were non-territorial due to sickness or handicap, and 33 were undetermined due to lack of observation data. No observations indicated that healthy adult males were non-territorial. Of the marked yearlings 37% were territorial, 55% non-territorial, and 8% intermediately positioned (Table 4). When classifying all adult males as territorial, 79.3% of the total male population was territorial, 18.7% was non-territorial, and 2.0% was in between.

Male territories were predominantly established at the forest edges and in the adjacent farmland with hedgerows, coverts and shrubby areas (Fig. 6). Territory sizes of adult and yearling males did not differ significantly; the mean size was 8.0 ha (Table 5). Mean size of the much larger home ranges of non-territorial males was 32.2 ha (Table 6). The mean size of territories was significantly negatively correlated with the number of territorial males (Fig. 8).

The overall breeding season-territories overlapped greatly, but territory boundaries changed from month to month (Figs 6 and 9), resulting in much less overlap between neighbouring territories on a monthly basis. Major factors responsible for changes of territory boundaries seemed to be movements of females and habitat changes due to growth of vegetation and field crops.

Males showed high territory fidelity from year to year. Of 43 surviving territorial males, 41 occupied the same or partly the same territory in consecutive years; complete shifts of territory from one year to the next were only observed for two males.

Female breeding ranges were unevenly distributed and overlapped greatly. The mean of home range sizes for yearling females was higher than for adult females (9.8 ha vs. 7.5 ha, Table 7), although not significantly. Females showed much faithfulness to the home range they had occupied in the preceding season; in total only 16% settled in non-overlapping ranges.

Yearling females shifted home range during the breeding season four times as often as adults (25.6% vs. 6.3%, Table 8). Predation by foxes seemed to be responsible for up to half of these shifts of home range.

Territorial adult and yearling males were observed without females in 67% and 83%, respectively, of all records made during 1 March to 30 June. Records of males accompanied by females increased from mid-March and peaked in May when they made up more than 40% of the observations of territorial males (Fig. 11); from late May the proportion decreased.

The highest number of females simultaneously observed with a territorial adult or yearling male was 12 and 7, respectively (Fig. 12). The total number of different females with which the individual males was seen throughout the breeding season was considerably higher: a maximum of 22 females was recorded for one male through the breeding season in 1981 (Table 9).

Adult males were more successful in attracting females than yearling males. The mean number of females observed accompanying adult and yearling territorial males differed significantly and was 2.5 and 1.8, respectively (Table 10). For the whole breeding season the mean number of different females recorded with adult and yearling territorial males was 3.9 and 2.9, respectively (Table 10), but this difference was not significant.

In all breeding seasons yearling females were seen in company with significantly more different territorial males than adult females which accompanied up to six different males during the same breeding season, averaging 1.9 males; yearling females accompanied up to seven different males, averaging 2.5 (Table 11, Fig. 13).

Less than one fourth of adult females and less than half the yearling females who had the opportunity, associated with the same territorial male during two or more successive breeding seasons.

The results are discussed, implicating the available knowledge on pheasant biology up to 1995, based on field studies and experiments performed in other countries.

## Dansk resumé

Territorialitet, home range i ynglesæsonen, haremers størrelse og stabilitet, og hønens trofasthed over for territoriale kokke, blev undersøgt i Kaløs fasanbestand i 1975-83. Det 367 ha store undersøgelsesområde bestod af skov og landbrugsarealer (Fig. 1).

Fasaner *Phasianus colchicus* blev efter at være fanget i fælder køns- og aldersbestemt. I alt blev 751 fasaner (296 kokke, 455 høner, Tabel 1) ringmærket og fik påsat en nummeret plastikhalskrave (Fig. 4). Fasanerne blev derefter sat fri og efterfølgende observeret gennem hele året, men kun observationer fra ynglesæsonen marts - juni er medtaget i denne rapport (Tabel 2).

Størrelse og sammensætning af Kalø-bestanden er opsummeret i Tabel 3, og den gennemsnitlige bestandsstørrelse pr. 100 ha var 27,3 fasaner, varierende mellem 19,9 og 33,8 (Fig. 5). Det gennemsnitlige antal kokke og høner i bestanden var hhv. 12,5 og 14,8.

Af 173 mærkede voksne kokke var 136 territoriale og 4 ikke-territoriale pga. sygdom eller handicap; 33 voksne kokkes territorial-status kunne ikke bestemmes pga. utilstrækkeligt antal observationer. Ingen observationer indicerede, at sunde, voksne kokke var ikke-territoriale. Af de mærkede, unge kokke var 37% territoriale og 55% ikke-territoriale; 8% udviste ikke entydig adfærd. Når alle voksne kokke blev klassificeret som territoriale, var 79,3% af samtlige kokke i bestanden territoriale, 18,7% var ikke-territoriale og 2% kunne hverken klassificeres som territoriale eller ikke-territoriale.

Kokkenes territorier etableredes fortrinsvis i skovkanter og i det tilstødende agerland med levende hegn, krat og småbevoksninger (Fig. 6). Der var ikke signifikant forskel på størrelsen af voksne og unge territoriale kokkes territorier, der gennemsnitligt var 8,0 ha (Tabel 5). Ikke-territoriale kokke havde home ranges, der i gennemsnit var 32,2 ha (Tabel 6). Der var signifikant negativ korrelation mellem gennemsnitlig territoriестørrelse og antal af territoriale kokke (Fig. 8).

Territorier beregnet for hele ynglesæsonen overlappede meget, men territoriernes grænser ændredes fra måned til måned (Fig. 6 og 9), så der var mindre overlap mellem nabeterritorier på månedsplan.

Fasankokkene udviste stor stedtrofasthed fra år til år. Af 43 overlevende territoriale kokke besatte 41 det samme eller delvis det samme territorium det efterfølgende år. Totalt skift af territorium fra et år til det næste blev kun registreret for to kokke.

Hønernes home range i ynglesæsonen var ujævnt fordelt i området

og overlappede meget. Unge høners gennemsnitlige home range var større (omend ikke signifikant) end de voksne høners, 9,8 ha mod 7,5 ha (Tabel 7). Overlevende fasanhøner var stedtrofaste over for deres home range fra den foregående sæson, idet kun 16% etablerede sig i ikke-overlappende home ranges.

Unge høner skiftede i løbet af ynglesæsonen home range fire gange så ofte som voksne (hhv. 25,6% og 6,3%, Tabel 8), og op mod halvdelen af disse skift syntes at kunne tilskrives forstyrrelser eller prædation fra ræve.

Territoriale voksne og unge kokke blev observeret uden høner i hhv. 67% og 83% af alle observationer i marts - juni. Andelen af observationer af kokke, der blev ledsaget af høner, steg fra midten af marts og toppede i maj, hvor de udgjorde over 40% af samtlige registreringer af territoriale kokke (Fig. 11). Fra sidst i maj faldt andelen igen.

Det højeste antal høner, som blev observeret samtidig med en voksen eller ung territorial kok, var hhv. 12 og 7 (Fig. 12). Det totale antal forskellige høner, som den enkelte kok blev set med gennem ynglesæsonen, var betragteligt højere: et maximum på 22 høner blev registreret for en kok i ynglesæsonen i 1981 (Tabel 9).

Det gennemsnitlige antal høner, som blev set ledsage voksne og unge territoriale kokke, var signifikant forskellige: hhv. 2,5 og 1,8 (Tabel 10). For hele ynglesæsonen var det gennemsnitlige antal forskellige høner, som blev observeret sammen med voksne og unge territoriale kokke, hhv. 3,9 og 2,9 (Tabel 10), men forskellen var ikke signifikant.

I samtlige ynglesæsoner blev unge høner set sammen med signifikant flere territoriale kokke end voksne høner (op til hhv. 7 og 6 kokke pr. ynglesæson), og de ledsagede i gennemsnit hhv. 2,5 og 1,9 kokke pr. ynglesæson (Tabel 11, Fig. 13).

Mindre end 25% af de voksne høner og mindre end 50% af de unge høner, som havde muligheden, knyttede sig til den samme territoriale kok i to eller flere på hinanden følgende ynglesæsoner.

Resultaterne diskuteres og sammenlignes med den tilgængelige viden om fasanernes biologi på basis af feltundersøgelser og eksperimenter udført i andre lande i perioden frem til 1995.



# 1 Introduction

In countries where the ring-necked pheasant *Phasianus colchicus* has been introduced, studies have shown a polygynous mating system, based on the defence of territories by males (e.g. Taber 1949, Collias & Taber 1951, Burger 1966, Lachlan & Bray 1976, Göransson 1980, 1984, Wasilewski 1986, Ridley & Hill 1987, Koubek & Kubišta 1990a, b, 1991). The most common explanation for this mating system is that females either choose the territory providing the best resources for breeding and caring for the young, ('resource defence polygyny', Emlen & Oring 1977), or choose the male, based on characteristics of the male himself (proven for pheasants by Ridley & Hill (1987), von Schantz et al. (1989), Göransson et al. (1990), Grahn et al. (1993a, b), von Schantz et al. (1994), Mateos & Carranza (1995)), or both. Besides defending the territory, the male defends the harem of females that has accumulated in his territory against other males ('harem defence polygyny', Emlen & Oring 1977; 'territorial harem defence polygyny', Ridley & Hill 1987), and this mate guarding reduces the risk to females of rape, predation and excessive energy expenditure (Ridley & Hill 1987), thus improving breeding success.

Pheasants live in flocks more or less segregated by sex during winter, males more loosely associated than females (Hill & Ridley 1987). On the verge of spring, males disperse to establish and defend territories in which they display courtship to females (e.g. Taber 1949), preferably along the edges of permanent cover (Gates & Hale 1974, Woodburn 1991, Robertson et al. 1993). Boundary disputes between neighbouring males are most frequent during the first few weeks of establishment (Hill & Robertson 1988b), when the majority of territories are occupied (Gates & Hale 1974, Göransson 1984, Koubek & Kubišta 1991). Not all males, however, obtain territories, and in many populations a proportion of non-territorial males remains (e.g. Taber 1949, Burger 1966, Lachlan & Bray 1976, Göransson 1980). Territorial defence and courtship displays decrease towards the end of the breeding season and terminate at the beginning of the annual moult, which for males occurs in June/July (Cramp & Simmons 1980).

Females disperse from their winter flocks later than the males (Gates & Hale 1974, Göransson 1984, Ridley & Hill 1987) to visit territory holders, and females are often still observed in smaller groups as they traverse territories. Later on, they settle into their breeding ranges. The term 'harem' generally signifies the group of females accompanying the territorial male at a given time. As pointed out by Ridley & Hill (1987), several aspects of territorial harem defence in pheasants resemble those in ungulates. Pheasant males try to attract females to their territories, but do not, however, control the movements of females. Harems are loosely knit; female pheasants move freely through male territories, joining and leaving

harems, and it seems that males are unable to prevent them from doing so (Göransson 1980, Ridley & Hill 1987, Göransson et al. 1990).

This report presents the results of an investigation of territoriality, breeding home range, harem size and stability, and faithfulness of females to territory-holding males, in a Danish pheasant population studied in the period 1973-84. The discussion of these results is based on the available knowledge on pheasant biology, based on field studies and experiments performed in other countries up to 1995.

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## **3 Study area**

The 367 ha study area consists of a rolling terminal moraine, falling gently towards the coast at the bottom of Kalø Bay in Eastern Jutland, Denmark (Fig. 1). A sandy, low-lying elevated sea-floor, formed during the last glaciation, predominates the western part of the study area. The more elevated areas consist of heavy clay soils and loam.

Of the study area 291 ha belong to the Kalø estate, including the Hestehave forest, 170 ha, agricultural areas, 95 ha, coverts, hedges, gardens, 25 ha, and a pond of one ha. The 76 ha neighbouring area consists primarily of farmland divided by hedgerows and small wooded areas.

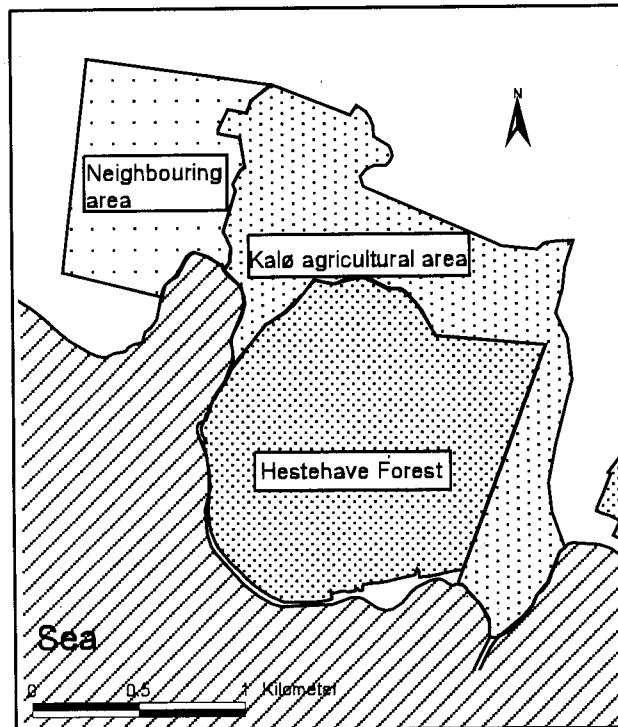


Figure 1. The study area including 170 ha of forest and 121 ha of agricultural land belonging to Kalø estate, plus additionally 76 ha primarily farmland.

The Hestehave forest consists of 108 ha (64%) deciduous stands, primarily beech *Fagus silvatica*, and 56 ha (33%) coniferous stands dominated by Norway spruce *Picea abies* and sitka spruce *P. sitchensis*. The remaining 6 ha (4%) consist of forest roads and unwooded areas.

When the study was initiated in 1973, 8 ha (5%) of the forest contained new plantings less than 10 years of age; 38 ha (22%) deciduous stands older than 80 years allowed a dense herb vegetation on the forest floor. The remaining 118 ha consisted of 66 ha 21-80 years old deciduous stands and 52 ha of more than 10 years old coniferous stands; the latter allowed only little herbaceous vegetation on the forest floor. In November 1981, a strong gale brought down nearly all coniferous stands older than 30 years; this led to a radically changed study area during the last two years of field studies.

In the farmland the crops included barley, winter wheat, seed grass, beets, turnips and rape; from 1980 onwards maize for cattle was grown instead of beets and turnips. Permanent pastures were grazed by cattle, but in some years the grass was harvested for silage.

One covert (2 ha) in the north-western part of the area was altered during the study period. In 1977 a stand of dying spruce was replaced with different bushes and trees, and an adjacent field of 0.3 ha was planted with Norway spruce.

The grassy salt meadows included dry and sandy areas with scattered clumps of dog rose *Rosa rugosa* and lower wet parts with reed *Phragmites communis*.

A pond of 1 ha was artificially established in the mid-1950s immediately north of the Hestehave forest. To the west the study area was bordered by a group of weekend cottages, to the north-west by a road and a few houses.

## 4 Methods

Field work was carried out between October 1973 and March 1984. Trapping of pheasants began in the autumn of 1973; different colour marking devices were tested to minimise damage to the birds, and to ensure durability and visibility in the field. Study methods and techniques were determined during the spring of 1974.

The pheasants were trapped in baited walk-in traps through October-March. Until the autumn of 1976 45-50 mobile, self-catching traps (Fig. 2) were distributed over the study area. Then, the mobile traps were replaced by 16 permanent traps (Fig. 3), which could be released by a cord from a distance of 100 m or more. The number of recaptured, marked birds was thereby minimised. Pilot-studies in 1974 had indicated that repeated trapping left the birds increasingly shy and alert. The permanent traps were supplemented with a few mobile traps in some coverts and hedges, where permanent traps had proved less effective.

As some male pheasants avoided capture, the method was modified and the trapping season was extended to include June from the spring of 1982. Live decoy males were placed in cages in combination with traps in the centre of territories of unmarked males. In this way nearly all territorial and non-territorial males were trapped.

The trapped birds were sexed from plumage and aged on the basis of presence or absence of *Bursa fabricii*, and measurements of lengths and shaft diameters of proximal primaries (Greenberg et al. 1972). At capture, the pheasants were divided into two age classes: yearlings and adults. Yearlings included individuals born during the preceding season, thus reaching the age of 10 months on 1 April.

The birds were marked with a numbered aluminium leg band and three coloured plastic leg bands; furthermore, a 5.5 x 15.5 cm



Figure 2. Self-catching trap.

curved yellow and black neck collar (poncho) of hard plastic engraved with a code was mounted (Fig. 4). The double marking technique was used to prevent lack of individual identification as collars had often proven to break and be lost. In total, 751 pheasants (296 males, 455 females) were trapped and marked during 1973-1984 (Table 1); 174 of the 751 pheasants (65 males, 109 females) were never observed after being marked. During the breeding season 27 (15.6%) of the 173 adult females and 17 (9.8%) of the 173 yearling females were not observed at all. In fact, they were not seen again until some time after termination of the breeding season.

In the Kalø estate part of the study area pheasant shooting took place only in the autumns of 1974 and 1975; one day each year. In the remaining study area pheasant shooting occurred during autumn each year. A total of 38 marked pheasants were shot during the study period, 24 of these were shot in the first two years, 1974 and 1975.



Figure 3. Permanent trap released by a cord.



Figure 4. Male pheasant with Alu-leg band, 3-colour leg bands & a neck collar (poncho).

Until 1977 the pheasant population declined. As remains of pheasants were often located at dens of red fox *Vulpes vulpes*, a fox control programme was implemented with effect from the summer of 1977. A few straying domestic cats *Felis silvestris* were killed as well.

Table 1. Sex and age composition of 751 pheasants trapped in 1973-1984.

Year	Males			Females			Total
	Adult	Year-ling	All	Adult	Year-ling	All	
1973-74	8	31	39	23	38	61	100
1974-75	6	24	30	16	61	77	107
1975-76	8	19	27	11	44	55	82
1976-77	1	14	15	4	21	25	40
1977-78	4	20	24	7	20	27	51
1978-79	0	26	26	4	39	43	69
1979-80	6	12	18	5	26	31	49
1980-81	1	30	31	4	30	34	65
1981-82	12	19	31	1	21	22	53
1982-83	5	25	30	6	35	41	71
1983-84	2	23	25	7	32	39	64
All years	53	243	296	88	367	455	751

Observations of pheasants were made throughout the year, primarily from one hour before to two hours after sunrise, and from 1-2 hours before to one hour after sunset. Observations were carried out daily during 1 March - 30 June; for the rest of the year 2-4 times weekly. The birds were observed from vehicles driven on permanent and temporary tracks in the forest and farmland. All sightings of marked and unmarked birds were recorded and the locations plotted on maps in the field. Numbers and identification marks of females observed with each male were noted.

The visual observation technique has its limitations compared to e.g. radio-tracking. The chance of discovering males that were not engaged in territorial activities, and females that were not in flocks or associating with a territorial male, was small. This is reflected in the low numbers of birds observed in March and June (Table 2). Especially in June observations of females are few, considering the skewed sex distribution revealed by trapping (see Table 1).

Males were classified as territorial or non-territorial according to appearance and categories of behaviour. Territorial behaviour included crowing and crowing-reply, an upright alert posture with inflated wattles ("red head"), erected ear tufts, and distended plumage; agonistic behaviours like run threat, lateral strut, parallel-walk, peck threat, and kicks with spurs were also included (Jørgensen 1977). The more skulking non-territorial males did not exhibit these behaviours or postures. Only territorial males performed courtship displays like lateral-display and tidbitting; on rare occasions, where mating or mating attempts by non-territorial males were observed, they took place without courtship displays (i.e. rape).

Territories and home ranges were determined on the basis of field observations made during 1 March - 30 June in 1975-1983 (Table 2). The beginning of the breeding season with male establishment of territories is included in this period. Yet, in 1976 and 1982 territorial behaviour was observed as early as the latter half of February. Male territoriality usually ceased by the end of June although a few males continued their territorial displays until mid-July.

The calculations of territory and home range size included 260 marked pheasants observed 10 or more times during a single breeding season (1 March - 30 June): 75 adult males, 70 yearling males, 54 adult females, and 61 yearling females. Size of territories and home ranges was estimated by combining the outermost positions to form a convex polygon (Mohr 1947). The convex polygon method was chosen in order to compare ranges from other studies, as most authors have used this method. Outstanding single observations of birds, at least 500 metres from the closest neighbour position, were omitted from the calculations.

Table 2. Total monthly number of observations of marked male and female pheasants during 1975 - 1983.

Number of observations	March	April	May	June
Males	174	2,032	2,657	928
Females	279	1,533	1,669	206

The locations of territories held by males for two or more consecutive years were compared to determine their territory fidelity. Similarly, it was investigated whether females changed their home ranges. When territories and home ranges, respectively, overlapped by 75% or more during two consecutive years they were designated as identical; when overlapping by 25-75%, they were designated as partly identical; and when overlapping by less than 25% a shift was defined. A shift of home range within the breeding season was defined when both of the following conditions were fulfilled: when a female moved to a new site without being seen in the original home range later on in the breeding season, and when the centre of the second home range was removed by more than 500 m from that of the original home range.

## 5 Results

Data on size and composition of the Kalø pheasant population are summarised in Table 3. The mean population size per 100 ha was 27.3 birds, varying between 19.9 in 1977 and 33.8 in 1975 (Fig. 5). The mean number of males and females per 100 ha was 12.5 and 14.8, respectively.

Analysis revealed that territory size varied significantly (adult males:  $t = 3.48$ ,  $df = 110$ ,  $p < 0.001$ ; yearling males:  $t = 2.57$ ,  $df = 25$ ,  $p < 0.02$ ) until the number of observations of adult and yearling males exceeded 18 and 14, respectively. However, in order to achieve sufficient material for the various analyses, our material includes territories calculated on the basis of 10 or more observations (see p. 15). Thus, the achieved territory size for some of the males may be underestimated. Female home range sizes were uninfluenced by the number of observations, as long as it was  $\geq 10$  (adult females:  $t = 0.35$ ,  $df = 58$ ,  $p > 0.5$ ; yearling females:  $t = 0.18$ ,  $df = 59$ ,  $p > 0.5$ ).



Table 3. Size and composition of the Kalø pheasant population on 1 April during 1975 - 1983.

Year	1975	1976	1977	1978	1979	1980	1981	1982	1983
Marked adult males	21	22	14	15	12	21	13	29	26
Marked yearling males	16	11	5	13	18	8	23	11	17
Best estimate of unmarked males	15	14	11	13	15	10	17	10	13
Total number of males	52	47	30	41	45	39	53	50	56
Marked adult females	28	23	15	18	19	23	21	13	15
Marked yearling females	30	23	13	17	27	15	25	11	17
Best estimate of unmarked females	14	15	15	11	13	12	16	21	19
Total number of females	72	61	43	46	59	50	62	45	51
Total population	124	108	73	87	104	89	115	95	107
Number per 100 ha	33.8	29.4	19.9	23.7	28.3	24.3	31.3	25.9	29.2
% unmarked birds	23	27	36	28	27	25	29	33	33

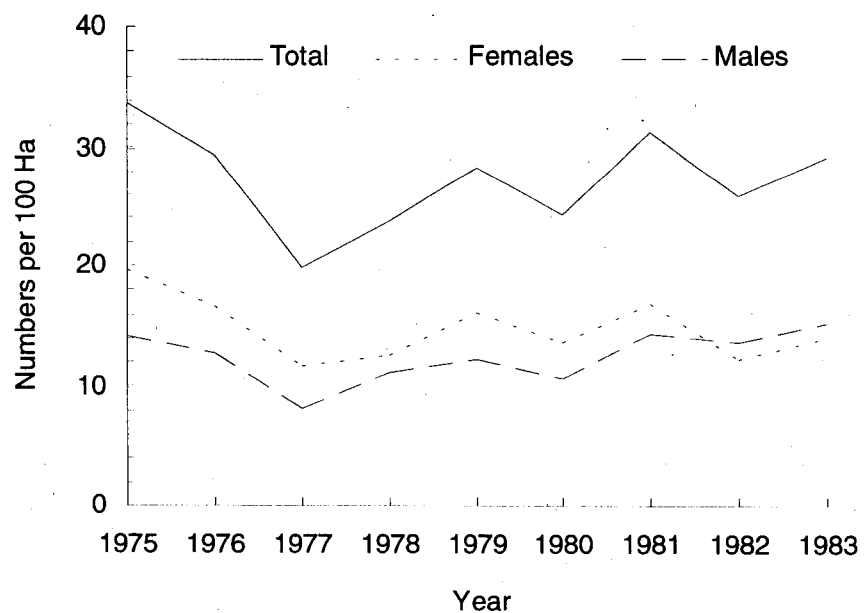


Figure 5. Population density of pheasants in the Kalø study area on 1 April in the years 1975-83.

## 5.1 Male territoriality

Of 173 marked adult males that stayed alive during the breeding season, 136 were territorial and four non-territorial, the latter due to sickness or handicap. The status of the remaining 33 birds could not be determined, due to lack of observations (Table 4); no observations indicated that healthy adult males were non-territorial.

Of 122 marked yearling males that stayed alive during the breeding season, 31 could not be categorised due to limited observation data. Of the rest 34 (37%) were territorial, 50 (55%) were non-territorial, and 7 (8%) were intermediately positioned (Table 4); during some observations the latter group displayed territorial behaviour and during others non-territorial behaviour.

When marked adult and yearling males were tested against unmarked males, evaluating the distributions of territorial males, non-territorial males, and males without determined status, no significant differences were found ( $\chi^2 = 2.86$ ,  $df = 2$ ,  $p < 0.24$ ). Including all 'defined' males in Table 4, and classifying all adult marked males as territorial, 79.3% of the male population was territorial, 18.7% non-territorial, and 2.0% in between.

## 5.2 Size and distribution of male territories and home ranges

For 75 adult males 112 territories were determined; 50 contributed a territory in one season, 15 in two seasons, 8 in three seasons, and 2 in four seasons. Mean size of territories ( $\pm$  SD) during 1975-83 was 8.0 ha  $\pm$  5.8 (Table 5), ranging within 0.7-27.9 ha. Furthermore, size of territories was determined for 28 yearling males, and mean territory size during 1975-83 was 8.3 ha  $\pm$  5.8 (Table 5), ranging within 1.3-23.5 ha. The territory sizes of adult and yearling males did not differ significantly (Mann-Whitney U,  $p < 0.6673$ ).

Mean home range size ( $\pm$  SD) for 37 non-territorial males was 32.2 ha  $\pm$  22.3 (Table 6), ranging from 3.5 to 89.4 ha. The smallest home ranges were probably underestimated, as non-territorial yearlings, due to their submissive and non-crowing behaviour, were observed less frequently than territorial males. Home range for five of the seven intermediately positioned males (see above) varied from 11.6 to 25.7 ha.

Territories were unevenly distributed in the study area. They were predominantly established at the forest edges and in the adjacent farmland with plenty of hedgerows, coverts and shrubby areas, and rarely in the dense parts of the forest (Fig. 6).

Table 4. Number of territorial, non-territorial and undetermined adult and yearling males during 1975 -1983.

Year	Marked										Unmarked					All					?' in % of N
	Adult					Yearling					N	T	D	?	N	T	D	M	?		
	N	T	D	?	N	T	D	M	?												
1975	21	17	1	3	16	2	8	0	6	15	11	2	2	52	34	10	0	8	15.4		
1976	22	22	0	0	11	3	6	2	0	14	6	2	6	47	31	8	2	6	12.8		
1977	14	13	1	0	5	0	4	1	0	11	10	1	0	30	24	5	1	0	0.0		
1978	15	13	2	0	13	5	5	1	2	13	6	1	6	41	26	6	1	8	19.5		
1979	12	10	0	2	18	5	8	2	3	15	6	2	7	45	23	10	2	10	22.2		
1980	21	17	0	4	8	1	3	0	4	10	8	1	1	39	30	4	0	5	12.8		
1981	13	9	0	4	23	4	10	1	8	17	10	3	4	53	27	13	1	12	22.6		
1982	29	16	0	13	11	5	4	0	2	10	6	2	2	50	40	6	0	4	8.0		
1983	26	19	0	7	17	9	2	0	6	13	10	2	1	56	45	4	0	7	12.5		
1975-83	173	136	4*	33	122	34	50	7	31	118	73	16	29	413	280	66	7	60	14.5		

N: Total number of males.

T: Number of territorial males.

D: Number of non-territorial males.

M: Territorial/non-territorial males.

?: Males without defined status.

T: All adult males + territorial yearling males + territorial unmarked males.

D': Non-territorial males; adults not included.

?: Males without defined status; adults not included.

\*: Sick or handicapped.

Table 5. Mean size and standard deviation of male territories during 1975 - 1983.

Year	Adult males		Yearling males	
	Ha ± S.D.	N	Ha ± S.D.	N
1975	4.22 ± 2.03	15	23.50	1
1976	9.40 ± 7.15	18	13.50 ± 6.77	3
1977	14.22 ± 8.36	13		0
1978	11.53 ± 4.41	13	11.28 ± 8.58	4
1979	8.77 ± 3.97	6	6.80 ± 1.68	5
1980	6.89 ± 5.02	14	4.10	1
1981	6.13 ± 3.92	6	5.42 ± 3.84	4
1982	4.74 ± 2.01	12	5.20 ± 2.97	3
1983	5.41 ± 2.42	15	6.67 ± 3.57	7
1975-83	7.96 ± 5.84	112	8.26 ± 5.83	28

Table 6. Mean size and standard deviation of home ranges for 37 non-territorial yearling males during 1975 - 1983.

Year	N	Size of home range
		Ha ± S.D.
1975	6	44.78 ± 25.15
1976	5	52.34 ± 34.56
1977	3	40.27 ± 25.91
1978	4	32.50 ± 10.11
1979	6	20.42 ± 10.57
1980	1	25.80
1981	6	18.75 ± 7.44
1982	4	24.90 ± 26.16
1983	2	24.95 ± 5.87
1975-83	37	32.20 ± 22.34

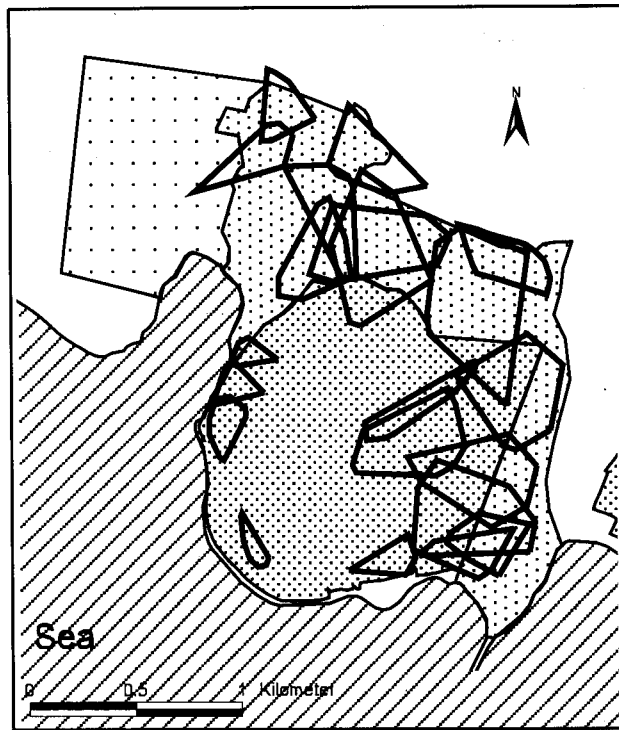


Figure 6. Locations of the 21 territories of marked male pheasants in the breeding season 1976.

### 5.3 Relation between territory size and density of territorial males

Determination of the total number of territorial males caused problems even though efforts in trapping, marking and observation were intense. On a yearly basis up to 23% of the registered males could not be classified with certainty as either territorial or non-territorial (see Table 5). The unclassified proportion included marked yearlings and unmarked birds; for analysis, all marked adult males were categorised as territorial.

When adding the estimated number of unmarked territorial males to all marked territorial males, the mean annual density of territorial males throughout the study period was 8.5/100 ha, varying between years from 6.5 to 11.7 (Fig. 7). These figures are minima, as part of the males with undetermined status probably were territorial. If, for instance, half of the "undetermined" males actually were territorial, this would increase the mean density to 9.7 territorial males per 100 ha, varying between 6.8 and 12.8 (Fig. 7).

Trapping efficiency may influence the calculations of densities. Thus, the introduction of a new trapping method in spring 1982 to supplement the already employed (see p. 12), obviously caused an increase in the relative number of marked adult males in 1982 and 1983 (Table 3).

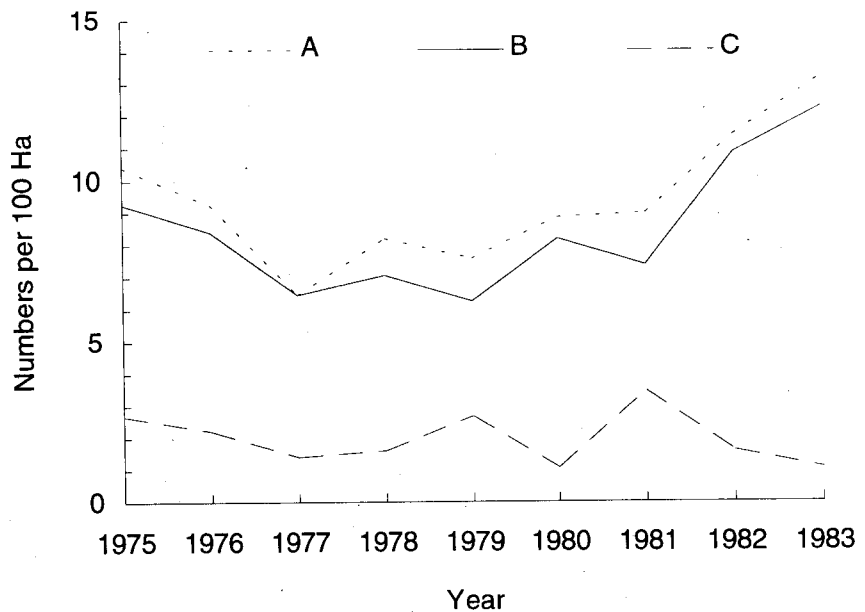


Figure 7. Densities of territorial and non-territorial males during 1975-83. A: territorial males + half of the "undetermined" males (see text); B: Territorial males; C: Non-territorial males.

The mean size of territories was significantly negatively correlated with the number of territorial males (Spearman Correlation Coefficient  $R_s = -0.76988$ ,  $p < 0.0152$ ), indicating that size of territories decreased with an increased number of territorial males (Fig. 8). The lower limit of the mean territory size seems to be 4-5 ha (Fig. 8).

#### 5.4 Overlap and stability of territories

The overall breeding season territories overlapped greatly, as exemplified by the 1976-season (see Fig. 6). But when the monthly occurrence of each territorial male was analysed, a diverging pattern emerged: the territory boundaries changed from month to month, resulting in less occurrence of overlap between territories on a monthly basis. A case story may illustrate this. In 1978 a 5-year-old male occupied a territory at the northern edge of the Hestehave forest (Fig. 9). Through the period of March to June the male was observed 37 times: 5, 13, 13, and 6 times in the respective months. Territory size and boundaries varied from month to month; in March and April the sub-territory was larger than in May and June. The overall breeding season territory was substantially larger than the monthly sub-territories. In March the male displayed territorial behaviour in the part of the territory that was situated in a winter-wheat field with 5-10 cm high vegetation. In April the territory was moved westward to a field of newly sown barley, an uncultivated area with shrub and grass, and the forest edge. The latter had now

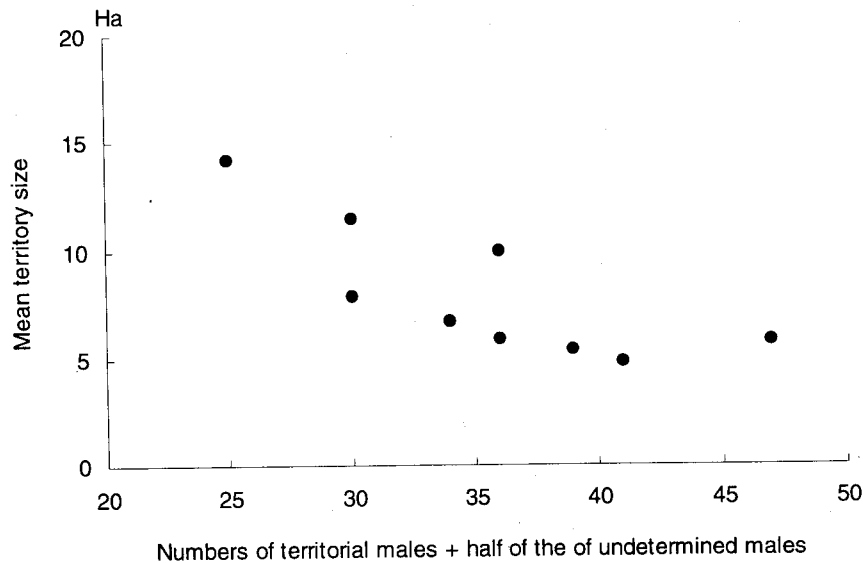


Figure 8. Mean territory size related to annual number of territorial males (including half of the "undetermined" males).

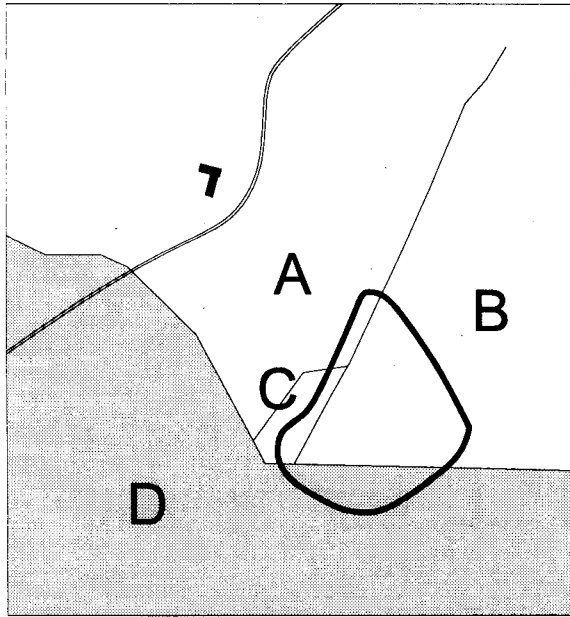
become the preferred habitat. In May the male was primarily observed in the barley field and in the uncultivated area. In June the male was almost exclusively observed in the barley field.

### 5.5 Territory fidelity from year to year

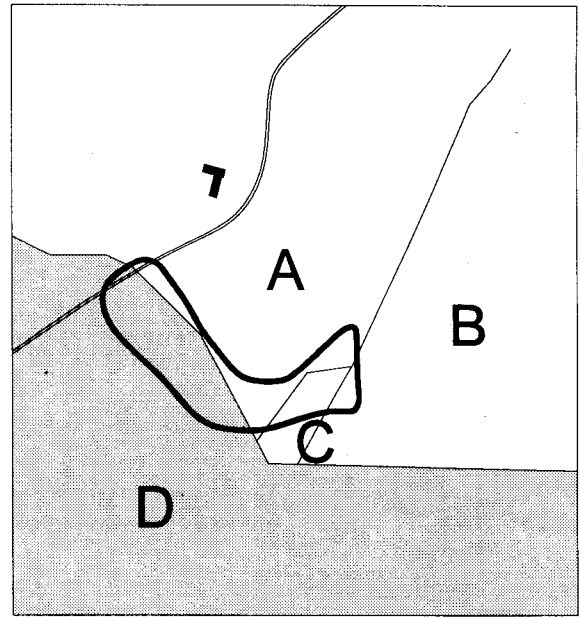
Males with defined territories survived and held territories during two or more consecutive breeding seasons on 62 occasions during the study period. Territories were defined for the successive breeding season for 43 of these; 12 males (28%) occupied the same territories in two successive years, 29 (67%) occupied partly the same, and 2 (5%) changed territory. One of the latter moved from a territory in the middle of the Hestehave forest to a vacant territory at the forest edge, including open fields. The other one which was displaced by a two year old male, established a territory in a habitat similar to the one it gave up.

Of 19 males for which territories were not determined the second year 12 (63%) were observed within or near the territory they occupied the previous season; all displayed territorial behaviour, and five were observed accompanying females. It thus seems likely that the 12 males occupied territories, but lack of observations prevented their ultimate determination. One of the remaining seven males may have shifted area. It was trapped on 6 March, 500 m away from the territory that was occupied the previous year. The remaining six males were not observed during the breeding season, but were recorded at later occasions.

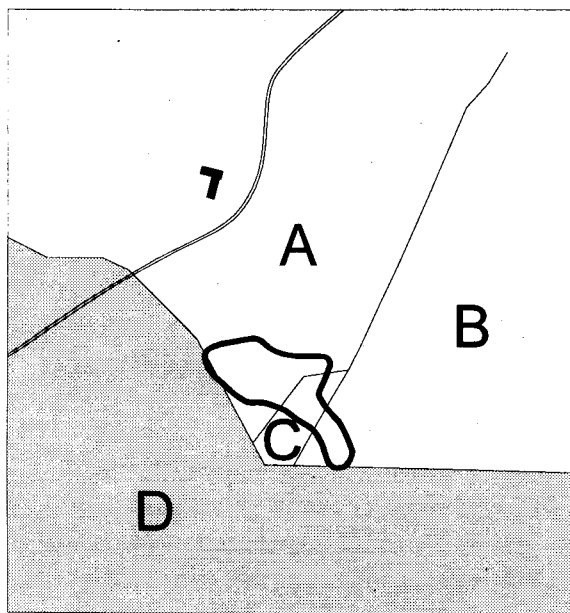
March



April



May



June

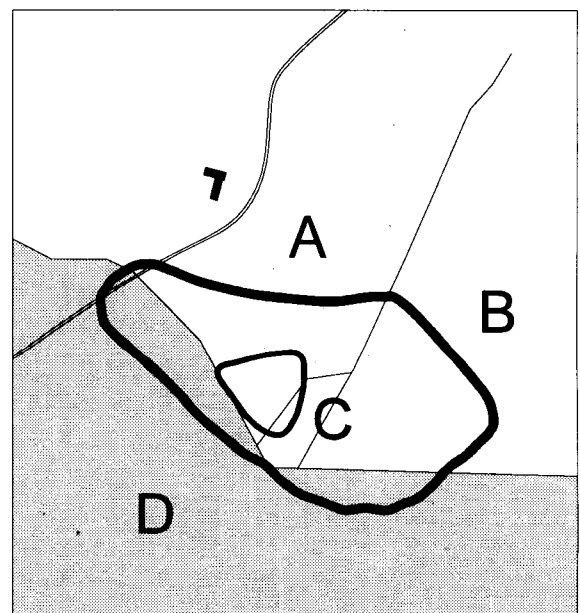


Figure 9. Territory plasticity during spring, exemplified by monthly location of territory of male no. 442070 in the period March to June 1978. The area encircled by the bold line in June indicates the overall season breeding range and includes spring barley (A), winter wheat (B), shrub and grass (C), and forest (D).



## 5.6 Size of female home ranges

In the period 1975-83 home range size of adult females during 1 March - 30 June were calculated in 60 cases for 54 different birds; 49 contributed for one year, 4 for two years, and 1 for three years. During the same period home range size of 61 yearling females was registered. Another 25 females which were also located 10 or more times were omitted from calculations of home range, as they changed home range during the breeding season (see below).

Home range sizes ( $\pm$  SD) of adult ( $7.1 \text{ ha} \pm 6.4$ ) and yearling females ( $9.8 \text{ ha} \pm 9.5$ ) (Table 7) did not differ significantly (Mann-Whitney U,  $p < 0.2584$ ). Spearman Correlation analysis showed no significant correlation between female home range sizes and the population size ( $R_s = -0.46667$ ,  $p < 0.2054$ ) or number of females present ( $R_s = -0.48333$ ,  $p < 0.1875$ ).

As for male territories, female home ranges were unevenly distributed and overlapped greatly.

Table 7. Mean size and standard deviation of female home ranges during 1975 - 1983.

Year	Adult females		Yearling females	
	Ha $\pm$ S.D.	N	Ha $\pm$ S.D.	N
1975	3.28 $\pm$ 2.38	10	6.81 $\pm$ 8.57	10
1976	7.51 $\pm$ 6.47	12	11.16 $\pm$ 8.68	12
1977	9.95 $\pm$ 8.27	12	15.10 $\pm$ 14.19	7
1978	4.56 $\pm$ 2.79	5	4.64 $\pm$ 2.50	5
1979	13.95 $\pm$ 5.02	2	10.02 $\pm$ 6.68	9
1980	8.20 $\pm$ 8.06	4	3.63 $\pm$ 0.38	3
1981	8.00 $\pm$ 6.28	10	13.38 $\pm$ 13.78	8
1982	9.23 $\pm$ 6.13	4	8.27 $\pm$ 5.27	3
1983	7.80	1	8.35 $\pm$ 10.14	4
1975-83	7.51 $\pm$ 6.35	60	9.82 $\pm$ 9.54	61

## 5.7 Female home range fidelity from year to year

Females for which home ranges could be determined for two or more successive years showed a high degree of fidelity to the site where they first settled: Of a total of 57 females, 24 (42%) occupied the same home range during two successive breeding seasons, 15 (26%) occupied partly the same, and 18 (32%) settled in a new range the following season. For nine of the 18 birds settling in a new range successive home ranges did not overlap at all; the distance between centres of the home ranges only exceeded 200 m in one case, when it was 500 m.

Home range fidelity did not differ between females being yearlings and females being two years or older in the first season that home range could be determined ( $\chi^2 = 2.25$ ,  $df = 2$ ,  $p > 0.30$ ).

## 5.8 Change of female home range

During the study period 4 adult (6.3%) and 21 yearling (25.6%) females changed their home range during the breeding season (Table 8), leading to the fact that a significantly higher proportion of yearling females than of adults changed home range ( $\chi^2 = 7.23$ ,  $df = 1$ ,  $p < 0.01$ ). The longest distance traversed in a change of home range was for a yearling which moved 1.500 m.

## 5.9 Presence of females in male territories

Territorial adult and yearling male pheasants were observed without females in 67% and 83%, respectively, of all records made during 1 March to 30 June (Fig. 10). The degree to which females were accompanied by territorial males varied throughout the breeding season (including July, Fig. 11). In early March territorial males were observed alone. Records of males accompanied by females increased from mid March and peaked in May when they made up more than 40% of the observations of territorial males. From late May the proportion decreased. The temporal distribution of females accompanied by territorial males varied from year to year. Termination of winter influenced the date for the first observation of females accompanied by males (Fig. 11).

During the first part of the breeding season females still concentrated in certain areas which meant that some males were seen with many females, whereas others were seen alone. These unstable spring groups were observed until the second half of April when the females dispersed; from the beginning of May more males were observed with smaller numbers of females. From this time females generally associated with specific territorial males. The highest

Table 8. Number of marked adult and yearling females which changed home range within the breeding season, 1975 - 1983.

Year	Adult females		Yearling females		All females	
	N <sub>1</sub>	N <sub>2</sub>	N <sub>1</sub>	N <sub>2</sub>	N <sub>1</sub>	N <sub>2</sub>
1975*	1	11	6	16	7	27
1976*	0	12	3	15	3	27
1977*	2	14	5	12	7	26
1978	0	5	1	6	1	11
1979	1	3	1	10	2	13
1980	0	4	0	3	0	7
1981	0	10	3	11	3	21
1982	0	4	2	5	2	9
1983	0	1	0	4	0	5
1975-83	4	64	21	82	25	146
% with shift	6.3		25.6		17.1	

N<sub>1</sub>: Number of females which changed home range.

N<sub>2</sub>: Total number of females with ≥ 10 observations during March - June.

\*: No control of fox.

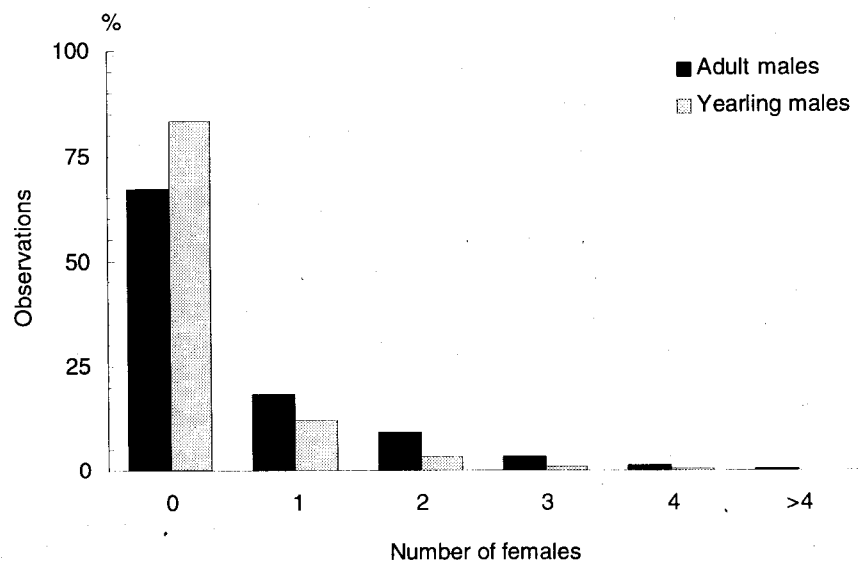


Figure 10. Relative proportions of observations, where territorial adult and yearling males were registered accompanying 0 - >4 females.

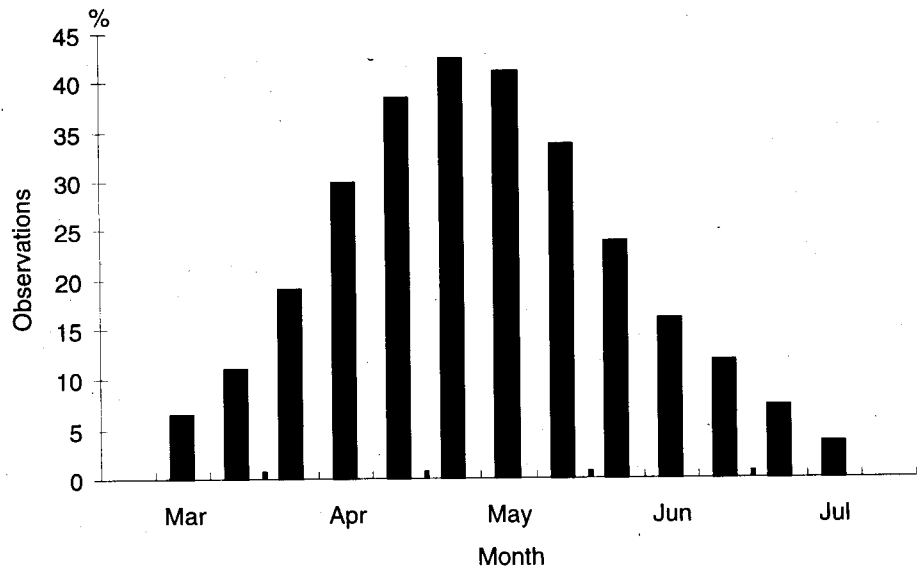


Figure 11. Mean frequencies of observations, where territorial males accompanied females during the period March to July 1975-83.

number of females simultaneously observed with a territorial adult or yearling male was 12 and 7, respectively (Fig. 12). During the total breeding season 7.1% of the adult males and 10.7% of the yearling males were not at all seen with females. The total number of females with which the individual male was seen throughout the breeding season was considerably higher than the maximum number simultaneously observed accompanying a male: a maximum of 22 females was recorded for one male through the breeding season in 1981 (Table 9).

The mean number ( $\pm$  SD) of females observed accompanying adult and yearling territorial males was  $2.5 \pm 1.95$  and  $1.8 \pm 1.42$ , respectively (Table 10); the difference was significant ( $\chi^2 = 8.746$ ,  $df = 3$ ,  $p < 0.033$ ; three or more females pooled). For the whole breeding season the mean number of different females recorded with adult and yearling territorial males was  $3.9 \pm 3.6$  and  $2.9 \pm 2.73$ , respectively (Table 10). This difference was not significant ( $\chi^2 = 2.124$ ,  $df = 3$ ,  $p < 0.547$ ; three or more females pooled).

Of the females adjoining territorial males, adult females accompanied up to six different males during the same breeding season, averaging 1.9 males. Yearling females accompanied up to seven different males, averaging 2.5 (Table 11, Fig. 13). In all breeding seasons yearling females were seen together with significantly more different territorial males than adult females ( $\chi^2 = 20.884$ ,  $df = 4$ ,  $p < 0.001$ ; five or more males pooled). Among the adult and yearling

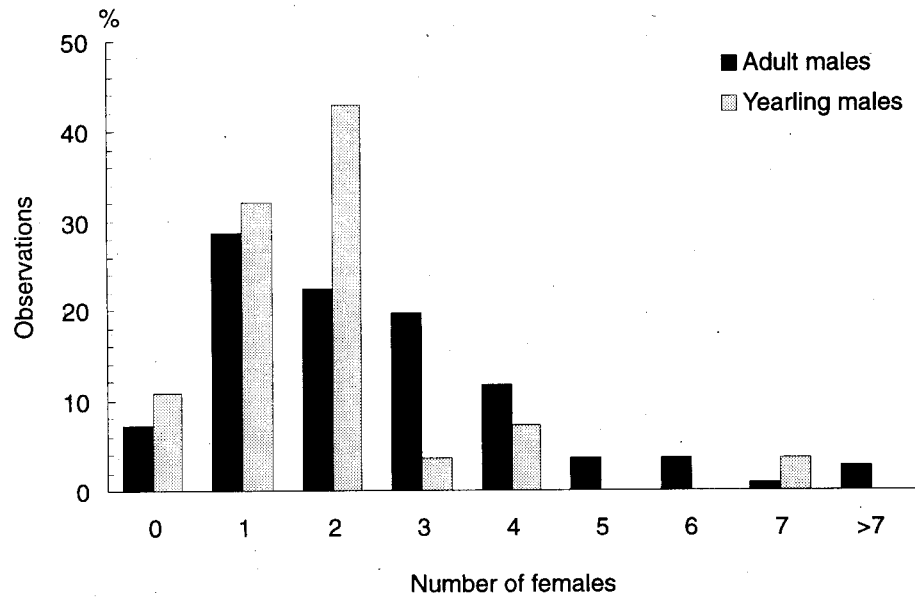


Figure 12. Relative distribution of the highest number of females seen simultaneously accompanying the single territorial male during the period March to June 1975-83.

Table 9. Number of female pheasants recorded with territorial adult and juvenile males during the breeding season;

A: The highest number of females recorded simultaneously with a single territorial male.

B: The highest total number of different females served in company with a single territorial male during the breeding season.

Year	Adult males		Yearling males	
	A	B	A	B
1975	9	14	3	3
1976	8	11	3	5
1977	6	14	-	-
1978	6	11	2	4
1979	4	8	4	9
1980	4	9	2	5
1981	12	22	7	13
1982	5	8	4	5
1983	7	12	2	3

Table 10. Mean numbers of female pheasants seen in company with territorial males.

A: Mean of the highest numbers of females observed in company with territorial males.  
 B: Mean number of different females observed in company with territorial males during the period March till June.

Year	Number of adult males	Number of females	Number of different females	Number of yearling males	Number of females	Number of different females
		A	B		A	B
1975	15	2.9	4.1	1	3.0	3.0
1976	18	2.5	3.6	3	1.7	2.7
1977	13	2.3	3.9	0	-	-
1978	13	2.2	3.7	4	1.2	2.3
1979	6	2.7	5.3	5	2.2	4.2
1980	14	1.9	3.4	1	2.0	5.0
1981	6	4.5	7.3	4	2.8	4.8
1982	12	2.7	3.8	3	2.3	3.0
1983	15	2.1	2.9	7	1.0	1.1
1975-83	112	2.5	3.9	28	1.8	2.9

females 79.4% and 56.4%, respectively, accompanied one or two territorial males; two adult and two yearling females were observed in six or seven different male territories during the same breeding season.

### 5.10 Fidelity of females to territorial males during successive years

Nineteen adult females which stayed within the same area/home range for at least two successive years, had the opportunity to associate with the same surviving territorial male during more than one season. Only four (21%), however, did so; three were observed during two successive breeding seasons, and the fourth in four seasons. All four associated with adult males during the first breeding season.

Of yearling females 28 had similar opportunities to associate with the same territorial male during at least two successive seasons; 13 (46%) were observed with the same male, 12 during two seasons, and one during three. Of the 13 accompanying males, 10 were adults and three were yearlings during the first breeding season; two of the yearling males were territorial, one non-territorial.

Table 11. Number of different territorial males associated with single females during the breeding seasons of 1975 to 1983.

Adult females							
Year	Number of territorial males						Mean
	1	2	3	4	5	6	
1975	12	11	1	0	0	0	1.5
1976	6	9	5	1	0	0	2.1
1977	4	3	5	2	0	0	2.4
1978	10	4	0	1	0	0	1.5
1979	5	7	1	0	0	1	2.0
1980	8	8	1	1	0	0	1.7
1981	6	9	2	2	0	1	2.2
1982	3	3	3	0	0	0	2.0
1983	4	4	1	2	0	0	2.1
1975-83	58	58	19	9	0	2	1.9
%	39.7	39.7	13.0	6.2	0.0	1.4	

Yearling females								
Year	Number of territorial males							Mean
	1	2	3	4	5	6	7	
1975	7	15	6	0	0	0	0	2.0
1976	5	3	6	3	3	1	0	3.0
1977	1	3	4	3	2	0	0	3.2
1978	7	2	4	2	0	0	0	2.1
1979	9	7	2	3	1	0	1	2.3
1980	4	5	3	0	0	0	0	1.9
1981	3	8	6	1	2	0	0	2.6
1982	0	2	3	2	1	0	0	3.3
1983	6	1	3	3	3	0	0	2.8
1975-83	42	46	37	17	12	1	1	2.5
%	26.9	29.5	23.7	10.9	7.7	0.6	0.6	

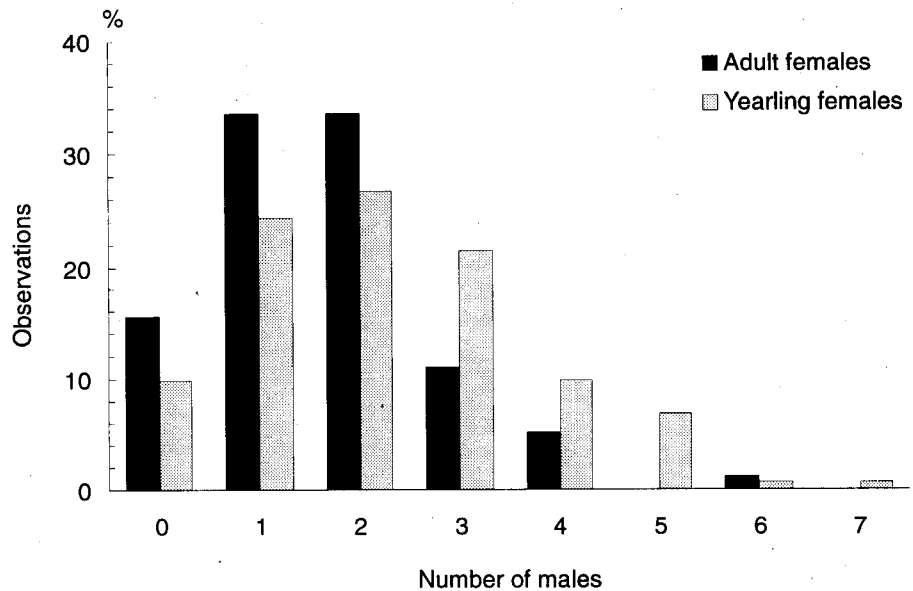


Figure 13. Relative distribution of the number of different territorial males, with which adult and yearling females associated during the period March to June 1975-83.

## 6 Discussion

### 6.1 Territoriality in male pheasants

Male pheasants which are dominant in winter flocks seem to establish their territories earlier than males of lower social rank and in the most preferred habitats (Collias & Taber 1951, Göransson 1980, 1984, Fröberg & Helgée 1985). Collias & Taber (1951) and Göransson (1984) observed that the high ranking males often were the oldest ones; yearlings occupied their territories later in the season than did older males (Göransson 1984), and in less preferred habitat, as the highest quality territories were already taken (Fröberg & Helgée 1985). Neither the social rank of males in winter flocks nor habitat quality parameters were investigated for the Kalø pheasant population.

In most pheasant localities excessive areas of less preferred habitat are available for territory-acquisition, but some males apparently prefer not to occupy low-quality territories, which females do not visit. Instead such non-territorial males stay in or close to other male high-quality territories, testing territory-holders and looking for a chance to mate with harem members. Observations of non-



territorial males copulating with females have been reported by Taber (1949) and Burger (1966); Göransson (1980) observed unsuccessful mating attempts by non-territorial males.

As in the present study non-territorial males have been reported from several other pheasant populations (Burger 1966, Swenson 1978, Robertson & Whelan 1987, Hill & Ridley 1987, Smiddy 1988, Hill & Robertson 1988a, Koubek & Kubišta 1990a, Robertson et al. 1993, plus those mentioned below in this paragraph). According to Taber (1949) and Collias & Taber (1951) these males are usually birds of low rank in the winter groups. As in the present study, where no healthy adult males were registered to be non-territorial, only yearling males were reported to be non-territorial by Lachlan & Bray (1976) and Göransson (1980, 1984). But, Ridley (1983, referred to in Hill & Robertson 1988b) found that 13% of non-territorial males were adults. Occurrence and number of non-territorial males seem to be associated with the density of males in the population (Taber 1949, Burger 1966, Lachlan & Bray 1976, Göransson 1980, Hill & Robertson 1988a, Robertson et al. 1993). While the density of territorial males within study areas may be fairly constant from year to year, the density of non-territorial males seems to correlate with male density, as demonstrated by Hill & Robertson (1988a) and Robertson et al. (1993) in populations with a highly variable male density in succeeding years mainly due to variations in number of released birds. Gates & Hale (1974) did not at all identify non-territorial males in their low density population.

## 6.2 Size of male territories and home ranges

At the Kalø study area the mean territory size for the whole breeding period was 8.0 ha. This figure is based on data from both adult and yearling males (see Table 5), as the territory sizes did not differ significantly between the two age groups. Smaller territories were observed in most other studies. In North America the mean size varied from 1.2 to 5.3 ha (Twining 1946, Taber 1949, Ball 1950, Burger 1966); in the UK and Ireland it varied between 1.8 and 4.5 ha (Lachlan & Bray 1973, 1976, others, see Hill & Robertson 1988b); in Italy, Cesaris & Meriggi (1985) recorded a mean territory size of 0.85 ha. Göransson (1980) and Fröberg & Helgée (1985) reported mean territories of 5.2 ha and 8.7 ha, respectively, from the same area in southern Sweden. Mean territory size in a Polish population was 6.1 ha (Wasilewski 1986), and in a Czechoslovak population it was 4.1 ha (Koubek & Kubišta 1990a).

The most important reason for the variations in territory size may be the period taken into consideration. Ridley & Hill (1987) only included observations from 1-10 April for calculations of territory size, assuming that most territories at that time were established and well defined; Koubek & Kubišta (1991), on the other hand,

reported of major changes in territory size during three distinct periods between 20 March and 20 May. The variation in presented territory size may furthermore be ascribed the diversity in methods of collection and treatment of data. Positions of territorial males are obtained using visual observations or triangulations (records of crowing calls, or radiotelemetry). Calculations of territory size also vary; most authors have used the convex polygon method, but Wasilewski (1986) used the elliptic range model. Additionally, some of the variation in territory size may have been influenced by differences in the habitat quality; habitats, however, are difficult to compare.

Territorial male density may also influence territory size. As in the present study, where mean size of territories was significantly negatively correlated with the number of territorial males (Fig. 8), smaller territories were observed to correlate with higher territorial male density by Burger (1966) and Lachlan & Bray (1976, although not significantly), but not by Göransson (1980). Ridley (1983, referred to by Hill & Robertson 1988b), found that territory size declined when the proportion of the boundary shared between a male and his neighbour increased.

Territory size was neither correlated to age of males in the Kalø population nor in Göransson's (1980) population, but Ridley & Hill (1987) recorded an increase in territory size during the second year for eight males watched in two consecutive years.

Non-territorial males in the Kalø study area were resident in home ranges considerably larger than territories (Table 6). Their ranges frequently overlapped one or several territories, and non-territorial males were tolerated to some degree by territory holders. In most cases, however, they were chased off as soon as they approached the harem (pers. obs., and Jørgensen 1977). This may have been the main reason why non-territorial males were often observed moving several hundred metres during one day. These results agree with the results obtained by Taber (1949), Burger (1966), and Göransson (1980, 1984), and with those of Grahn et al. (1993a), who found that the most "attractive" males (to females) showed a higher degree of territoriality, i.e. they made shorter daily movements, had smaller ranges, and crowed more frequently. Thus, non-territorial males make longer daily movements in larger home ranges.

### **6.3 Stability of territories**

Each territorial male monopolises an area throughout spring and early summer. In the 1940s and 1950s several authors, however, doubted whether pheasant males held territories with clearly defined boundaries (Wight 1945, Twining 1946), or held territories or 'crowing areas' that were plastic and subject to frequent readjustments

(Leedy & Hicks 1945, Baskett 1947, Taber 1949, Ball 1950, Robertson 1958). Kozłowa (1947) observed strictly defined "cruising routes" within each male domain in the pheasant's native Tadjikistan, but did not regard this as a territory, because she never observed a male chasing an intruder.

Later on, much stability of territory spacing has been reported. In some populations, territories with well defined boundaries occurred in similar areas from year to year (Lachlan & Bray 1973, 1976, Göransson 1980, Koubek & Kubišta 1990a). Almost identical territories were occupied repeatedly, especially in "central areas" preferred by the pheasants, and even with new males in succeeding years (Göransson 1980, Koubek & Kubišta 1990a). Well defined boundaries may be a matter of density (Burger 1966, Gates & Hale 1974, Göransson 1984). Gates & Hale (1974), in their sparse population, defined the area used by a territorial male as its home range, but found that males fought over infringements of an 'individual distance' in a 'moving zone of intolerance', that was not confined to a certain defended area (= territory).

Although the overall breeding season territories overlapped greatly in the present study, the territorial boundaries changed according to month (see Fig. 9), resulting in much less overlap of neighbouring territories. Similar changes of territory boundaries during the breeding season were reported by Burger (1966) and Koubek & Kubišta (1991), as well as by the above mentioned authors from the 1940s and 1950s. These changes may result from growth of herb vegetation (Koubek & Kubišta 1991) and farmland crops, movements of females, pressure by males, death of neighbouring male (expansion of territory, see also Göransson 1980) (Taber 1949, Burger 1966), and farming practises (Taber 1949, Robertson 1958). In the Kalø population, observations indicated that movements of females and habitat changes due to growth of vegetation and field crops were the major factors responsible for changes of territory boundaries.

#### **6.4 Territory fidelity from year to year**

Males showed a high degree of faithfulness to the sites in which they first settled; while 41 out of 43 territorial males occupied the same or partly the same territory in consecutive years, complete shifts of territory from one year to the next were only observed for two males. Similar high fidelity was observed by Lachlan & Bray (1976), who found that none of 21 territorial males took up a new territory in successive springs. Göransson (1980, 1984) reported that a male changed its territorial site in only two out of 36 occasions over a period of six years. A British study (Hill & Ridley 1987) recorded a mean distance of 66 m between consecutive spring ranges of adult males at Fulwell, England.

When non-territorial yearling males in our study area became territorial in the succeeding spring they established their territory within the home range of the previous year. Gates & Hale (1974) concluded from their data that males remained faithful throughout their adult lives to the area in which they first bred, and this conclusion is obviously valid for our results as well.

## 6.5 Home range of females

The mean size of home ranges calculated for the whole breeding season was larger for yearling females ( $9.8 \text{ ha} \pm 9.5$ ) than for adults ( $7.5 \text{ ha} \pm 6.4$ ), although not significantly (Table 7). This may indicate that yearlings moved more than adult females, and thus seem to have been less attached to a specific area (or male) than adults. Yearlings are reported to move further than adults during the period of dispersal from winter flocks to their breeding ranges (Taber 1949, Gates & Hale 1974, Hill & Ridley 1987, Hill & Robertson 1988b). In general, breeding activity of adult females precedes that of yearlings, as older females are the first to disperse from winter flocks and among the first to enter harems (Taber 1949, Robertson 1958, Gates & Hale 1974). According to Collias & Taber (1951) age is associated with dominance; Gates & Hale (1974) observed that adult females competed better for space than juveniles, indicating that many yearlings were being buffeted from territory to territory through intrasexual interactions in harems. The period of dispersal and harem formation is included in our overall breeding season home ranges, and thus larger home ranges of the yearlings may reflect increased movements caused by social interactions.

The mean breeding home range of the females at Kalø compares well with the mean of breeding ranges of  $12.5 \text{ ha}$  obtained by radiotelemetry of females in South Dakota, USA (April-August and June-August, Kuck et al. 1970), and means of female spring and summer ranges of  $7.8 \text{ ha}$  and  $11.3 \text{ ha}$ , respectively, in Texas, USA, where monthly ranges during March - June were  $6.8$ ,  $9.0$ ,  $8.2$ , and  $5.5 \text{ ha}$  (Whiteside & Guthery 1983). In another area in South Dakota, mean female range through June-October was  $36.4 \text{ ha}$  (Hanson & Progulske 1973). Mean home range of radio-marked females recorded between 20 March and 11 April in an Irish population was  $28.4 \text{ ha}$  (Robertson & Whelan 1987). In England, female spring home ranges averaged  $2.9 \text{ ha}$  (Ridley & Hill 1987). It does not, however, seem fruitful to compare these home ranges directly, as none of them was calculated for exactly the same period of female breeding activity. Estimates of home ranges for the whole breeding season, or as at Kalø for the period March - June, yields no information on the variation during spring and summer in the use of an area by females, according to time of dispersal, harem formation, nest building, incubation, and rearing of the brood.

Coinciding with nest establishments Gates & Hale (1974) observed home range adjustments of females which seemed to reflect a dispersal from the centres of harem activities to activities at the onset of egg-laying; 80% of the females nested in ranges in which they had not been previously observed during the pre-nesting period. In a study in Wisconsin, USA, 94% of the females established their nests on the peripheries of the home ranges they had occupied during the preceding 30 days (Dumke & Pils 1979). In the same study, 82% of re-nesting females favoured the periphery of the ranges occupied between 1st and 2nd nest; initial nests were also placed apart from the activity centres of associated males. Nine radiomarked females at Fulwell, England, all nested on the periphery of their daily feeding ranges (Ridley & Hill 1987).

Hill & Robertson (1988b), defining a home range for the laying period in a British study, obtained an average laying range of females of 16 ha, 9 ha smaller than the average pre-nesting range. Also, they found the size of the range during the laying of a re-nest clutch to be smaller (11 ha) than that of the first nest (18 ha). They stated that there is generally no relationship between the size of pre-nesting ranges and the laying ranges. In 63% of their laying ranges the nest was placed on the edge of the range. Furthermore, during feeding bouts throughout the incubation period, females avoided the nest site area. This probably is a strategy that reduces the risk of predation to the female and to the clutch (Hill & Robertson 1988b).

Average size of home ranges of females with broods during the first two weeks of a chicken life ranges between 2 - 11 ha (Kuck et al. 1970, Hanson & Progulské 1973, Warner 1979, Hill & Robertson 1988b); Warner (1979) reported an exponential increase in brood ranges during the first nine weeks, up to about 50 ha.

## 6.6 Home range fidelity from year to year

Females in our study area showed much faithfulness to the home range they had occupied in the preceding breeding season; in total only 16% settled in non-overlapping ranges, although still close to the former range except in one case. During spring dispersal in Wisconsin, 85% of the adult females returned to the same breeding areas as the year before (Gates & Hale 1974), and the authors concluded that females typically returned each spring to the same home ranges provided that the areas themselves remained suitable for nesting. Göransson's (1980) limited data on this issue ( $n = 4$ ) indicated that females return to the same territory or the same surviving male in two consecutive breeding seasons. Hill & Ridley (1987) recorded a mean distance of 169 m between consecutive spring ranges of adult females at Fulwell, England.

## 6.7 Shifts of female home ranges

Yearling females in the Kalø study area shifted home range during the breeding season four times as often as adults (Table 8). In the first three years of the study when fox control was not exercised, 8% and 33%, respectively, of adult and yearling females shifted home range. In the following six years with fox control 4% and 18% shifted home range. Predation by foxes may thus have been responsible for up to half the shifts of home range, and yearling females may be especially vulnerable to disturbance caused by predators. In our study more than half (51.7%) the annual mortality of females occurred during April - June (unpubl. data). Göransson (1980) and Dumke & Pils (1979) also recorded a high female mortality during April - June and found that foxes were responsible for the main part. Grahn (1993) reported an average breeding season mortality of females of 26%, peaking in late May; the main predators were raptors and red fox. In six pheasant studies reviewed by Hill & Robertson (1988b), avian and mammal predators were responsible for 20 - 57% of nest losses; in some of the studies agricultural disturbances accounted for 9 - 37% of the nest loss. Nest predation accounted for 44% of clutch fates for wild females in South Dakota (Leif 1994). In Wisconsin predation was the primary cause of disruption of first nest clutches whereas hay mowing was responsible for primarily re-nest clutches (Dumke & Pils 1979).

## 6.8 Relationship between male and female pheasants

Territorial males attract females to their territories by crowing and courtship displays (e.g. Hill & Robertson 1988b). As implied in a polygynous mating system, some males are better at attracting females than others; in our study area several males that established a territory have probably even totally failed breeding as they were never observed accompanying a female. Mating opportunities are thus distributed unevenly across the male population (Ridley & Hill 1987). The higher maximum and mean numbers of females seen with adult males than with yearlings (Table 10) indicate that adult males were more successful in attracting females. Similar results were reported by Göransson (1980) and Ridley & Hill (1987).

There is growing evidence that the female choice of mate is based on secondary sexual characters and ornaments, such as spur length (von Schantz et al. 1989, Göransson et al. 1990, von Schantz et al. 1994), tail length (Geis & Elbert 1956, Mateos & Carranza 1995), length of ear tufts and presence of black points in the wattles (Mateos & Carranza 1995), all or some of which seem to be reliable indicators of physical condition and viability. Females selecting long-spurred males as their mates showed an increased production of hatchlings and surviving offspring, the spurs both being an 'hon

est' signal of phenotypic condition and genetic fitness (von Schantz et al. 1994).

The average group sizes of 2.5 and 1.8 of females adjoining adult and yearling males, respectively (Table 10), correspond to observed means of harem sizes between 1.2 and 4.9 in other studies (Twining 1946, Taber 1949, Robertson 1958, Swenson 1978, Göransson 1980, Fröberg & Helgée 1985, Robertson & Whelan 1987, Ridley & Hill 1987, Hill & Robertson 1988a, Koubek & Kubišta 1991, Anon. 1992). Means of harem sizes during the whole breeding season may not, however, be reliable indicators of male attractiveness. During the first part of the breeding season females often change territories, and they may choose between several males before deciding upon a certain male. Therefore, Grahn et al. (1993a) only used harem sizes from the period between the median day of clutch initiation until 30 June to estimate male attractiveness, and 'harem' size was defined as the average number of females per day detected by radio-tracking within 100 m of the males. The most attractive males in their study showed a higher degree of territoriality; i.e. they crowded more frequently (see also Winterbottom 1993), and made shorter daily movements in shorter ranges than did less attractive males.

Yearling females moved over larger areas than adults (see pp. 25-27, Tables 7 and 8), this probably being the reason why yearling females were observed with significantly more territorial males than adults (see Table 11). In the Kalø study area less than a quarter of adult females and less than half the yearling females who had the opportunity, associated with the same territorial male during two or more successive breeding seasons (p. 30), totalling 36% (n = 47). This is less than could be expected given a home range fidelity of females from year to year of 68%, and a territory fidelity of males of 95% (with more than 25% overlapping home ranges, resp. territories, see p. 26 and p. 23). These findings may contribute a modification to the suggestions made by Göransson (1980) and Ridley & Hill (1987) on the basis of limited data (n = 4 and 9, respectively) that females are loyal to surviving partners in successive years.

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