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Traditionality of Black Grouse *Tetrao tetrix* leks

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Many lek mating systems are characterized by traditional sites, which are used from year to year. We counted individual Black Grouse *Tetrao tetrix* on 6–17 leks between 1987 and 1994 to study the traditionality of leks. We correlated male (adults and yearlings separately) and female numbers from each year against the corresponding figures of the previous year. There was a significant association in numbers of adult and yearling males both within and between successive years. Female counts were not correlated with past female or male numbers. Thus, it seems that the habit of young males to recruit preferentially to large leks, or to avoid the smallest leks, maintains the traditionality in Black Grouse leks.

1. Introduction

Leks are assemblies of displaying males that females visit for the sole purpose of mating (Bradbury & Davies 1987, Höglund & Alatalo 1995). A typical character of leks of several avian and mammalian species is the between-year site fidelity, i.e. the same arenas are used in successive years (e.g. Koivisto 1965, Clutton-Brock et al. 1988, Bradbury et al. 1989, Wiley 1991). Moreover, certain leks seem to be larger than others constantly from year to year (Bradbury et al. 1989). The mechanisms by which this constancy of leks is maintained have remained unclear. The site fidelity of individuals may be one factor that promotes lek site constancy. However, in species with a high annual mortality and population turnover rate this might not be enough for the maintenance of traditionality. An additional mechanism could be the tendency of young males to recruit into larger leks, which would produce a correlation between numbers of attending males in successive years (Bradbury et al. 1989).

Black Grouse *Tetrao tetrix* females visit and mate preferably on larger leks (Alatalo et al. 1992). In addition to females directly responding to lek size, the association between female and male numbers may be partly a result of traditionality, or alternatively, both sexes may be independently affected by similar lek site requirements. A prediction regarding between-year correlations can be deduced from the "hotspot" hypothesis from the evolution of leks (Bradbury & Gibson 1983): if males were to settle at sites where the probabilities of encountering females are high, they should be able to use the information on female traffic of the previous year when making their settlement decision. Black Grouse males seldom establish a permanent territory until their second year of age (Alatalo et al. 1992). This would allow them to follow a rule predicted by the "hot spot" hypothesis, namely, settle where females were abundant in the previous spring. In this paper we test the mechanisms that generate traditionality in the black grouse by correlating

numbers of displaying adult males and visiting young males and females in successive years.

2. Methods

We studied leks of black grouse during 1987–1994 in Petäjävesi, Keuruu and Uurainen (62°10´N, 25°05´E), and during 1993–1994 in Konnevesi (62°36´N, 26°20´E), all localities situated in Central Finland in the boreal zone. Black grouse leks are found on open sites, usually on bogs or frozen lakes, and occasionally on fields. Our data set includes leks from all these habitat types.

Data on male and female numbers were gathered yearly from 6–17 lek sites during 1987–1993. However, most leks were observed only in two successive years. Most sites were watched for several mornings (mean = 5.2, s.d. = 3.8), and leks with a single observation morning were omitted from analyses. The leks were observed between 0230 and 0800 h from tents or hides, and individuals on a lek were counted repeatedly throughout the morning.

Males that defended a territory were regarded as territorial males, except on lakes (with no fixed territories, see Koivisto 1965, Hovi et al. 1996), where the number of regularly (= daily) attending males was used. These males were almost invariably in adult plumage, with individually recognizable differences in tail condition and spottings in under tail coverts. We expressed the numbers of females as the number of different visits to a lek (from first sight to departure from a lek) divided by the number of observation mornings. Mornings before the onset of the actual breeding season (first female visits) were excluded, taking into account the top season only. In fact, this measure is a rate of female visits and not a number of individual females visiting the leks. The exact amount of females was unknown in many cases, because on most leks they were not individually marked. For simplicity, we refer to "female numbers" in this paper. Occasionally visiting males, which were usually yearlings, were not included in the male counts, but they constituted their own group. Their numbers were expressed in the same way as those of females, because their numbers varied considerably on a daily basis.

We tested the association between adult and juvenile males, and females within a year by including the whole data set (n = 66 lek years). Figures from two successive years, t and t–1 in a given lek, were used as a pair for analysis of traditionality (n = 23 year pairs). The population density in our study area varied somewhat during the study period, and different sites were observed at different phases of the population cycle. Therefore, numbers for each site were made relative to the varying population level by averaging male and female numbers across sites within years, and fixing the mean values to unity. So, for instance, male numbers higher than 1 indicated leks larger than the average. Parametric statistics were used, except for the number of yearling males, which did not meet the criterion of normality (Lilliefors' two-tailed $P < 0.05$). All probabilities are for two-tailed tests. The significance values for the correlation coefficients have been Bonferroni-corrected to minimize the table-wise error rate (Rice 1989).

3. Results

The numbers of yearling males (= Y, CV = 129%) fluctuated significantly more among different leks than the numbers of territorial males (= M, CV = 48%) or females did (= F, CV = 56%), as indicated by the differences in their variances (Y versus M: $F = 3.14$, $P < 0.01$; Y versus F: $F = 2.66$, $P < 0.05$; M versus F: $F = 1.18$, $P > 0.05$; $n = 66$). Note that this variation occurs between leks after the yearly variation has been removed. Also, the yearly means of yearling numbers fluctuated fourfold, while the between-year variation was much less among adult males and females (Fig. 1).

Within years the numbers of adult males and females were positively correlated ($r = 0.52$, $n = 66$, $P_{corr} < 0.01$). Also, the number of young males was highly related to lek size in terms of adult, territorial males ($r_s = 0.65$, $n = 66$, $P_{corr} < 0.001$). In contrast, female and yearling counts were not related to each other ($r_s = 0.24$, $n = 66$, $P_{corr} > 0.05$).

The numbers of territorial males in successive years were positively correlated ($r = 0.64$, $n = 23$, $P_{corr} < 0.05$, Table 1). This means that lek sizes in relation to general population level were fairly constant from year to year. Additionally, the number of young males showed a significant correlation with the number of adult males of the previous season ($r_s = 0.63$, $n = 23$, $P_{corr} < 0.05$, Fig. 2, Table 1). The

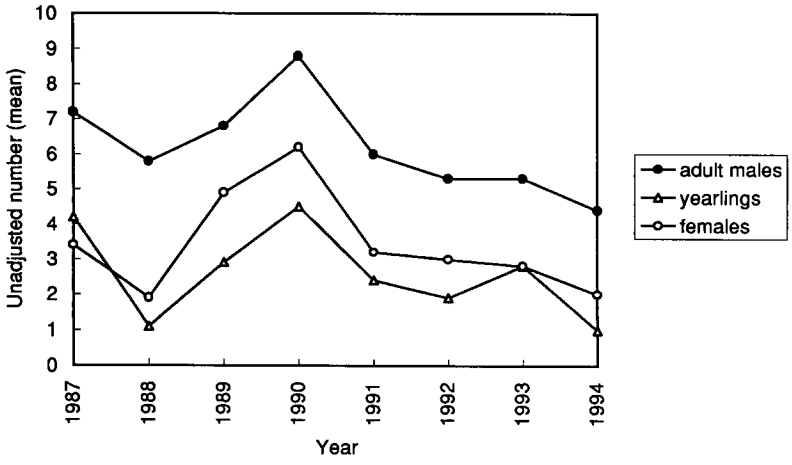

Fig. 1. The changes in average lek size (the number of adult males), the number of yearling males and the number of females during the study period 1987–1994. The number of females and young males are expressed as rates of visits to leks per morning.

reverse was not true, however: leks with many young males in the previous year (t–1) did not have many adult males in year t ($r_s = 0.37$, $P_{corr} > 0.1$).

To control for the intercorrelation between the number of yearlings in year t, the number of adult males in year t and the number of adult males in year t–1, we performed Kendall's partial correlation analysis for those three variables. When controlling for adults in year t–1, adults and yearlings were significantly correlated ($\tau = 0.46$, $n = 23$, $P < 0.01$). Consequently, yearlings were also related to adults of the past year (adults in year t controlled for; $\tau = 0.30$, $n = 23$, $P < 0.05$). Instead, the relationship between numbers of adult males of two successive years disappeared after controlling for yearlings ($\tau = 0.17$, $n = 23$, $P > 0.05$). To conclude, the association between yearlings and adult males, and on the other hand, between yearlings and adult males in the previous year, seemed to be the only important factors generating traditionality.

4. Discussion

Counts of yearling males showed large variation between years and leks. The former is most likely caused by variation in breeding success of black grouse in our study area, while the latter may be, at least partly, caused by the tendency of young males to visit the leks unevenly. In fact, there were more visiting young males on large leks, and additionally, more on leks that were large in the previous season. At first glance it might seem impossible for a newcomer to settle on a site of high past activity. However, adult black grouse males gather on lekking sites in October to display, and this autumn lekking is noted by females and probably young males, too (Hjorth 1970, P. T. Rintamäki unpublished). It is possible that young males settle at localities where there were large leks in the previous autumn. Alternatively, the surroundings of a large lek might produce more surviving offspring and thus have more young males next spring, because males do not disperse very far from their birth site (Willebrand 1988).

Males older than one year display on the same sites from year to year (Koivisto 1965), and this site fidelity extends even to the level of territory, at least in the dominant males (Koivisto 1965, Rintamäki et al. 1995a). On the other hand, the annual mortality rate of adult males is very high (Angelstam 1984, Rintamäki et al. 1995a), which is likely to weaken

Table 1. Correlation matrix for the number of adult males, young males and females in successive years (t) and (t–1). The coefficients are for Spearman's rank correlation, except those in boldface, which are parametric (Pearson). Sample size is 23 for within-lek comparisons between years and 66 for comparisons within years. Asterisks denote Bonferroni-adjusted probability values, *p < 0.05, **p < 0 .01.

	Young males (t)	Adult males (t)	Females (t)
Adult males (t)	0.65 **		
Females (t)	0.21	**0.52** **	
Young males (t–1)	0.43	0.37	– 0.08
Adult males (t–1)	0.63 *	**0.64** *	**0.14**
Females (t–1)	0.14	**0.34**	**0.24**

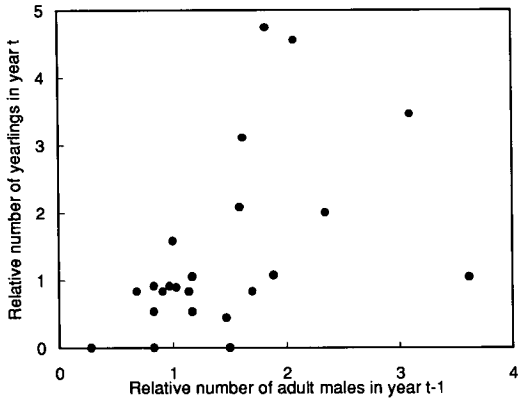

Fig. 2. The association between the number of yearling males and the number of adult males in the previous year ($r_s = 0.63$, $n = 23$, $P_{corr} < 0.05$). Each data point represents one lek with counts from two successive years. The numbers have been controlled for the yearly variation.

the effect of site fidelity on traditionality. In fact, the partial effect of adult male numbers in successive years was insignificant.

The number of females and males were correlated, as found earlier by Alatalo et al. (1992) with a smaller data set. This correlation most probably reflects a preference to mate on larger leks. This preference had no significant contribution for the traditionality, however. Females, especially those older than one year, have very limited breeding dispersal like birds in general (Greenwood 1980, Willebrand 1988). In other words, once they have chosen a lek where to breed, they usually do not make a choice between leks in following seasons. Additionally, they also seem to be faithful to their previous mates, if alive (Rintamäki et al. 1995b). This behaviour, which should promote traditionality, seems to be offset by high annual mortality, which is even higher than that of males (Angelstam 1984). Local high survival is not a likely mechanism in regard to females, because of their far-reaching natal dispersal, which does not contribute to local recruitment (Willebrand 1988).

It is evident that young males do not respond, or do not get the cue of the female numbers of the previous season, and this kind of "hot spot" explanation does not achieve support. Instead, there is a strong tendency for young males to go where the older males are. In a playback experiment where male vocal display was emitted from loudspeakers on lake leks, we found that young males were attracted by the auditory stimulus (M. Hovi et al., unpublished), which is in line with this result. This could be seen as a variant of the "hot shot" mechanism, but instead of being attracted by a certain superior male, the yearlings perceive a large lek as an attractive site for females.

Why young should males settle on leks with several adult competitors? Yearlings with low attractivity and weak competitive abilities seldom achieve any copulations during the season, and therefore should avoid sites with many adult males (Parker & Sutherland 1986, Sutherland & Parker 1992). In an analysis by Alatalo et al. (1992), it was found that on large leks the proportion of young males was in fact lower than on small leks. On the smallest leks, the chances of a yearling obtaining any matings are very low, if there is a dominant adult male (see Hovi et al. 1995). Perhaps the optimum for a recruiting male would be a lek of intermediate size.

To conclude, the constancy in lek sizes is suggested to be mainly produced by the tendency of young males to avoid the smallest leks. This might be related to the benefits of young males in terms of occasional copulations (a kind of hot shot mechanism), or perhaps future status as a territorial male. The "hot spot" hypothesis gained no support since male numbers did not respond to female numbers of the previous year.

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Selostus: **Teeren (*Tetrao tetrix*) soitimen traditionaalisuus**

Tutkimme teeren soitimia vuosina 1987–1994 Keski-Suomessa selvittääksemme soidinten pysyvyyden ja traditionaalisuuden taustalla olevia mekanismeja. Tarkkailimme vuosittain 6–17 eri soidinpaikkaa, joilta määritettiin vanhojen (+2-kv) ja nuorten (2-kv) koiraiden sekä naaraiden lukumäärät. Kaksi jälkimmäistä muuttujaa mitattiin soidinvierailufrekvensseinä aamua kohti. Korrelaatioanalyysi

osoitti vanhojen ja nuorten koiraiden lukumäärien korreloivan sekä vuosien sisällä että vuosien välillä, kuitenkin siten, että aikuisten määrä ei ollut riippuvainen edellisvuoden nuorten määrästä. Naaraiden määrä korreloi ainoastaan saman vuoden aikuisten koiraiden määrän kanssa. Tämän laskenta-aineiston perusteella ja aiempiin teeren dispersaalikäyttäytymistä koskeviin tietoihin nojautuen voitaneen päätellä nuorten koiraiden mahdollisesti rekrytoituvan mielellään keskimääräistä suuremmille soitimille, mikä ainakin osaksi selittää, miksi tietyt soitimet ovat suurempia kuin muut vuodesta toiseen.

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