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A 33-year study of hazel grouse *Bonasa bonasia* in the Bohemian Forest, Šumava, Czech Republic: effects of weather on density in autumn

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The only long-term census of hazel grouse Bonasa bonasia in Central Europe was conducted during 1972-2004 on a 100-km² area of the Bohemian Forest, Šumava, Czech Republic. To obtain a density index in October, I recorded indirect signs of hazel grouse, such as dust bathing sites, feathers, droppings or tracks, and reactions to a whistle that imitates the male territorial song along fixed routes covering 80 km in total. During the 33 years of counting, I found no statistically significant trend in the fluctuating numbers. I also looked for the influence of weather on hazel grouse abundance. Analysis by stepwise multiple regression suggested that six weather variables were correlated with the annual rate of change of hazel grouse density in autumn, explaining 44% of the variation in density: mean temperature and total precipitation in April (highly significant positive correlations) and mean temperature and total precipitation in May and September (significant negative correlations). The results for April and May seem to indicate a positive effect of rainfall and temperature in April on reproductive success in the pre-laying period, but a negative effect of rainfall in May on chick survival.

Key words: Bohemian Forest, Bonasa bonasia, Czech Republic, hazel grouse, population monitoring, weather

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Except for the Alps, the Bohemian Forest is the largest area occupied by hazel grouse *Bonasa bonasia* in central Europe. Before 1950, the density of this species in the spruce-dominated landscape was low, but numbers increased later, apparently due to natural succession of birch *Betula pendula* and alder *Alnus glutinosa* after 1945 on abandoned fields and meadows. In addition, spruce *Picea abies* was planted, mostly on small plots, creating mosaics of different forest types with a high density of forest edge throughout the region. The increase in the amount of young mixed forests was accompanied by a pronounced increase in hazel grouse numbers (Kučera 1975, Klaus 1991).

Different factors affect the reproductive success of tetraonids, including the physical condition of the female prior to laying (Siivonen 1957, Moss & Watson 1984) and weather conditions during in-

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cubation (Semenov-Tjan-Shanskii 1960), hatching or when the chicks are very small (Bump et al. 1947, Slagsvold & Grasaas 1979). Predation on eggs or chicks can also be important (Angelstam et al. 1985, Marcström et al. 1988). Cold and wet weather increases the mortality of young chicks, which have poorly developed thermoregulatory abilities (Bump et al. 1947, Slagsvold & Grasaas 1979). Studies showing that reproductive success correlates with weather factors have identified two critical periods. These are the pre-laying period and the first weeks after hatching, with small grouse species being most affected in the early period, and large grouse species being most affected in the latter period (Swenson et al. 1994). In my study, I tried to determine whether hazel grouse numbers have been stable during the last 33 years and whether weather affected numbers in autumn.

Some results obtained during shorter periods of the study, e.g. dependence of hazel grouse on tree species diversity and age of forests, were described earlier (Klaus 1991, 1995, 1996).

Material and methods

Study area and census technique

During 1972-2004, I studied a hazel grouse subpopulation in the central part of the Bohemian Forest, district Klatovy, Czechia. The 'Šumava National Park', covering 68,520 ha, was established in 1991 and parts of my study area were incorporated into the park. Up to now, the entire study area has been subjected to forest management practices of varying intensity. On a 100-km² area, I mapped 140 hazel grouse 'sites' along fixed routes totalling 80 km (Klaus 1995). Sites were located by indirect indications, e.g. dust-bathing places, droppings, feathers and tracks, and by use of a whistle that imitated the territorial song of the male. These methods were described by Wiesner et al. (1977) and Swenson (1991a). I prefer the term 'site' to 'territory', because I did not always obtain a response to the whistle at sites occupied by hazel grouse. Typically, all 'sites' were found within habitats described in the literature as being suitable for hazel grouse (Swenson 1991b, Bergmann et al. 1996). The distance between different 'sites' was ≥ 500 m. In the first four years of my study, the presence of hazel grouse was tested on about 40 sites previously found by Kučera (1975). Afterwards 50-60 sites were tested each year, with the route varying only slightly between years. On every site the whistle was used for 15 minutes. If there was no response, I searched for indirect signs of hazel grouse. The results of these two tests indicated whether the site was occupied. Most effective was the control of known dust-bathing sites, because they were used traditionally year after year. The proportion of dust bathing sites tested remained about the same in all years. In the second half of October, I estimated the proportion of sites occupied after the break-up of broods. All data on density are indices rather than direct counts. The 'density index' of a given year was defined as the quotient between the number of occupied sites and the number of sites tested for the presence of hazel grouse.

Origin of weather data

All weather data were kindly provided by the meteorological station of Churanov ($49^{\circ}04'N$, $13^{\circ}36'E$, at 1,118 m a.s.l.) located at the eastern edge of the study area. The station represents the hazel grouse habitats in the higher elevations of the study area. Unfortunately, no weather data were available for habitats at lower elevations.

Statistics - stepwise multiple regression analysis

The yearly indices of densities were transformed into 'annual rates of change' by dividing the index of a given year by the index of the preceding year. These finite rates of change were then regressed on 20 weather variables (total monthly precipitation and mean monthly temperature of January through October for all years studied (1972-2004), using stepwise multiple regression analysis (backward mode, SPSS; Norukis 1993). The resulting 17 models were checked stepwise and the 'partial regression coefficients' obtained.

Results and discussion

Population dynamics

Hazel grouse abundance fluctuated during the 33 years of study (Fig. 1). The small long-term decline was not significant ($R^2 = 0.0044$) and in fact numbers tended to increase during 1994-2004. Prior to our study period, Kučera (1975) found a continuous increase in hazel grouse density in the same area between 1963 and 1971, 18-27 years after the start of the extensive forest succession covering large parts of the Bohemian Forest (Klaus 1995). The fluctuations that have been found in my study area up to now are less pronounced than those found in more northerly hazel grouse habitats (Semenov-Tjan-Shanskii 1960, Rajala 1966, Beshkarev et al. 1994, Ranta et al. 2004). According to Angelstam et al. (1985) and Cattadori & Hudson (2000) fluctuations of grouse usually decline as one moves south. Based on Figure 1, I infer that fluctuations were more pronounced before 1982. In a later study, I will investigate whether the observed variation in hazel grouse numbers follows a cyclic pattern.

Effects of weather

The statistically relevant variables that were found in the stepwise multiple regression analysis are summarised in Table 1. Of the 20 variables tested, six were significantly correlated with the annual rate of change of hazel grouse density in autumn. Mean monthly temperature and total precipitation in April were positively (highly significant) correlated with changes in hazel grouse density in autumn. For two different

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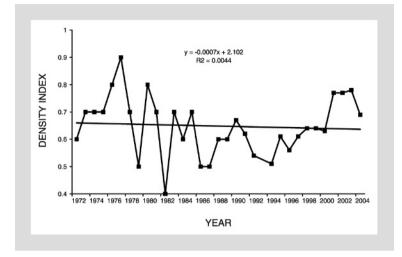


Figure 1. Variation in the density index of hazel grouse in autumn (yearly ratio of the number of occupied sites /number of controlled sites) during the 33 years of study in the Bohemian Forest, Šumava, Czech Republic.

hazel grouse study areas (southwestern Finland and southern Poland) Swenson et al. (1994) found that high temperatures in March were positively correlated with hazel grouse density. These authors argued that the reproductive success of hazel grouse is largely determined by the availability of nutritionally rich food and the ability of females to find it during the prelaying period. During this period, female hazel grouse forage primarily on newly sprouted forbs (Swenson 1991b). The selection of places with the earliest plant phenology has been documented for other grouse females (Siivonen 1957) and was often observed by me, when hazel grouse were found foraging along small streams with highly diverse ground vegetation that became available earliest in the season (see White 1993). In most parts of my study area, high temperatures and rainfall in April accelerated snow melting. In my study area, laying begins in mid-April.

Using a different method, Eiberle & Matter (1984) examined correlations between the number of hazel grouse harvested by hunters in Kanton Graubünden, Switzerland, during 1919-1961, and temperature and precipitation during bi-monthly periods within and prior to the year of harvest. They found only one significant correlation (P < 0.05) with the number of hazel grouse harvested, and that was mean temperature during March and April in the year of harvest. My results support the findings of Eiberle & Matter (1984).

As shown in Table 1, higher precipitation in May is negatively correlated with change in hazel grouse numbers in autumn. As in other mountain areas of central Europe (Müller 1992 for the Black Forest; C. Beyer and U. Wilmering, pers. comm.) hatching of hazel grouse chicks in my area often occurs in the last week of May, which probably explains the negative effect of rain in this month on numbers in autumn. Swenson et al. (1994) were unable to detect a negative effect of precipitation in May or June, the first few weeks after hatching, on hazel grouse density in autumn during a 14-year period in Finland and a 6year period in Poland. In contrast, a negative effect of rainfall just after hatching occurs in capercaillie Tetrao urogallus (Höglund 1952, Siivonen 1957, Semenov-Tjan-Shanskii 1960) and other species of larger grouse (see Swenson et al. 1994 for references).

Table 1. Results of stepwise multiple regression analysis of the correlation between hazel grouse density (annual rates of change) and weather variables (total monthly precipitation, mean monthly temperature) during 1972-2004. Results are only shown for the six statistically relevant variables of the final model of the backward mode.

Dependent variable, standardised IndQ	Unstandardised correlation coefficients B	Standardised correlation coefficients Beta	Р
Mean temperature in April (°C)	+0.843	+0.850	0.000
Total precipitation in April (mm)	+0.659	+0.644	0.001
Mean temperature in May (°C)	-0.400	-0.403	0.017
Total precipitation in May (mm)	-0.328	-0.328	0.043
Mean temperature in September (°C)	-0.339	-0.333	0.054
Total precipitation in September (mm)	-0.470	-0.485	0.007

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I cannot explain the negative correlations between annual rate of change of hazel grouse numbers in October and temperature in May, when females incubate, and temperature and precipitation in September, when broods break up. I can only speculate that other dependent variables, such as food quality and/or predation, are involved. Altogether, the significant weather variables summarised in Table 1 explain 44% of the density variation in hazel grouse in autumn in our study area.

It would be interesting to follow the influence of weather on hazel grouse reproduction under the warmer and dryer conditions predicted by climate change. Such climate change may have favoured reproduction and increase in density over the last 10 years.

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