Zoological Studies **49**(4): 453-460 (2010)

Zoological Studies

Flocking Behavior and Sexual Segregation in Black Grouse *Tetrao tetrix* during the Non-Breeding Period

Michał Ciach*, Dominik Wikar, Małgorzata Bylicka, and Marta Bylicka

Department of Nature-Cultural Heritage, Animal Ecology and Wildlife Management, Faculty of Forestry, University of Agriculture, al. 29 Listopada 46, 31-425 Kraków, Poland

(Accepted January 11, 2010)

Michał Ciach, Dominik Wikar, Małgorzata Bylicka, and Marta Bylicka (2010) Flocking behavior and sexual segregation in Black Grouse *Tetrao tetrix* during the non-breeding period. *Zoological Studies* **49**(4): 453-460. Black Grouse tend to form flocks outside the breeding period and to segregate sexes during flocking. However, the mechanisms of sex-specific and mixed flock formation remain unclear. In 2002-2005, we studied flocking behavior of Black Grouse during the non-breeding period in open habitats of the Kotlina Orawsko-Nowotarska valley (southern Poland). The results were grouped into 4 seasons: autumn, early winter, winter, and early spring. Relative abundances of Black Grouse did not differ among seasons. Birds were observed in unisex, containing only males or females, and mixed flocks. Male flocks dominated, and differences in their size among seasons were close to being significant. There was a tendency of male flock size to increase in winter, when the extended snow cover appeared. Female flocks were recorded less often, and differences in their size were not significant among seasons. Mixed flock size did not differ among the defined seasons. However, a tendency of the mixed flock size to decrease as the seasons progressed was found. The sex structure in mixed flocks significantly differed among seasons. In autumn and early winter, males dominated the mixed flocks. This rapidly decreased in winter and early spring. Males gradually left the mixed flocks, probably joining unisex flocks during the winter, and hence mixed flock size decreased together with sex-structure changes. http://zoolstud.sinica.edu.tw/Journals/49.4/453.pdf

Key words: Flocking behavior, Sex ratio, Non-breeding period, Black Grouse, *Tetrao tetrix*.

Aggregations of birds can be a result of breeding biology events, a response to food availability, or an anti-predatory behavior. Individual birds may benefit from group formation because of the dilution effect, but also because increased vigilance decreases the hunting success of the predator (Pulliam 1973, Lima and Dill 1990). On the other hand, an increase in a group's size may lead to stronger competition (Krause and Ruxton 2002). Hence, there might be an optimal flock size determined by predation risk and food availability. Organisms also develop morphological traits and behavioral mechanisms to decrease predation risk (Caro 2005). However, morphological traits may differ due to sexual dimorphism, which can subsequently induce different anti-predatory behavioral mechanisms at the species level.

Black Grouse *Tetrao tetrix* show lekking (arena) behavior during courtship, when males become territorial (de Vos 1983). Sexual selection in this species is most likely mediated by both male-male competition and female preference (Höglund et al. 1995, Rintamäki et al. 1995a, Alatalo et al. 1996, Höglund et al. 1997, Karvonen et al. 2000, Rintamäki et al. 2001). Male reproductive success depends on their social dominance, including localization of their territory, which is occupied during the lek (Rintamäki et al. 1995a b).

*To whom correspondence and reprint requests should be addressed. E-mail:mciach@ar.krakow.pl

However, the lek system and sexual selection in Black Grouse are essential to their ecology and behavior throughout almost all seasons, considering for example, the autumn male lekking activity (Rintamäki et al. 1999) and female territoriality in the breeding season (Angelstam et al. 1985). Outside the breeding season, Black Grouse tend to form flocks, which is the dominant social strategy during winter (Koskimies 1957, de Vos 1983). There is a tendency for the sexes to segregate during flocking (de Vos 1983), but mixed flocks are also recorded. The mechanisms of sex-specific flock formation and movements among flocks remain unclear.

The aim of this study was to analyze changes in flock sizes and sex structure during the non-breeding period in a local Black Grouse population in the Western Carpathians. We hypothesized, that changes in flock size may depend on winter conditions, particularly the lasting snow cover, when food resources become less available, and the birds' visibility increases. Flocking behavior, resulting from changes in climatic conditions, may induce sex-specific flocking behavior. We also predicted that mixed flock size would decrease and the sex structure would change as the non-breeding period progresses. The process by which mixed flocks disband remains unknown, and a flow of birds between mixed and unisex flocks may exist.

Over the last century, Black Grouse numbers have declined over much of Europe (Cramp and Simmons 1980, Storch 2000). Large-scale extinctions and the short-distance movements of this species (Warren and Baines 2002) have resulted in isolated populations which exhibit low genetic variation (Höglund et al. 2007). The Polish population of Black Grouse has declined tremendously in recent decades (Tomiałojć and Stawarczyk 2003) and is presently divided into isolated subpopulations. The species is included in the *Polish Red Data Book* as endangered (Głowaciński 2001), and the Kotlina Orawsko-Nowotarska valley holds one of the most important subpopulations in Poland. Knowledge of Black Grouse biology and ecology in the Carpathians remains very basic. However, behavioral studies are useful in conservation biology (Buchholz 2007, Caro 2007) and can provide appropriate conservation tools.

MATERIALS AND METHODS

Study area

The Kotlina Orawsko-Nowotarska (500-600 m in elevation) is an extensive homogeneous valley located in the Western Carpathians (southern Poland and northern Slovakia). It borders the Beskidy Zachodnie (Western Beskid) mountain ranges in the north and foothill ranges in the south. The local climate of the valley is continental and differs from neighboring mountain ranges. The mean temperature of the warmest month (July) is 15.6°C, and in the coldest month (Jan.), it is -6.0°C, with a mean annual temperature of 5.3°C. Owing to the mountainous terrain, thermal inversions frequently occur, and temperatures can fall to -35°C. The 1st snow usually falls at the beginning of the 2nd third of Oct., and the last snow usually falls during the first third of May. There is lasting snow cover for a mean of 83 d from 26 Dec. to 18 Mar. (Konček 1974).

The Kotlina Orawsko-Nowotarska is dominated by extensively farmed open valley habitats, including meadows, pastures, abandoned land, and a small extent of cultivated land. Part of the terrain is covered by extensive high peat bogs overgrown with mountain pine *Pinus mugo* and *Pinus* × *rhaetica* as well as Scots pine *Pinus sylvestris*-Norway spruce *Picea abies* forests (Pawłowski 1977). These habitats create a mosaic of open terrain crossed by streams, drainage ditches, afforested areas, and communication routes. In non-breeding seasons, predators such as the Raven *Corvus corax* and Common Buzzard *Buteo buteo* are commonly seen in the study area (Ciach et al. 2006).

Observations were conducted on 3 marked transects with a total length of 31.5 km located in open areas among Czarny Dunajec (49°44'N; 19°85'E), Piekielnik (49°47'N; 19°76'E), and Ludźmierz (49°46'N; 19°97'E). The major part of the transect area (ca. 70%) was a mosaic of hayed or grazed meadows and unused land. The remaining part was covered by afforested areas, fragments of peat bogs, and cultivated fields. The transects and their locations as well as the study area are described in detail elsewhere (Ciach et al. 2006).

Transect surveys

We conducted the study in 2002-2005, during 3 non-breeding periods, each of which covered the

months of Oct. (or late Nov. during the 1st period) to Mar. Surveys of the Black Grouse population size and structure were conducted regularly on 3 marked transects in the middle and at the end of each month. All transects were surveyed in the morning on the same day. Transect belts on which birds were counted ranged 200-1,000 m on each side of the transect and were delimited by characteristic objects (clumps of trees, forests, roads, or buildings) and the topography. The observers moved on foot (at a speed of 2-3 km/h) and carefully surveyed the terrain with binoculars. Birds within eyesight were counted across the entire breadth of the belt. Flock size (including single birds) and the sex of the birds (according to plumage coloration) were recorded. The length of the transects and the width of belts where birds were counted were established using GPS and a map with a 1:5,000 scale.

Data analyses

Due to small variations in the landscape among transects, as well as their relatively short lengths, data from the 3 transects were combined. Results were grouped into 4 seasons (Table 1) defined on the basis of mean daily temperatures and dates of appearance and disappearance of lasting snow cover (Konček 1974). Weather conditions recorded in the 3 non-breeding periods were similar and congruent with characteristics given for the defined seasons. Relative abundance was expressed as number of birds per 10 km of transect. All records of bird aggregation and sex were grouped into the above-defined seasons. Due to the low sample sizes in each study period, data from all years were pooled. Statistical procedures were performed using the Statistica 7.1 software (StatSoft 2005) according to Zar (1999).

When we analyzed mixed flock size changes, we assumed that small flocks recorded in autumn and early winter were single families. Based on brood sizes, their survival, and possible low summer mortality (Hanson and Soikkeli 1984, Baines 1991, Spidsø et al. 1997, Caizergues and Ellison 2002, Warren and Baines 2002), groups of up to 6 individuals (2, 2, 5, 6, and 6 individuals), which were recorded in autumn and early winter, were excluded from Kendall's rank correlation analysis.

RESULTS

Relative abundance

Black Grouse abundance did not significantly differ among the 4 seasons (with years grouped together) (Kruskal-Wallis analysis of variance (ANOVA) $H_{3,34} = 0.038$; $p = 0.998$). The median abundances were 6.7, 6.0, 5.4, and 6.5 individuals (ind.)/10 km in autumn, early winter, winter, and early spring, respectively (Fig. 1). The highest abundance of 22.5 ind./10 km was noted during winter.

Bird aggregations

Black Grouse were observed as single birds, or in unisexual or mixed flocks. Male flocks dominated (Table 2), with female and mixed flocks recorded less often. There were no significant differences among seasons in the frequency of various (mixed or unisexual) types of flock (Kruskal-Wallis ANOVA $H_{3,136} = 4.64$; $p = 0.2$). However, due to the small sample sizes, the frequency of mixed flocks declining in winter and early spring could not be excluded (Table 2).

Male flocks

Differences in male flock size among seasons were close to being significant (Kruskal-

Table 1. Characteristic differences in defined seasons according to Konček (1974) and the number of Black Grouse censuses

Season	Autumn	Early winter	Winter	Early spring
Dates	25 Sept.-22 Nov.	23 Nov.-25 Dec.	26 Dec.-18 Mar.	19 Mar.-12 Apr.
Number of days	59	33	84	24
Mean daily temperature (°C)	0-10	< 0	< 0	0-5
Extended snow cover	none	none	present	none
Number of counts on transects	7	6	17	4

Wallis ANOVA $H_{3,81}$ = 7.12; p = 0.068) (Fig. 2). In autumn, there was a median flock size of 2 males. The largest recorded flock contained 17 cocks. In early winter, a median flock size of 3 males was recorded. The largest recorded flock was 19 cocks. The median size of flocks in winter was 6 males, and the largest recorded was 32 cocks. In early spring, there was a decrease in flock size. The median size of flocks was 2 males, and the largest recorded was 10 cocks.

Female flocks

Female flocks size did not significantly differ among seasons (Kruskal-Wallis ANOVA $H_{3,33}$ = 1.44; p = 0.7) (Fig. 3). In autumn, only single hens or groups of 2 were recorded. In early winter and winter, the median flock size was 2 females. However, larger flocks were recorded as well: up to 8 hens in early winter and up to 13 hens in winter. In early spring, mostly single hens were recorded, and the largest flock contained 7 females.

Mixed flocks

Mixed flock size did not significantly differ among the seasons (Kruskal-Wallis ANOVA $H_{3,22}$ = 2.62; p = 0.45). The median flock sizes in autumn, early winter, and winter were 10, 7 and 11 individuals, respectively. The sizes of flocks in autumn ranged 6-22 individuals, in early winter,

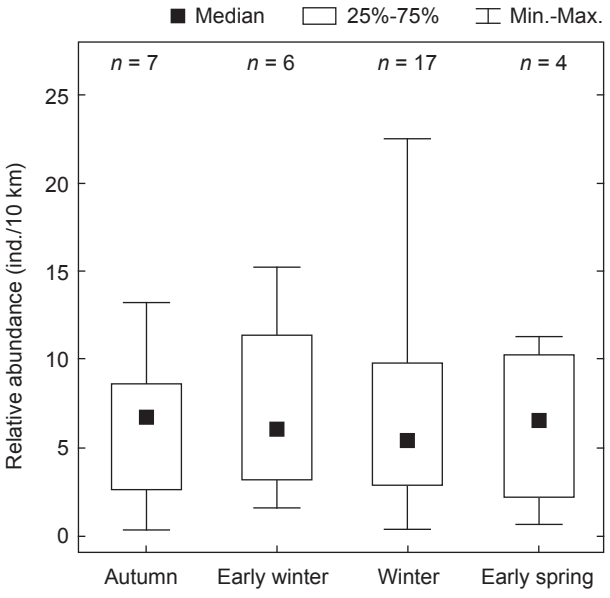

Fig. 1. Black Grouse *Tetrao tetrix* relative abundances in subsequent seasons in the Kotlina Orawsko-Nowotarska valley (southern Poland) during the non-breeding periods of 2002-2005 (*n*, the number of counts on transects).

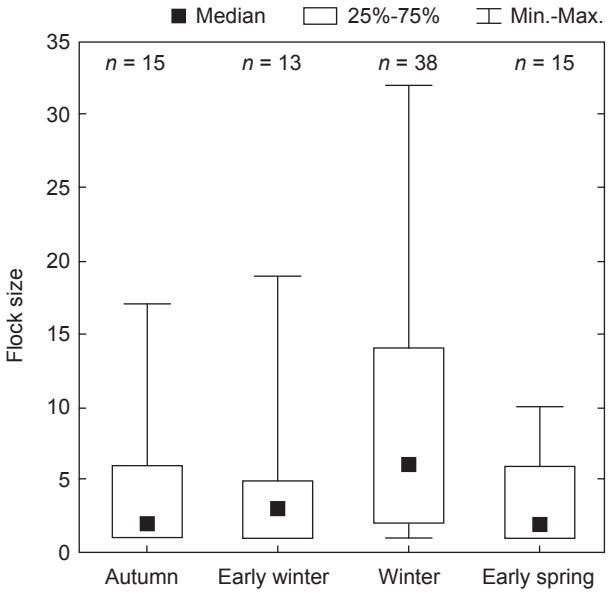

Fig. 2. Median flock size with the 25%-75% confidence interval, and minimum and maximum of the unisexual male Black Grouse *Tetrao tetrix* flocks observed in subsequent seasons in the Kotlina Orawsko-Nowotarska valley (southern Poland) in 2002-2005 (*n,* the number of records).

Table 2. Frequency of records of flocks of Black Grouse *Tetrao tetrix* in subsequent seasons in the Kotlina Orawsko-Nowotarska valley (southern Poland) in 2002-2005 during the non-breeding period

Type of flock	Autumn		Early winter		Winter		Early spring	
	n	(%)	*n*	(%)	*n*	(%)	*n*	(%)
♂♂	15	53.6	13	46.4	38	66.7	15	65.2
♀♀	7	25.0	8	28.6	12	21.1	6	26.1
♂♂ and ♀♀	6	21.4	7	25.0	7	12.3	2	8.7
Total	28	100	28	100	57	100	23	100

2-25 individuals, and in winter, 6-18 individuals. In early spring, only 2 mixed flocks were recorded of 4 and 6 individuals each.

However, after excluding records of groups of up to 6 individuals recorded in autumn and in early winter (considered to be single families, see "METHODS"), a significant decrease in mixed flock size as the seasons progressed was found (Kendall' s rank correlation τ = -0.36; $p < 0.05$) (Fig. 4).

The sex structure within mixed flocks significantly differed among seasons (Fig. 5). Males dominated in autumn and early winter, and they constituted 67.1% (n = 76) and 81.5% (n = 65) of all individuals, respectively. The proportions of males in the mixed flocks significantly differed between these 2 seasons (G test with correction, G = 3.83; p = 0.05). In winter and early spring, percentages of males in mixed flocks decreased at 46.9% (n = 81) and 30% (n = 10), respectively, and did not significantly differ between these 2 seasons (G = 1.06; $p > 0.05$). The proportion of males was higher in autumn than in winter and early spring (G test with correction, G = 6.6; $p < 0.02$ and G = 5.0; $p < 0.05$, respectively). Similarly, the proportion of males was higher in early winter than in winter and early spring (G = 19.2; $p < 0.001$ and G = 10.4; $p < 0.01$, respectively).

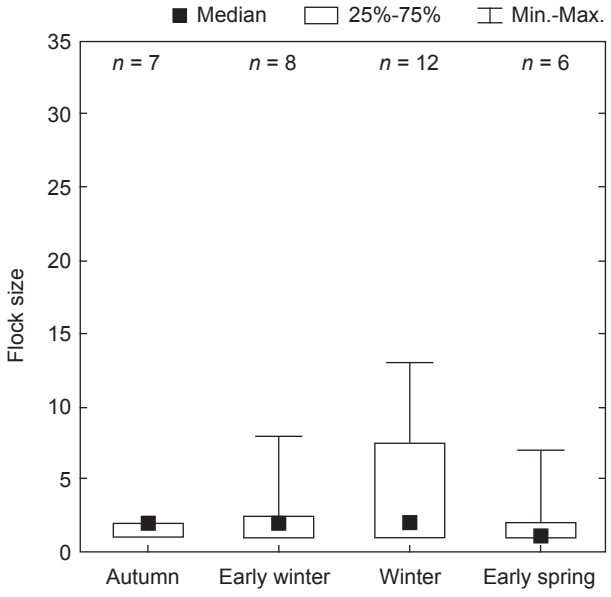

Fig. 3. Median flock size with the 25%-75% confidence interval, and minimum and maximum of unisexual female Black Grouse *Tetrao tetrix* flocks observed in subsequent seasons in the Kotlina Orawsko-Nowotarska valley (southern Poland) in 2002-2005 (*n,* the number of records).

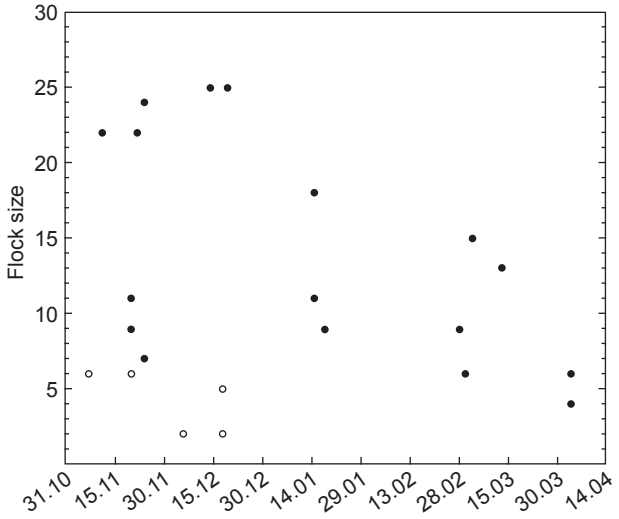

Fig. 4. Black Grouse *Tetrao tetrix* mixed flock size changes during the non-breeding period in the Kotlina Orawsko-Nowotarska valley (southern Poland) in 2002-2005 (open signs, records excluded from the statistical analyses, see "METHODS").

DISCUSSION

The relative abundance of Black Grouse remained stable during the non-breeding season within the Kotlina Orawsko-Nowotarska valley.

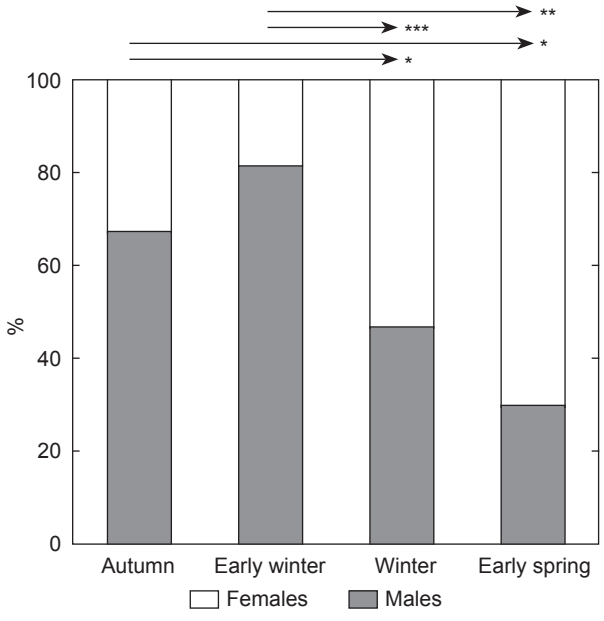

Fig. 5. Sex structure in Black Grouse *Tetrao tetrix* mixed flocks in subsequent seasons of the non-breeding period in the Kotlina Orawsko-Nowotarska valley (southern Poland) in 2002-2005 (arrows indicate differences between periods; *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

An immigration of some birds from neighboring mountain ranges (Tatra Mts. and Babia Góra Mt.) for the entire non-breeding period cannot be excluded. However, Caizergues and Ellison (2002) found that dispersal movements took place in Oct. and Apr., i.e., outside our study period. Hence, increased flock size in winter was probably not a result of increased number of birds in the study area.

Along with the stable abundance, changes in the flocking behavior of Black Grouse males were recorded during the winter. This behavior, which was also reported in other tetraonine studies (Hanson and Soikkeli 1984, Hines 1986), may be related to climatic conditions (Koskimies 1957). In our study, flock sizes gradually began to increase in early winter, when the temperature dropped below 0°C. However, the process was particularly visible in winter, when extended snow cover exists. The appearance of snow cover during winter seems to be a major flocking factor. It induces changes in the birds' visibility, which may result in anti-predatory flock formation (see also Marjakangas 1990).

Snow cover limits food accessibility, which may lead to foraging concentrations. Flocking may have resulted from communal foraging, especially when available food resources are distributed in clusters. In summer and autumn, Black Grouse mainly feed on berries, flowers, seeds, grassland herbs, and dwarf shrubs (Pulliainen 1982, Starling-Westerberg 2001, Beeston et al. 2005). During the presence of extended snow cover, when the availability of preferred food is low, the role of tree buds increases, especially of birches *Betula pendula* (Pulliainen 1982, Beeston et al. 2005). Thus, birds living in habitats where trees are grouped in clusters may show a higher tendency to form flocks than those living in woodlands, as indicated by studies on other tetraonines (Hines 1986). In the Kotlina Orawsko-Nowotarska valley, birches are unevenly distributed, and this may lead to foraging concentrations.

Adult mortality is one of the main factors determining the abundance of local Black Grouse populations (Lindström et al. 1997). The major cause of winter deaths in Black Grouse is predation by the Goshawk *Accipiter gentilis* (Angelstam 1984, Caizergues and Ellison 1997, Spidsø et al. 1997, Selås 2003). High energy demands due to low temperatures and low availability of preferred foods may force the grouse to increase the time used for foraging, making them more vulnerable to Goshawk predation. Flocking behavior, which reduces the need for vigilance by each individual, may thus be especially favorable during winter. Presumably, Black Grouse adult cocks allow young individuals to join during this hazardous season. They may form a kind of protection to guard adult males against predators, while being the 1st prey of predators at the same time. This hypothesis was confirmed by the age-dependent Black Grouse mortality rate. Adult male mortality is lowest during winter, whereas young and non-territorial males show the highest mortality during this season (Angelstam 1984). In this way, family relations of aggregated birds may be important as well. The hypothesis of kin selection as a factor that explains the evolution of leks (Höglund 2003) may also explain flocking behavior in non-breeding seasons. Flocking in winter may be supported by family relations, where young males join their relatives, and males from 1 family tend to stay in closely related groups. Thus, social relations may be a basis of winter flock formation. However, further studies are needed to support that hypothesis.

A lower tendency of female Black Grouse to form flocks may result from their dispersal movements and migration between winter and breeding ranges. Adult hens show fidelity to their winter range (Caizergues and Ellison 2002). However, they possess, along with young birds, good dispersal abilities and perform movements between fragmented habitats (Marjakangas and Kiviniemi 2005). Philopatry in males and dispersal movements of females (Höglund et al. 1999, Caizergues and Ellison 2002) in isolated populations may induce an overall decrease in the number of females. Black Grouse tend to form larger flocks in regions with high densities (Hanson and Soikkeli 1984). If we apply this at the sex level, rarer flocking behavior by females in our study might result from a lower density of their population.

De Vos (1983) pointed out that the Black Grouse show a tendency to segregate in unisex flocks due to sex-related differences in habitat choice. Black Grouse females are smaller and may seek out denser cover than males (Marti 1985). This, together with their more-cryptic plumage, even in winter conditions, may make them less vulnerable to Goshawk predation (Angelstam 1984). In addition, competition for high-quality food plants may be stronger, especially in late winter, than among males. Thus, the smaller flock sizes of Black Grouse females may be shaped by both dispersal and hiding

possibilities, and the avoidance of competition.

Apparently, extended snow cover did not influence the formation of mixed flocks. Mixed autumn and winter flocks may primarily consist of adult hens and yearlings of both sexes, as suggested for other tetraonines (Ellison 1973). Bigger flocks may result from associations of single family groups. This probably takes place during summer and autumn, and during the latter, some of the families are still separated. The decrease in mixed flock size during the non-breeding period along with sex-structure changes indicates that males gradually leave mixed flocks. Our results suggest that these males probably join winter unisex flocks. When males have departed, females (adults and young) probably gradually disperse at the beginning of the breeding (lek) season. However, elucidating the processes of mixed flock formation and disbanding, as well as within-flock kin relations, requires further studies.

Acknowledgments: We wish to express our gratitude to members of the Ornithological Section of the Foresters' Scientific Club of the Faculty of Forestry, Univ. of Agriculture, Kraków, Poland for their help with the fieldwork. Particularly we wish to sincerely thank M. Stańczyk, M. Mężyk, M. Barczyk, P. Dec, and B. Kwarciany. We want to thank L. Ellison, J. Höglund, V. Selås, and anonymous reviewers for critical and valuable comments on this paper.

REFERENCES

Alatalo RV, T Burke, J Dann, O Hanotte, J Höglund, A Lundberg et al. 1996. Paternity, copulation disturbance, and female choice in lekking Black Grouse. Anim. Behav. **52:** 861-873.

Angelstam P. 1984. Sexual and seasonal differences in mortality of the Black Grouse *Tetrao tetrix* in boreal Sweden. Ornis Scand. **15:** 123-134.

Angelstam PK, M Jaarola, NE Nordh. 1985. Are female Black Grouse *Tetrao tetrix* territorial? Ornis Fenn. **62:**124-129.

Baines D. 1991. Factors contributing to local and regional variation in Black Grouse breeding success in northern Britain. Ornis Scand. **22:** 264-269.

Beeston R, D Baines, M Richardson. 2005. Seasonal and between-sex differences in the diet of Black Grouse *Tetrao tetrix*. Bird Study **52:** 276-281.

Buchholz R. 2007. Behavioural biology: an effective and relevant conservation tool. Trends Ecol. Evol. **22:** 401-407.

Caizergues A, LN Ellison. 1997. Survival of black grouse *Tetrao tetrix* in the French Alps. Wildl. Biol. **3:** 177-186.

Caizergues A, LN Ellison. 2002. Natal dispersal and its consequences in Black Grouse *Tetrao tetrix*. Ibis **144:** 478-487.

Caro T. 2005. Antipredator defenses in birds and mammals. Chicago, IL: Univ. of Chicago Press.

Caro T. 2007. Behavior and conservation: a bridge too far? Trends Ecol. Evol. **22:** 394-400.

Ciach M, D Wikar, M Bylicka. 2006. Birds community of open habitats of Kotlina Orawsko-Nowotarska valley in non-breeding season. Berkut **15:** 55-65.

Cramp S, KEL Simmons, eds. 1980. The birds of the western Palearctic. Vol. 2. Oxford, UK: Oxford Univ. Press.

de Vos GJ. 1983. Social behaviour of Black Grouse, an observational and experimental field study. Ardea **71:** 1-103.

Ellison LN. 1973. Seasonal social organization and movements of Spruce Grouse. Condor **75:** 375-385.

Głowaciński Z, ed. 2001. Polish red data book of animals. Vertebrates. Warszawa, Poland: Państwowe Wydawnictwo Rolnicze i Leśne. (in Polish with English summary)

Hanson WR, M Soikkeli. 1984. Group size and sex ratios among Finnish Black Grouse. Ornis Fenn. **61:** 65-68.

Hines JE. 1986. Social organization, movements, and home ranges of Blue Grouse in fall and winter. Wilson Bull. **98:** 419-432.

Höglund J. 2003. Lek-kin in birds – provoking theory and surprising new results. Ann. Zool. Fenn. **40:** 249-253.

Höglund J, RV Alatalo, RM Gibson, A Lundberg. 1995. Mate-choice copying in Black Grouse. Anim. Behav. **49:** 1627-1633.

Höglund J, RV Alatalo, A Lundberg, PT Rintamäki, J Lindell. 1999. Microsatellite markers reveal the potential for kin selection on black grouse leks. Proc. R. Soc. Lond. B **266:** 813-816.

Höglund J, T Johansson, C Pelabon. 1997. Behaviourally mediated sexual selection: characteristics of successful male Black Grouse. Anim. Behav. **54:** 255-264.

Höglund J, JK Larsson, HAH Jansman, G Segelbacher. 2007. Genetic variability in European Black Grouse (*Tetrao tetrix*). Conserv. Genet. **8:** 239-243.

Karvonen E, PT Rintamäki, RV Alatalo. 2000. Female-female aggression and male mate choice on Black Grouse leks. Anim. Behav. **59:** 981-987.

Konček M, ed. 1974. Climate of Tatry Mountains. Bratislava, Slovakia: Vydavateľstvo Slovenskej Akadémie Vied. (in Slovakian)

Koskimies J. 1957. Flocking behaviour in Capercaillie, *Tetrao urogallus* (L.), and Blackgame, *Lyrurus tetrix* (L.). Finn. Game Res. **18:** 1-32.

Krause J, GD Ruxton. 2002. Living in groups. Oxford, UK: Oxford Univ. Press.

Lima SL, LM Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68:** 619-640.

Lindström J, E Ranta, M Linden, H Linden. 1997. Reproductive output, population structure and cyclic dynamics in Capercaillie, Black Grouse, and Hazel Grouse. J. Avian Biol. **28:** 1-8.

Marjakangas A. 1990. A suggested antipredator function for snow-roosting behaviour in the Black Grouse *Tetrao tetrix*. Ornis Scand. **21:** 77-78.

Marjakangas A, S Kiviniemi. 2005. Dispersal and migration of female Black Grouse *Tetrao tetrix* in eastern central Finland. Ornis Fenn. **82:** 107-116.

Marti C. 1985. Unterschiede in der Winterökologie von Hahn

und Henne des Birkhuhns *Tetrao tetrix* im Aletschgebiet (Zentralalpen). Der Ornithol. Beob. **82:** 1-30.

Pawłowski B. 1977. Flora of Polish mountains. *In* W Szafer, K Zarzycki, eds. Flora of Poland. Warszawa, Poland: Państwowe Wydawnictwo Naukowe, pp. 189-252. (in Polish)

Pulliainen E. 1982. Breeding, foraging, and wintering strategies of the Black Grouse, *Lyrurus tetrix* L., in the Finnish taiga - a review. Aquilo Ser. Zool. **21:** 68-75.

Pulliam HR. 1973. On the advantages of flocking. J. Theor. Biol. **38:** 419-422.

Rintamäki PT, RV Alatalo, J Höglund, A Lundberg. 1995a. Male territoriality and female choice on Black Grouse leks. Anim. Behav. **49:** 759-767.

Rintamäki PT, RV Alatalo, J Höglund, A Lundberg. 1995b. Mate sampling behaviour of Black Grouse females (*Tetrao tetrix*). Behav. Ecol. Sociobiol. **37:** 209-215.

Rintamäki PT, J Höglund, RV Alatalo, A Lundberg. 2001. Correlates of male mating success on black grouse (*Tetrao tetrix* L.) leks. Ann. Zool. Fenn. **38:** 99-109.

Rintamäki PT, E Karvonen, RV Alatalo, A Lundberg. 1999. Why do Black Grouse males perform on lek sites outside the breeding season? J. Avian Biol. **30:** 359-366.

Selås V. 2003. Vulnerability of Black Grouse (*Tetrao tetrix*) hens to Goshawk (*Accipiter gentiles*) predation in relation to vole cycles. J. Ornithol. **144:** 186-196.

Spidsø TK, O Hjeljord, JG Dokk. 1997. Seasonal mortality of Black Grouse *Tetrao tetrix* during a year with little snow. Wildl. Biol. **3:** 205-209.

Starling-Westerberg A. 2001. The habitat use and diet of Black Grouse *Tetrao tetrix* in the Pennine Hills of northern England. Bird Study **48:** 76-89.

StatSoft. 2005. Statistica (data analysis software system), vers. 7.1. www.statsoft.com

Storch I. 2000. Grouse. Status survey and conservation action Plan 2000-2004. WPA/BirdLife/SSC Grouse Specialist Group. Gland, Switzerland and Cambridge, UK: IUCN and Reading, UK: World Pheasant Association.

Tomiałojć L, T Stawarczyk. 2003. The avifauna of Poland. Distribution, numbers and trends. Wrocław, Poland: Polskie Towarzystwo Przyjaciół Przyrody pro Natura. (in Polish with English summary)

Warren PK, D Baines. 2002. Dispersal, survival, and causes of mortality in Black Grouse *Tetrao tetrix* in northern England. Wildl. Biol. **8:** 91-97.

Zar JH. 1999. Biostatistical analysis. 4th ed. Upper Saddle River, NJ: Prentice Hall.