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Female age and breeding performance in a cyclic population of black grouse *Tetrao tetrix*

Arto Marjakangas & Laura Törmälä

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The breeding performance in yearling and adult female black grouse *Tetrao tetrix* was studied in a 6-7 year cyclic population during 1989-93 in central Finland. Eighty yearlings and 108 adults, radio-marked in late winter, survived until the breeding season. Adults were larger, had more body mass at capture, initiated laying earlier and had larger eggs and clutches than yearlings. Yearlings and adults lost 11.8 and 20.9%, respectively, of their first nests to egg predators. Hatching dates and success of eggs were similar for both age classes. The proportion of females losing the entire brood was 32% for yearlings and 27.1% for adults. Brood size in late summer and number of chicks produced per female initiating breeding did not differ between age classes.

Key words: black grouse, breeding performance, female age, population dynamics, radio-telemetry, Tetrao tetrix

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It is a common pattern among birds that young individuals start breeding later in the season, lay fewer eggs, and fledge fewer young than their older conspecifics (e.g. Sæther 1990). Several mechanisms, or a combination of mechanisms, may explain the age-specific performance. For instance, young individuals may be less experienced in food acquisition, or they may have lower physiological efficiency, lower social status, or poorer parental skills than older birds (Curio 1983, Sæther 1990, Martin & Sæther 1994). Young birds may also restrain reproduction, or fecundity and longevity may correlate (Curio 1983, Sæther 1990). In the latter case, breeding performance of individual birds does not change with age.

Females of grouse species (Phasianidae, Tetraoninae) mostly breed as yearlings (Johnsgard 1983, Hannon & Smith 1984, Bergerud 1988). Age-specific breeding performance is more common in promiscuous than in monogamous grouse species (Hannon & Smith 1984, Bergerud 1988). Most studies, however, have focused on nesting parameters, while data on chick production are scarce (Redfield 1975, Keppie 1982, Hannon & Smith 1984, Myrberget 1986).

The black grouse *Tetrao tetrix* is a promiscuous lekking grouse species distributed over central and northern Eurasia (Johnsgard 1983). Black grouse prefer to inhabit early successional stages of boreal forests (Swenson & Angelstam 1993). Willebrand (1992) showed a dramatic age-specific difference in chick production in female black grouse in Sweden: adults fledged about 10 times more chicks per female than yearlings. A smaller difference was observed in southern central Finland (Valkeajärvi & Ijäs 1994). Willebrand (1992) suggested that the large difference in age-specific breeding performance was caused by unfavourable habitat structure in his study area, and that the difference might be less pronounced in more suitable habitats. There was no difference in selection of nesting habitat between yearling and older female black grouse (Brittas & Willebrand 1991).

Black grouse show 6-7 year cycles in numbers in most of Finland (Lindén 1988, 1989, Lindström, Ranta, Kaitala & Lindén 1995). Lindén (1989) suggested that a non-stable age structure, together with differential breeding performance of yearling and adult females, might have an important role in these cycles. Recently, Lindström et al. (1995) showed that population age-structure is unlikely to yield cycles. However, using a model with delayed density-dependence in breeding success and differential performance of yearlings and adults, Lindström (1996) was able to produce population dynamics closely resembling those observed in the Finnish black grouse. Thus, it is important to know the age-related breeding performance of black grouse.

We assessed age-specific breeding performance in female black grouse from populations fluctuating in 6-7 year cycles (Marjakangas 1995). This paper presents data on mass, size, timing of nesting, clutch and egg size, nest loss, hatching success, brood loss, fledging success, and brood size of radio-marked yearling and adult female black grouse. Timing of nesting may be important because early-nesting females may be more likely to renest if their first nests are destroyed by predators (e.g. Hannon, Martin & Schieck 1988). Egg size is important because more viable chicks may be produced from larger eggs (e.g. Moss, Watson, Rothery & Glennie 1981).

Study areas

The study was conducted during 1989-93 south of Kajaani in eastern central Finland (~ 64°N, 27-28°E). Female black grouse were radio-marked each year at 1-4 sites, 5-10 km apart. The terrain is hilly or slightly undulating (125-350 m a.s.l.) and the major habitat types were forests and bogs. Forests were dominated by Scots pine *Pinus sylvestris* (76%), interspersed with Norway spruce *Picea abies* and deciduous trees, mostly birch *Betula pubescens* and *B. pendula* (Aarne 1995). Bogs (mostly pine bogs) comprised 45% of the forestry land area, and 64% of the bogs had been drained for forestry (Aarne 1995). Forests were mostly relatively young, and clear-cuts and plantations were common. The ground layer was dominated by bilberry *Vaccinium myrtillus* and lingonberry *V. vitis-idaea* in forests and bog whortleberry *V. uliginosum* and Labrador tea *Ledum palustre* in bogs.

Female black grouse were also radio-marked in two other study areas in 1989, Tyrnävä (~65°N, 26°E) and Ylivieska (64°N, 25°E) in western central Finland. The terrain in Tyrnävä and Ylivieska was mostly flat, elevated 20-60 and 75-125 m a.s.l., respectively. Birch was more abundant and bogs covered a higher percentage of the area than in Kajaani (Aarne 1995).

In 1989, females were tracked within 10-15 km from the capture sites in each study area. During 1990-93, with improved searching techniques, the area where nests of radio-marked females were located, covered 1,000-1,500 km^2.

Methods

Radio-marking and tracking

Each capture site was a winter feeding station installed on an open bog and supplied with oats for black grouse. Winter feeding is a game management effort carried out by hunters in southern and central Finland. Feeding stations effectively attract individual black grouse within a radius of 2-3 km (Valkeajärvi & Ijäs 1989). Black grouse visiting feeding stations remain shy and also feed on natural winter foods (Marjakangas 1992). Thus, black grouse captured at feeding stations constitute a representative sample of the local population.

Females were captured in wire-netting traps baited with oats during mid February to early April each year. Birds were weighed to the nearest 5 g with a spring scale, and wing length was measured in mm with the wing flattened and straightened. The birds were classified as yearlings (hatched the previous season) or adults on the basis of the shape and pigmentation of the ninth and tenth primaries (Helminen 1963). They were marked with a numbered aluminium leg band and fitted with a 17-g necklace radio transmitter (1.6-2.2% of body mass) with an expected life time of 6-10 months and released immediately after marking. Necklace radio transmitters weighing 2-3% of body mass are preferable to backpacks for gallinaceous birds (Marcström, Kenward & Karlbom 1989).

Female black grouse were located once a week by triangulation using portable receivers and hand-held and vehicle-mounted 4-element yagi-antennas. When consecutive locations indicated no movement, we approached birds until they either flushed or their remains were found. The disappearance of many females during breeding dispersal in April resulted in considerable loss of data in 1989, because tracking was restricted to a radius of 10-15 km around the capture sites. In 1990-93 missing hens were located from aircraft following Kenward (1987) over an area of 60 × 60 km, with some found at distances of 20-35 km from the capture site (Marjakangas, Aspegren & Kyllönen 1991).

Nests were mostly located at the onset of incubation. Eggs were counted and numbered, and length and breadth (maximum diameter) were measured with calipers to the nearest 0.05 mm. We tested 2 or 3 eggs from each clutch in water to identify incubation stage (Westerskov 1950). The presence of females at the nest was checked by triangulation once or twice a week, and usually two more visits were made to ascertain nest fate. The most important nest predator was the red fox *Vulpes vulpes* (Marjakangas 1996). Other potential nest predators in the study areas were raccoon dog *Nyctereutes procyonoïdes*, pine marten *Martes martes*, badger *Meles meles*, mink *Mustela vison*, short-tailed weasel *M. erminea*, least weasel *M. nivalis*, brown bear *Ursus arctos*, red squirrel *Sciurus vulgaris*, raven *Corvus corax*, hooded crow *C. corone*, jay *Garrulus glandarius* and black-billed magpie *Pica pica*. Females that lost their first nests were flushed once a week to detect possible renests.

Nests were visited after hatching and unhatched eggs and dead chicks were recorded. Hens with young chicks were located by triangulation at least once a week, and interference was minimised. Females were flushed in late July - early August to estimate brood size. We believe our data on brood size to be reliable, because black grouse broods tend to crouch when approached (Brittas & Karlbom 1990), and we carefully searched an area of at least 25 m around the point where the female was flushed. If we were uncertain of brood size, the brood was relocated and flushed the next day.

Data analysis

The date of nest initiation (laying date) was calculated as

$$y = x - 1.8(a - 1),$$

where y = date of nest initiation (Julian date), x = date of the commencement of incubation, and a = clutch size. The laying interval was assumed to be 1.8 days (8 eggs/12-13 days, Siivonen 1957). Date of commencement of incubation was estimated by backdating after assessing the stage of incubation using egg flotation (Westerskov 1950, accurate for the first eight days of incubation), or by backdating from hatching dates, assuming an incubation period of 25 days (Klaus, Bergmann, Marti, Müller, Vitovic & Wiesner 1990). Egg volume was used as an estimator of egg size, and was calculated following Hoyt (1979):

$$V = kLB^2$$

where V = egg volume (ml), L = length and B = breadth of the egg (cm) and k = constant (function of egg shape), 0.51 for black grouse (Lindén 1983).

A nest was considered totally lost when the eggs had disappeared or were broken, or when the female abandoned her partially destroyed clutch. Partial nest loss meant that the female continued incubating her reduced clutch. The nests of 10 hens killed during incubation, one nest destroyed by man, and one abandoned for unknown reasons were excluded from the nest survival analysis.

Hatching success was expressed as the proportion of chicks per clutch leaving the nest after hatching. Females were considered to have lost their broods if none of the chicks that left the nest, either first or renest, survived until late July - early August. Fledging success was expressed as the proportion of chicks leaving the nest that survived until late July - early August.

Factorial analysis of variance was used to test for differences between age classes and years when data were distributed normally and had homogeneous variances. Proportions (hatching and fledging success) were normalised prior to testing using arcsin-transformation. Otherwise, non-parametric tests (Kruskal-Wallis test, Mann-Whitney U test) were used. Categorical variables were tested using Chi-square tests of goodness of fit and independence or two-tailed Fisher's exact test. Data were pooled over years and tested for differences between age classes using 2 × 2 contingency tables. Pooling is justified after testing for heterogeneity (Zar 1984) between years. However, we could not use this procedure because some annual data sets had insufficiently large frequencies for a Chi-square analysis (Zar 1984). Therefore, we first tested for between-year differences within age classes and, if none existed, we pooled data over years and tested for differences between age classes using 2 × 2 contingency tables. The sample size and thus, statistical power, is low in some of the comparisons.

Table 1. Morphometric characteristics and hatch dates of first nests of yearling and adult female black grouse in central Finland, 1989-93.

		Yearlings			Adults		
Variable	Year	N	mean	SD	N	mean	SD
Body mass, g	1989	6	848.3	49.6	10	894.0	34.0
	1990	23	884.6	41.2	26	926.3	46.8
	1991	12	884.2	46.4	36	935.7	39.2
	1992	22	862.5	37.1	21	934.0	42.0
	1993	16	873.8	37.0	15	885.0	49.6
Wing length, mm	1989	6	233.3	2.9	9	236.1	5.2
	1990	23	236.0	3.9	26	238.8	5.5
	1991	12	235.3	3.7	36	239.0	3.5
	1992	22	234.4	4.6	21	237.1	5.0
	1993	16	236.0	5.0	14	236.9	3.6
Clutch size	1989	6	7.8	1.0	8	7.9	1.0
	1990	16	7.5	1.0	23	8.6	0.8
	1991	13	7.8	1.0	33	8.0	1.2
	1992	21	8.3	0.8	20	9.0	0.9
	1993	13	8.2	1.1	13	9.0	1.2
Mean egg volume, ml	1989	6	31.8	1.1	7	32.3	0.9
	1990	16	31.8	1.4	22	32.1	1.4
	1991	13	31.8	1.7	33	32.7	1.6
	1992	21	31.2	1.4	21	32.2	1.5
	1993	14	31.9	1.5	13	31.6	1.2
Hatching date	1989	5	162.0	2.3	7	161.4	2.1
	1990	15	161.1	2.4	18	161.7	3.2
	1991	9	167.8	2.3	18	166.4	2.8
	1992	18	170.7	1.8	13	170.1	1.4
	1993	12	164.8	1.4	10	165.6	1.5

Table 2. Factorial analyses of variance of morphometric characteristics and variables at hatching of yearling and adult female black grouse in central Finland, 1989-93. Age class = A, year = Y.

Variable	Source	df	F	P
Body mass	A	1	40.955	0.0001
	Y	4	4.147	0.003
	A × Y	4	2.393	0.052
	error	177		
Wing length	A	1	12.119	0.001
	Y	4	1.641	0.166
	A × Y	4	0.406	0.804
	error	175		
Clutch size	A	1	11.294	0.001
	Y	4	4.378	0.002
	A × Y	4	1.145	0.338
	error	156		
Mean egg volume	A	1	3.622	0.059
	Y	4	0.929	0.449
	A × Y	4	0.994	0.413
	error	156		
Nest initiation date	A	1	5.249	0.023
	Y	4	45.450	0.0001
	A × Y	4	0.314	0.868
	error	155		
Hatching date	A	1	0.275	0.601
	Y	4	72.123	0.0001
	A × Y	4	0.958	0.434
	error	115		
Hatching success	A	1	0.137	0.712
	Y	4	2.101	0.085
	A × Y	4	0.604	0.660
	error	117		
Fledging success	A	1	0.087	0.768
	Y	4	0.501	0.735
	A × Y	4	0.292	0.882
	error	67		

Results

We radio-marked 297 female black grouse during 1989-93. Of these, 76 birds were killed and the radio signals of 33 birds were lost during late winter or early spring. Hence, 188 birds (80 yearlings and 108 adults) were present at the onset of nesting in early May.

We pooled data sets from the three study areas in 1989, because there were no between-area differences in body mass, wing length, date of nest initiation, clutch and egg size, hatching success, fledging success, and brood size (Kruskal-Wallis test, $P \geq 0.1$ for yearlings, $P > 0.1$ for adults), or in total nest or brood loss (χ^2 test, $P > 0.1$ for both age classes).

Morphometric characteristics

Adults were significantly heavier and had longer wings (indicating larger body size) than yearlings at capture (Tables 1 and 2). Body mass also varied significantly between years. Age and year also influenced body mass (see Table 2).

Nest initiation dates, clutch size, and egg volume

Adults initiated laying their first clutches earlier than yearlings each year. However, differences between age classes, although significant (see Table 2), were not large, mostly 1-2 days on average. Initiation dates varied significantly between years (see Table 2), parallelling snow melt; e.g., in 1990 snow melted early and mean nest initiation date was 5 May for yearlings and 3 May for adults, whereas the early spring of 1992 was relatively cold with late snow melt, and the respective mean dates were 12 and 11 May.

Adults laid significantly larger first clutches and slightly larger eggs than yearlings (see Tables 1 and 2). Clutch size was highest in 1992 and 1993 in both age classes. Variation between years was significant in clutch size but not in egg volume (see Table 2).

Nest loss, hatching success, and hatching date

Between-year differences in total loss of first nests (Table 3) were not significant for yearlings (χ^2 = 2.942, df = 4, P = 0.568) or for adults (χ^2 = 2.288, df = 4, P = 0.683). Eight of 68 yearlings (11.8%) and 18 of 86 adults (20.9%) lost their first nests to egg predators (χ^2 = 2.273, df = 1, P = 0.132).

Partial loss of first nests mostly involved loss of one egg, which happened in 19 of 23 cases (82.6%). Variation between years (see Table 3) was not significant for yearlings (χ^2 = 5.716, df = 4, P = 0.221) or for adults (χ^2 = 6.672, df = 4, P = 0.154). Eleven of 60 yearlings (18.3%) and 12 of 67 adults (17.9%) suffered partial loss of their first nests (χ^2 = 0.004, df = 1, P = 0.951).

Although dates of initiating first nests differed between age classes (see Table 2), dates of hatching were similar (see Tables 1 and 2). This was probably because adults had larger clutches (see Table 1) and, therefore, had longer laying periods. The hatching success of first nests was similar for both age classes (see Tables 2 and 3).

Renesting and females without nest

We lost the radio signal of one of eight yearlings that lost their first nests to egg predators. Thus, seven yearlings were potential renesters, but only one (14.3%) renested, while six of 18 adults (33.3%) that lost their first nests renested. The probability of renesting did not differ between age classes (Fisher's exact test, P = 0.626). The renest of the yearling female was successful; two of six adults abandoned their renests for unknown reasons during incubation, two renests were depredated, and two renests of

Table 3. Nesting and hatching success, brood loss and fledging success of yearling and adult female black grouse in central Finland, 1989-93. Sample sizes are given in parentheses.

		Year				
Variable	Age class	1989	1990	1991	1992	1993
Total nest loss, %	Yearlings	16.7 (6)	6.2 (16)	25.0 (12)	9.5 (21)	7.7 (13)
	Adults	12.5 (8)	14.3 (21)	29.6 (27)	22.2 (18)	16.7 (12)
Partial nest loss, %	Yearlings	20.0 (5)	0.0 (15)	22.2 (9)	31.6 (19)	16.7 (12)
	Adults	0.0 (7)	5.6 (18)	22.2 (18)	35.7 (14)	20.0 (10)
Mean hatching success, %	Yearlings	100.0 (5)	96.6 (15)	97.5 (9)	96.6 (18)	96.7 (12)
	Adults	100.0 (7)	98.6 (18)	96.8 (19)	95.5 (14)	99.3 (10)
Total brood loss, %	Yearlings	0.0 (3)	33.3 (12)	25.0 (8)	25.0 (16)	54.6 (11)
	Adults	14.3 (7)	31.2 (16)	37.5 (16)	15.4 (13)	37.5 (8)
Mean fledging success, %	Yearlings	34.3 (3)	47.7 (8)	26.3 (6)	48.6 (12)	46.3 (5)
	Adults	38.1 (6)	42.4 (11)	44.7 (10)	51.0 (11)	40.1 (5)

adults were successful. In 1992 when females initiated nesting relatively late no renests were found.

We found eight nests (belonging to three yearlings and five adults) which had been initiated during late May or early June. They had small clutches; we found five eggs in the nest of a yearling (two other yearlings abandoned their nests before the clutch was completed), and 4-8 eggs in the nests of the five adults. Most of these nests may have been renests (the first nests were possibly destroyed before we could find them) but, because we cannot be certain, they were excluded from analyses.

We did not find any nests for seven of 80 yearlings (8.8%) and five of 108 adults (4.6%). The occurrence of females without nests did not differ between age classes ($\chi^2 = 1.306$, df = 1, P = 0.253).

Brood loss, fledging success, and brood size

Total brood loss between hatching and late July - early August was low in 1989 and in 1992 (see Table 3), but brood loss did not vary between years within age classes (yearlings: $\chi^2 = 4.532$, df = 4, P = 0.339; adults: $\chi^2 = 2.814$, df = 4, P = 0.590). Considering all years, 32.0% of yearlings (N = 50) and 28.3% of adults (N = 60) surviving or being monitored until late July - early August lost their broods ($\chi^2 = 0.175$, df = 1, P = 0.676).

Fledging success reflected the relative reduction of brood size between hatching and late July - early August (see Table 3). There was little variation in fledging success between age classes and years (see Table 2). Brood size did not differ between age classes in any year (Table 4). Considering all years, the median brood size was two for yearlings and three for adults (Mann-Whitney U test, z = 1.19, P > 0.2). Chick production per female initiating breeding did not differ between age classes in any year (Mann-Whitney U test, P > 0.1). Yearlings (N = 76) and adults (N = 102) produced 1.29 and 1.34 chicks per female, respectively, during 1989-93 (Mann-Whitney U test, z = 0.044, P > 0.9).

Table 4. Brood size in early August of yearling and adult female black grouse in central Finland, 1989-93. Differences between age classes were tested using Mann-Whitney U tests.

	Yearlings			Adults				
Year	N	median	range	N	median	range	U/z	P
1989	3	1	1-5	6	3	1-6	6	0.548
1990	8	3	1-6	11	2	1-8	38	>0.100
1991	6	2	1-3	10	2	1-6	22.5	>0.100
1992	12	2.5	1-9	11	4	1-5	49	>0.100
1993	5	3	2-6	5	3	2-5	11	0.841

Discussion

Adult female black grouse were larger and had more body mass in late winter, and they laid earlier and had larger clutches and slightly larger eggs than yearlings. Despite these differences, nesting success and chick production were similar for both age classes. This pattern has also been observed in several other grouse species (reviewed by Hannon & Smith 1984, Zwickel, Lewis & McKinnon 1988).

Body mass was studied 2-3 months before initiation of nesting. The differences observed between age classes probably remained until the breeding season; thus Willebrand (1992) and Valkeajärvi & Ijäs (1994) found that adult female black grouse were heavier than yearlings during the spring mating period. Willebrand (1992) suggested that yearlings may be less efficient in selecting nutritious food necessary for ovary recrudescence. Larger body mass may explain why adult female black grouse initiated nesting earlier than yearlings, since Hannon et al. (1988) observed that heavy female willow ptarmigan *Lagopus lagopus* laid early. Similarly, larger body mass may explain why adults laid larger clutches and slightly larger eggs than yearlings.

Lindén (1983, 1989) reported that clutches of female black grouse and capercaillie *Tetrao urogallus* tended to be larger during the increasing phase of the 6-7 year population cycle than during the decreasing phase. This difference might be explained by varying age structure of the female population in different phases of the cycle: the proportion of older females may be higher during the increasing phase than during the decreasing phase (Lindén 1989). In our study, however, clutch size showed between-year variation within the age classes. Thus, clutch size is also subject to important sources of variation other than age structure of the female population. Our results on egg size differ from those of Lindén (1983, 1989), since we found no differences between years (see Tables 1 and 2).

Total loss of first nests due to predation did not differ between yearling and adult female black grouse in Sweden (Willebrand 1992), nor did it differ in our study. Such a result could have been expected, because yearlings and adults nest in similar habitats (Brittas & Willebrand 1991). Furthermore, the females studied did not show any age-related difference in flushing distances during incubation (Marjakangas 1995). However, relatively more adults than yearlings hatch a clutch because of the higher probability of

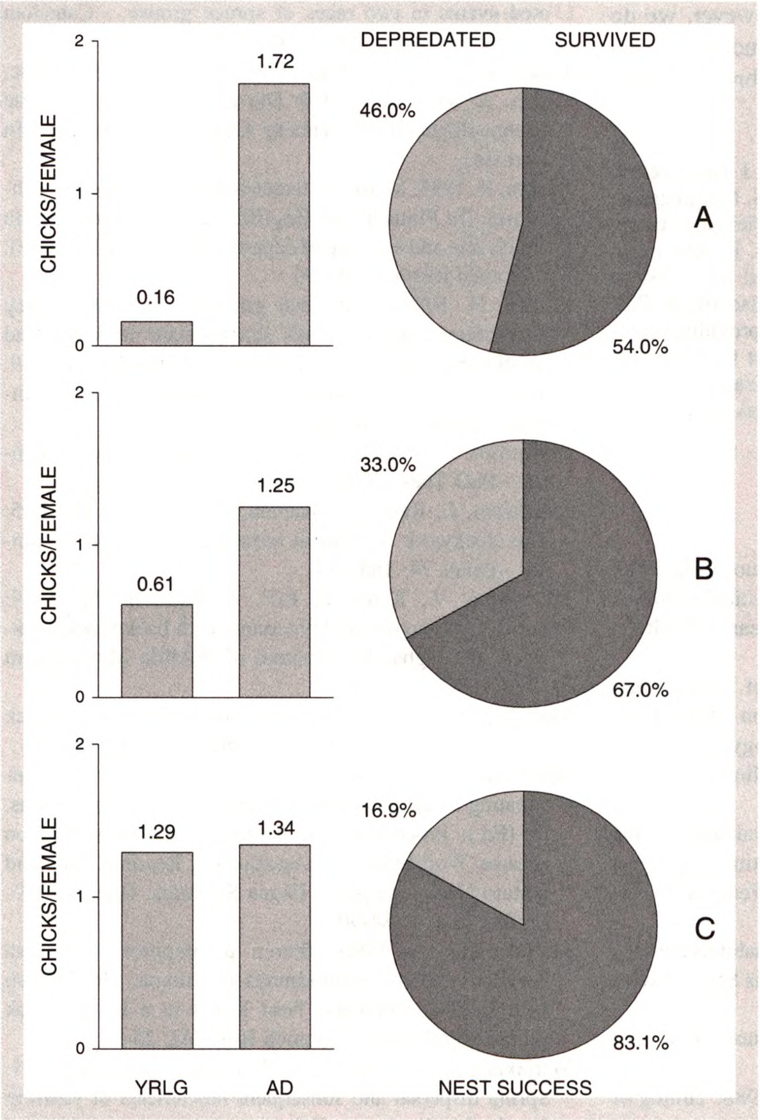

Figure 1. Chick production per female black grouse initiating breeding (columns) and success (depredated or survived) of first nests in yearling and adult female black grouse in A) central Sweden (Willebrand 1992), B) southern central Finland (Valkeajärvi & Ijäs 1994, and unpubl. data), and C) central Finland (present study). The proportions of surviving and depredated first nests were calculated with years and age classes combined.

renesting in adults (Willebrand 1992, Valkeajärvi & Ijäs 1994).

We did not find nests for 6.4% of the hens in our study. In Norway, three radio-marked female black grouse without nests were shot and their reproductive organs were examined (Storaas & Wegge 1985). All birds had laid eggs. It is probable that the females without nests observed in our study had been nesting and that their nests had been destroyed before we located them.

Our results on age-related chick production in female black grouse contrast with those of Willebrand (1992) and Valkeajärvi & Ijäs (1994) achieved using similar methods. In central Sweden, the number of chicks per female fledged by adults was about 10-fold compared to that fledged by yearlings (Willebrand 1992). A 2-fold difference was observed in southern central Finland (Valkeajärvi & Ijäs 1994), while there was no difference in our study areas, about 250 km north of the study area of Valkeajärvi & Ijäs (1994). The age-related difference in chick production observed by Willebrand (1992) and Valkeajärvi & Ijäs (1994) was mainly the result of higher probability of renesting and better brood survival in adult females.

Why do our results on chick production differ from those obtained by Willebrand (1992) and Valkeajärvi & Ijäs (1994)? Willebrand (1992) suggested that the large age-related difference was a result of the overall habitat structure in his study area. Forest stands were becoming too mature for black grouse, and the population was declining (Willebrand 1992). However, it is difficult to compare habitat structure and composition between these study areas, because appropriate habitat data are not readily available. Therefore, we used nest predation rate (total loss of first nests) to indicate the 'quality' of the landscape for breeding in the different areas. We believe that the extent of age-specific difference in chick production clearly parallelled nest predation rate in the three study areas (Fig. 1), i.e., populations showing relatively high, moderate, and no differences between age classes, had relatively high, moderate, and low nest predation rates, respectively. These findings suggest that yearlings may do as well as adults in good breeding habitats (in terms of nest predation).

These results suggest that possible variation in age structure of the female population (Lindén 1989, Lindström 1996) does not explain cycles in numbers of black grouse in our study areas. However, we do not know the number of offspring produced by yearlings and adults that are recruited to the breeding population.

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