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Original article

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In black grouse *Tetrao tetrix* the survival of juveniles from hatching until recruitment is a critical determinant of population growth. The proportion of juvenile survivors from hatching until recruitment declines continually, but juvenile mortality rates are commonly highest during approximately the first 10 days after hatching. Likely causes of mortality include adverse weather, predation and availability of food. Little is known, however, about how individual properties, such as body mass of hen or chicks and properties of the brood rearing environment (e.g. vegetation characteristics or weather conditions) interact with each other and/or with fluctuating levels of predator abundance in determining early brood survival, simply because such data are very scarce. Using an information-theoretic approach, our paper identifies determinants of early daily survival rates of black grouse chicks in a managed forest landscape of central Finland. During the three years of our study, the proportion of hens losing their broods within 10 days after hatching varied between 0.08 and 0.36.The variation in daily survival rates of chicks was largely mediated by a combination of four key explanatory variables. Brood survival clearly increased with the extent of bilberry *Vaccinium myrtillus* cover, and was further affected by interactions of temperature and hatching date as well as temperature and chick body mass. Low temperatures consistently resulted in lower daily survival rates. An increase in temperature, however, was more beneficial for early hatchers and heavy chicks. There was no difference in survival between broods from yearling and adult hens and we found no effect of predator density, be it as main effect or as interaction with other variables, on the daily survival rates of chicks. Improving black grouse breeding success can be regarded as a key management target which may be critical for their recovery. Our results suggest that such management should favour protection or local recovery of bilberry, as well as integrate weather and climate changes into the equation of hunting management.

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In Finland and much of Fennoscandia, both long-term breeding success and size of black grouse *Tetrao tetrix* populations have faced severe declines during the past decades (Helle et al. 2002, Ludwig et al. 2006). Declines in grouse breeding success in Finland and elsewhere are commonly associated with increased rates of nest loss due to increased predation (Marcström et al. 1988, Baines 1991, Caizergues & Ellison 1997, Kurki et al. 1997, 1998, Kauhala & Helle 2002, Ludwig 2007), but the processes determining early brood survival are generally more difficult to study and are therefore less well known. Survival of juveniles from hatching until recruitment to the breeding population in the

following year is a critical determinant of population growth in many species of grouse (Tetraonidae; Sandercock et al. 2005). Juvenile mortality rates in grouse are commonly the highest during approximately the first two weeks after hatching (Ludwig et al. 2006, Hannon & Martin 2006), and are therefore an important component of the variation in annual recruitment. The main causes of early brood mortality are generally considered to be predation, unfavourable weather conditions as well as chick and/or hen quality. For instance, high predation induced chick mortality during the first 10-14 days after hatching has been reported for capercaillie *T. urogallus* (Kastdalen & Wegge 1991), red grouse *Lagopus lagopus scoticus* (Park et al. 2002), ruffed grouse *Bonasa umbellus* (Larson et al. 2001), white-tailed ptarmigan *L. leucura* (Braun et al. 1993) and sharp-tailed grouse *Tympanuchus phasianellus* (Manzer 2004). On the other hand, exposure to cold and/or rainy conditions has been shown to be a major source of early mortality in willow ptarmigan *L. lagopus* (Erikstad & Andersen 1983, Erikstad 1985). Hen condition, which may be affected by e.g. weather conditions in the pre-nesting period, may further affect egg quality, and hence also chick quality and viability (e.g. Siivonen 1958, Moss & Watson 1984, Hannon & Martin 2006).

The role of weather conditions for breeding success in Finnish forest grouse such as black grouse, capercaillie or hazel grouse *B. bonasia* has been controversial (Lindström 1996). Recent results, however, have demonstrated that weather conditions, especially temperature, experienced by black grouse chicks during the first 10 days after hatching, strongly influence the annual breeding success (Ludwig et al. 2006). These results also underline the importance of accurately estimation and matching of the timing and the length of the weather period with the timing of hatching if one is to gain biologically meaningful inference. The effect of weather has further been shown to be exacerbated by climate change. Due to an advance of spring phenology, black grouse have advanced the timing of both the breeding and the hatching. Problematically, early summer has not advanced, i.e. has not warmed up, and hence grouse chicks are increasingly hatching under colder conditions (Ludwig et al. 2006). Little is known, however, about how individual properties (e.g. body mass of hen or chicks) and properties of the brood rearing environment (e.g. vegetation characteristics or weather conditions) interact with each other and/or with

fluctuating abundance of predators to determine early brood survival.

Human alteration of brood habitat can influence early juvenile survival through increased predator densities, direct disturbance and changes in the spatial and temporal distribution of food or lack of cover (e.g. Miquet 1990, Kurki et al. 2000, Storch 2000). In central and southern Finland, the majority of black grouse breeding habitat has been heavily altered by modern forestry practices such as clear-cutting and large-scale drainage during the past decades (Kurki et al. 2000, Ludwig et al. 2008), and the consequences of it on black grouse nesting success have recently been demonstrated (Ludwig 2007). Until now, little knowledge exists on how interactions of humanly altered habitat properties, weather, predators and individual characteristics of hens and chicks affect early brood survival.

The main scope of our study was to evaluate both potential direct and indirect causes of early mortality in black grouse broods in a managed forest landscape in central Finland. Using an information-theoretic approach and a unique data set on the individual brood level, we aimed at identifying the most important explanatory variables and the extent to which variables interact with each other. We took temporal and spatial variation into account.

Material and methods

Field methods

We monitored survival of black grouse broods at a total of seven different lekking sites in central Finland during 2003-2005. We located the sites in the communes of Jyväskylä Maalaiskunta, Jämsänkoski, Keuruu, Multia and Petäjävesi. The entire study area covers a surface area of 4,000 km^2, the farthest distance between two sites being approximately 100 km. Black grouse broods prefer young stages of boreal forests (Swenson & Angelstam 1993). Potential brood habitats in the study sites are dominated by landscapes heavily managed for timber production, consisting of a patchy mosaic of commercial forests at different successional stages varying from new clear cuts to harvestable forest stands. Approximately one third of the forestry surface consists of drained bogs (Ludwig et al. 2008). The major tree species are Scots pine *Pinus sylvestris*, Norway spruce *Pinus sylvestris*, European white birch *Betula pendula* and

downy birch *B. pubescens*. Ground vegetation is mostly dominated by species of *Vaccinium* (i.e. bilberry *V. myrtillus*, lingonberry *V. vitis-idea* and bog bilberry *V. uliginosum*), heather *Calluna vulgaris* and a mixture of different grass and herb species.

We captured hens in winter from feeding sites on the leks using oat-baited walk-in traps (Ludwig 2007). After capture, we aged hens and classified them as either yearlings (hatched the previous season) or adults on the basis of shape, wear and colouring of the outermost primary wing feathers (Helminen 1963) and weighed them to the nearest 5 g. Because hens gain weight rapidly just prior to the breeding season in April, we adjusted body mass of the few hens captured during that time (N = 7) by substracting the mean period specific increase in body mass. We took a blood sample by puncturing of the brachial vein and counted the number of the two most common extracellular blood parasites, microfilaria (Höglund et al. 1992) and *Trypanosoma* spp. (Rätti et al. 1993) according to Lebigre (2008). Because of highly skewed distributions of *Trypanosoma*, we defined this variable on a presence/absence basis. We also used blood samples to determine hematocrit levels of the birds by measuring the relative amount of red blood cells in the total volume of blood sampled (Lebigre 2008). We fitted hens with a necklace-mounted radio-transmitter (Televilt or Holohil; weight 15-20 g ∼ 1.6-2.2% of the average body mass and a life expectancy of 18-30 months). We used portable receivers and both handheld Yagi and omnidirectional car antennas to locate the females on the nest and subsequently the broods.

We normally localised the hens on their nests at the beginning of the incubation period and the timing of hatching was evaluated on the basis of previous investigations (H. Siitari, unpubl. data), by floating the eggs in hand-warm water in order to estimate the incubation status. On the day of calculated hatching, we revisited the nest to assess the nest status. If the nest was successful, we captured the brood, counted the chicks and weighed them individually to the nearest 0.1 g. In most cases, the day of hatching was exactly identified, as the chicks were mostly still on or very close to the nest. If the brood had left the nest, it was located by use of telemetry and captured, and the approximate age was determined on the basis of wing feather development and/or presence/absence of egg teeth. Using this technique the day of hatching could always be identified to ± 1 day. A nest was declared successful if ≥1 chick had left the nest. Unsuccessful hens were revisited regularly to check for re-nesting attempts.

After leaving the nest, broods were followed regularly (maximum once per day) during the first two weeks. The brood was normally not disturbed unless the chicks were to be counted. We estimated the location of the brood using triangulation, with at least 2-3 telemetry bearings collected from a close range. The chicks were counted at the age of approximately two weeks. An accurate estimate of the brood size is very difficult at this stage, and therefore we used brood survival as the dependent variable of interest. A brood was considered alive if at least one chick was sighted or heard. Each brood was counted again at the age of about two months. In two cases one or more chicks were found to be alive at the age of two months, while none was detected at two weeks. We used this information to correct the brood survival status at the age of two weeks. Also, if the brood was not found but the hen's behaviour clearly indicated chicks to be alive (e.g. hen is trying to confuse by staying close and faking a broken wing, or apparent attacks towards the observer), the brood was considered alive. On the day of hatching, we installed a data logger (Kooltrak Inc.) and a rain gauge close to the nest site which allowed us to monitor ambient temperature and precipitation. Both devices were placed in a shady place in order to avoid direct sunshine, and the data loggers were placed 0.5 m above the ground and were programmed to measure temperature by intervals of 30 minutes. Rainfall was measured and recorded, and the device was emptied every time the brood was located. During the first two weeks broods commonly move away from the nest, but normally stay within a distance of 1-2 km of the nest. However, we found very high correlations (mean r > 0.95) between neighbouring measurements of both temperature and rainfall up to several kilometres apart, which suggests that this is not a major source of bias.

After the chicks were counted at the age of two weeks, we revisited the brood sites in order to describe the environment. First, we sampled the field layer from five 2 × 2 m squares: one square at the exact position of the brood's GPS-coordinates, and one at 15 m south, north, west and east of the central square, respectively. Within each square the coverage of the different vegetation types and characteristics we expressed as proportions. The field layer we described by the following character-

istics: proportions of bilberry, heather and grassy vegetation (grasses, sedges, herbs) cover. Secondly, using the central square as the central point, we calculated the following metrics (according to Hyvämäki 2002): the number of trees/ha, number of shrubs/ha and tree canopy cover. We further evaluated the drainage status (drained/not drained) for each individual brood site and estimated the visibility of the brood's location by placing a grouse-sized object in the central square and evaluating the distance from which it could be seen from the four compass directions, at a height of approximately one metre. We then expressed the visibility as the geometric mean of the visibilities from the four directions. As we were investigating the causes of mortality during the first 10 days after hatching (Ludwig et al. 2006), only brood localisations in this period were used in the analyses. Likewise, we calculated mean temperature as well as total precipitation for this period. For each of the brood locations we averaged the variables of the five plots, and then for each brood we averaged data from all the locations that fell within the 10-day post-hatch period. For the categorical variable drainage the averaged variable expresses the proportion of sites used by a particular brood that which is drained.

We approximated relative mammalian predator densities for red fox *Vulpes vulpes* and marten *Martes martes* by monitoring snow tracks. In each of the sites, we investigated a polygon-shaped line transect of 10 km length by skiing along the line in mid winter. During 2003-2006, we investigated the lines on two subsequent days. On the first day, we marked old predator tracks and on the second day, we counted the new tracks that had crossed the line. The polygon was situated such that it would encompass the majority of potential brood rearing areas around each of the lekking sites. Because the indices of fox and marten were highly positively correlated (r=0.65), we combined the two indices to characterise the overall predator density. Also, preliminary model runs (see below) showed that this index performed better than when using fox and/or marten indices separately. The index was defined as the total number of tracks/10 km/24 hours. The method is essentially the same as the Finnish Wildlife Triangle Scheme, which has been proved very successful in a wide array of population and landscape ecological studies (e.g. Lindén et al. 1996, Kurki et al. 1997, Ludwig et al. 2006, Ludwig 2007).

Statistical analyses

We used the nest survival model procedure and the logit link function of program MARK to estimate daily brood survival rates (DSR). The nest survival procedure is suitable for modelling brood survival within a given period of time, as long as the fate of the brood is treated as a categorical variable (brood alive=at least one chick alive). The model allows for variable brood exposure time, i.e. accounts for the problem of counting broods of different age (Mayfield 1961). For every model, MARK produces the Akaike Information Criterion corrected for small sample size (AIC$_c$), allowing models to be ranked according to the amount of information loss (Burnham & Anderson 2002). For a given set of candidate models, the model with the lowest AIC$_c$ is considered the best model, i.e. the model with the least information loss. We also presented the difference in AIC$_c$ ($\triangle$AIC$_c$), Akaike weight (w) and deviance (dev; in respect to the full model).

We checked all variables for multicollinearity, and whenever pairs of independent variables were strongly correlated (r $\geq$ 0.5) one would be excluded based on the importance of the variable as established through previous research. The variables we used in the candidate models were the following: female age (two categories: first breeder & older), body mass of the hen (in g), hatching date (1 = earliest nest of the study), microfilaria (n), trypanosoma (presence/absence), hematocrites (in % red blood cells), clutch size (n), mean chick mass (in g), bilberry cover (in %), heather cover (in %), grassy vegetation cover (in %), tree density (number/ha), shrub density (number/ha), canopy coverage (in %), visibility (in metres), drainage (two categories: drained/not drained), rainfall (in mm), temperature (in °C) and predator track density (tracks/24 hours/10 km). For the analysis, we arcsine transformed variables that express proportions.

We accounted for variability induced by study site and year by introducing a dummy control variable for each year and site in all of the models. In this way, site and year dependent variation was effectively standardised across all candidate models, and the differences between candidate models largely reflect differences in the predictive ability of the explanatory variables. For ease of interpretation we did not include control variables in the tables.

In addition to year and site, we included a

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maximum of two main effects. This we did because large numbers of predictor variables with respect to n response variables result in data too thin to accurately estimate parameters (Hosmer & Lemeshow 1989), thereby compromising comparison of different effects. Furthermore, it is well known that the variance of the model increases exponentially with the number of parameters to be estimated (Burnham & Anderson 2002). Using all possible combinations with up to two main effects, we developed a total of 190 candidate models to predict early brood survival. In addition to the main effect models, we introduced biologically meaningful interactions between main effects whenever considered necessary, to investigate whether the effect of a variable was dependent on the effect of some other variable.

In order to establish a subset of 'best' models, we selected all models that performed better, in terms of AIC_c, than the model including only site and year variables. That is, from an information theoretic point of view, we are interested in all the models i for which the following condition is fulfilled:

$$AIC_{cthreshold} - AIC_{ci} \geq 2 \qquad (1)$$

where $AIC_{cthreshold}$ represents the AIC_c of the site + year model. From that group of models, even

the worst will be better, in terms of its AIC_c, than the threshold model (Burnham & Anderson 2002). Such a procedure commonly suffers from model selection uncertainty (Burnham & Anderson 2002). It needs to be understood, however, that we are mostly interested in the relative importance of explanatory variables, rather than a particular 'best' model. We therefore made further inference based on the entire subset of selected models. We present Akaike weights w_i for each variable that is present in at least one selected model, and average the parameter estimates (and confidence intervals) across the models where a given variable occurs (Burnham & Anderson 2002). Variables with 95% confidence intervals that include zero can be considered as not significant.

Results

During 2003-2005, we monitored a total of 81 successfully hatched broods (out of 136 nests) and the number of locations per brood during the first 10 days varied within 3-9. Early brood loss varied between years ($\chi^2 = 6.19$, $P = 0.045$); the frequencies of complete brood loss during the first 10 days were 0.36, 0.26 and 0.08 for 2003, 2004 and 2005, respectively. Mean values for all variables, both for

Table 1. Mean values (untransformed data for all sites and years combined; N = 81) and standard deviations of the variables used in the models, both for successful (Alive) and unsuccessful broods (Dead), along with t-test and P-values. Units for each variable are explained in the methods section.

	Dead		Alive			
	Mean	SD	Mean	SD	t	P
Hen body mass	876.38	47.04	884.89	50.20	0.69	0.24
Clutch size	8.85	1.31	8.66	1.08	0.66	0.51
Chick body mass	23.54	1.71	24.17	1.77	1.39	0.17
Hatching date	10.80	1.55	9.25	0.55	1.19	0.24
Microfilaria	21.29	21.30	44.23	58.97	1.70	0.09
Trypanosoma	0.45	0.50	0.49	0.51	0.32	0.79
Hematocrites	0.53	0.03	0.52	0.03	1.33	0.19
Temperature	11.52	2.26	12.36	1.94	1.50	0.11
Rain	24.48	19.38	27.80	20.62	0.63	0.53
Predator track density	10.61	11.43	4.78	6.34	2.87	< 0.01
Bilberry cover	19.20	14.18	35.09	16.20	3.01	< 0.01
Heather cover	2.12	4.63	2.52	4.28	0.95	0.73
Grasses & herbs	58.30	29.16	45.62	25.53	1.82	0.07
Canopy	37.34	21.62	37.51	17.47	0.08	0.93
Drainage	26.85	26.58	44.19	34.54	2.05	0.04
Trees	1021.14	532.61	1372.20	769.91	1.89	0.06
Shrubs	42.10	30.57	68.59	42.72	2.56	0.01
Visibility	4.91	2.55	5.13	2.59	0.33	0.74

Table 2. Best models of brood DSR in decreasing order of importance. AIC_c = Akaike Information Criterion, AIC_c = Difference in AIC as compared to the best model, w = Akaike weight, Dev. = Deviance, L = Likelihood, K = Number of parameters. K includes the indicator variables for site and year (included in every model). Note that the interaction models (indicated by *) also include the respective main effects. The threshold model (including only indicator variables for site and year without main effects) is shown as a reference, at the bottom of the table.

Model	AIC_c	AIC_c	w	L	K	Dev.
Hatching date*temperature, Ageday1*Temperature	66.07	0.00	0.173	1.00	11	435
Chick body mass*temperature, Chickmass*Temperature	66.24	0.17	0.158	0.92	11	437
Bilberry, microfilaria	66.85	0.78	0.117	0.68	10	464
Bilberry, drainage	67.02	0.95	0.107	0.62	10	466
Hatching date*chick body mass, Ageday1*Chickmass	67.21	1.14	0.098	0.57	11	447
Bilberry, rain	67.90	1.83	0.069	0.40	10	475
Bilberry	68.30	2.23	0.057	0.33	9	499
Bilberry, canopy	68.61	2.54	0.049	0.28	10	482
Bilberry, HT	69.25	3.18	0.035	0.20	10	488
Bilberry, chick body mass	69.43	3.36	0.032	0.19	10	490
Bilberry, body mass	69.63	3.56	0.029	0.17	10	492
Bilberry, trees	69.76	3.69	0.027	0.16	10	493
Bilberry, shrubs	69.95	3.89	0.025	0.14	10	495
Bilberry, grasses	70.00	3.94	0.024	0.14	10	496
Threshold model	72.06	5.99	0.008	0.05	8	558

successful and unsuccessful broods, as well as t-tests and P-values for comparisons between groups, are shown in Table 1.

Out of more than 200 candidate models (190 main effect models plus the interaction models), 14 models fulfilled the condition $AIC_{cthreshold} - AIC_{ci} \geq 2$, where $AIC_{cthreshold}$ represents the AIC_c of the model including site and year only (Table 2). The set of best models can be clearly structured into two groups; three out of the five best models were interaction models involving the variables temperature, hatching date and chick body mass. All other models included main effects only, and each of the remaining models included the variable bilberry cover. Inspection of the relative Akaike weights (w), revealed strong model selection uncertainty, the weight of the best model being only 0.173. However, considering the number of models in the candidate set this is hardly surprising. We therefore gained further inference by calculating relative weights,

Table 3. Averaged Akaike weights (w_{hat}), averaged parameter estimates (β_{hat}), and its standard error (SE_{hat}), lower (LCI_{hat}) and upper confidence intervals (UCI_{hat}) for all variables, including interactions (indicated by *), present in at least one best model. Note that β_{hat} for temperature, chick body mass* hatching date are based on the main effects from the interaction models.

| Variable	w_{hat}	β_{hat}	SE_{hat}	LCI_{hat}	UCI_{hat}
Bilberry	0.571	4.397	2.047	0.386	8.408
Temperature	0.331	-1.821	2.912	-7.528	3.885
Chick body mass	0.288	-1.085	1.663	-4.345	2.174
Hatching date	0.270	0.791	0.413	-0.018	1.600
Hatching date*temperature	0.173	-0.098	0.039	-0.174	-0.023
Chick body mass*temperature	0.158	0.336	0.209	-0.074	0.747
Microfilaria	0.117	0.022	0.013	-0.004	0.048
Drainage	0.107	0.019	0.011	-0.002	0.040
Chick body mass*hatching date	0.098	0.111	0.053	0.007	0.215
Rain	0.069	-0.036	0.024	-0.082	0.010
Canopy	0.049	-2.013	1.544	-5.040	1.014
HT	0.035	8.514	8.193	-7.544	24.572
Body mass	0.029	4.731	5.572	-6.190	15.652
Trees	0.027	0.000	0.001	-0.001	0.001
Shrubs	0.025	0.006	0.010	-0.013	0.025
Grasses	0.024	0.574	0.964	-1.315	2.462
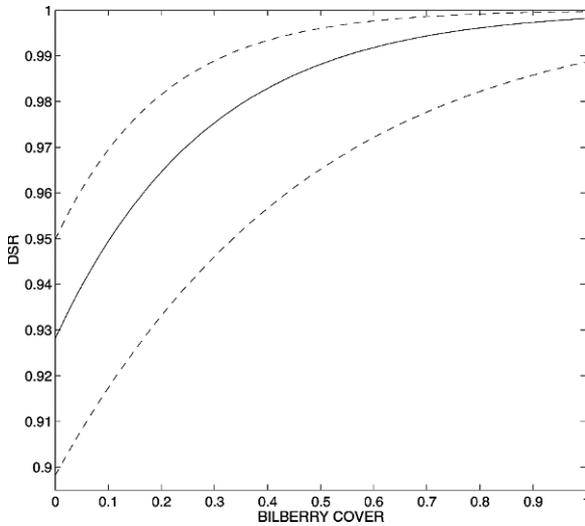
Figure 1. Early daily survival rates (DSR; during the first 10 days after hatching) for black grouse chicks as a function of bilberry cover, for all years and sites combined.

averaged β-estimates as well as averaged upper and lower confidence intervals for all variables being present in at least one of the selected models (Table 3).

Being present in 11 out of 14 models, the variable bilberry cover was clearly the best predictor (Fig. 1). The averaged β-estimate as well as an averaged confidence interval that excludes zero, suggest a
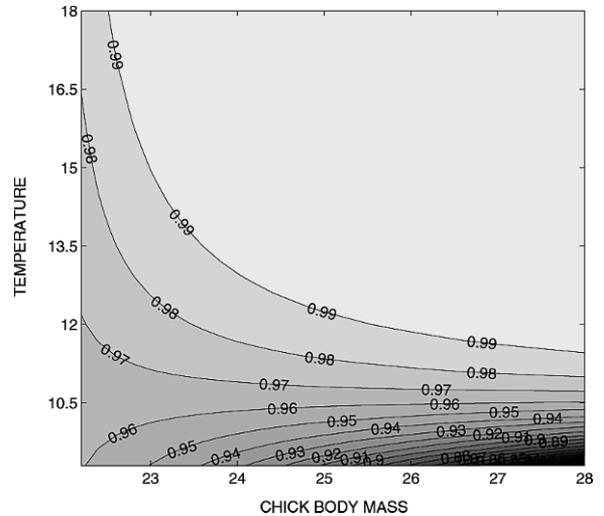

Figure 2. Isoclines of early daily survival rates (DSR; during the first 10 days after hatching) for black grouse chicks as a function of the interaction temperature*hatching date for a given year (2003) and a given site. Hatching date is expressed as days of June, temperature expresses the experienced daily mean temperature (in °C) during the first 10 days after hatching.

Figure 3. Isoclines of early daily survival rates (DSR; during the first 10 days after hatching) for black grouse chicks as a function of the interaction temperature*chick body mass for a given year (2003) and a given site. Temperature expresses the experienced daily mean temperature (in °C) during the first 10 days after hatching and chick body mass is expressed in grams.

strong positive effect of bilberry cover on DSR of broods during the first 10 days after hatching. We found no interaction of bilberry with other variables. The effects of temperature, hatching date and chick mass, on the other hand, were clearly dependent on interactions with each other, as none of the respective main effect models was included in the candidate set. As is often the case with interactions, the β-estimates may not be indicative of the effect's direction (positive/negative). In order to understand it better, we visualised DSR as a function of the two most important interactions, i.e. temperature*hatching date and temperature*chick mass (Figs. 2 and 3).

Predator track density was not included in any of the best DSR models, despite the fact that predator track density was significantly higher for unsuccessful nests (see Table 1). Furthermore, DSR of broods did not seem to depend on hen age, as age was not included in any of the best models either. Cross tabulation of brood fate against age showed no significant effect ($c^2 = 0.33$, $P = 0.53$, $N = 81$).

Discussion

The statistical approach we used allowed us to evaluate the relative importance of different covariates on early brood survival, both among and be-
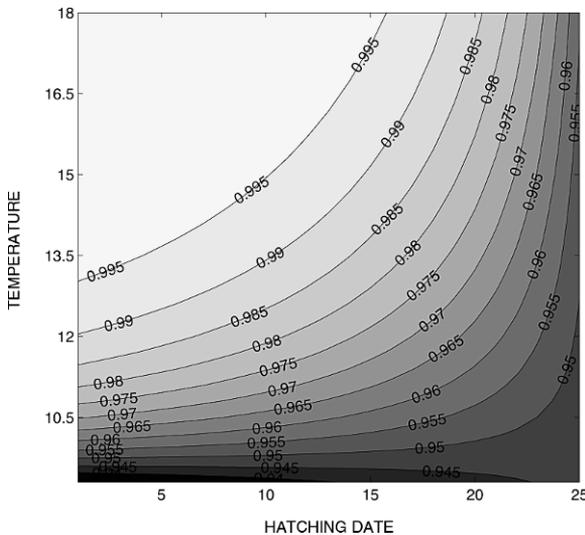
tween different levels (i.e. individual brood and environment). When having a large number of closely related models, such as in our case, designation of a single best model may not be satisfactory, because that model is likely to be highly variable. In other words, the 'best' model is likely to vary from data set to data set, even if replicate data sets would be collected under the same underlying process. In such a case, model and parameter averaging provides more stabilised inference (Burnham & Anderson 2002).

We defined early brood survival as whether or not at least one chick survived the first 10 days after hatching. Using brood size, as a continuous variable, rather than a binary outcome, may eventually provide more information. However, we checked broods without using pointer dogs, and often under difficult conditions, and a reliable estimate of brood size at the age of 10-14 days was difficult at the least. However, using two brood counts (at two and eight weeks of age), as well as features of individual hen behaviour, provided a solid basis for inferring whether or not at least one chick was still alive at this point of time. The proportion of hens without a brood during late summer is also commonly used in population studies based on line transects or wildlife triangle monitoring data (e.g. Kurki et al. 2000) to assess breeding success. This proportion will be made up by those that lose the nest, lose the brood during the early but critical stage, or lose the brood after the critical early stage. The use of the first 10 days after hatching as the critical period, on the other hand, is justified by a recent study (Ludwig et al. 2006). In our study, we demonstrated that the effects of weather conditions experienced after hatching are very critical for survival, but then rapidly fade after a period of 10 days. Similarly, intense mortality during the first 10-14 days has been documented in a number of grouse species (e.g. Lindén 1981a, Erikstad & Andersen 1983, Kastdalen & Wegge 1991, Braun et al. 1993, Caizergues & Ellison 2000, Larson et al. 2001). Such mortality has been experimentally shown to be due in part to chick viability, which ultimately is influenced by maternal condition and egg quality (Moss & Watson 1984). For instance, according to the 'early vegetation' hypothesis by Siivonen (1958), resource availability before and during egg-laying may affect hen condition and hence egg quality. In our study, chick body mass was strongly correlated with fresh egg mass $r=0.568$, $P < 0.000$), and negatively correlated with egg quality, here defined as fresh egg mass - chick body mass ($P = -0.365$, $P = 0.001$). Hen body

mass, on the other hand, was related to neither chick body mass nor egg quality ($r=0.178$, $P=0.112$ and $r = 0.066$, $P = 0.558$, respectively). Hence, in our study, the effect of chick body mass is not necessarily mediated by hen condition.

In our study, variation in early brood survival was mediated by the extent of bilberry cover, as well as through the interactions of temperature, chick body mass and hatching date. Being present in 11 out of 14 selected models, cover of bilberry was by far the single most important main effect. The lack of any interaction with other variables suggests the effect to be independent of other covariates. The proportion of bilberry has previously been shown to be of high importance to grouse chicks (e.g. Baines et al. 1994, Storch 1994, Wegge et al. 2005) and in capercaillie adults, summer home-range size was negatively correlated with proportion of bilberry cover (Storch 1993). The importance of bilberry is likely to be food mediated. Due to the high energy requirement in early life (Lindén 1981b), chicks rely on a protein rich invertebrate diet (Baines et al. 1994, Wegge et al. 2005). While chicks may prey upon a wide array of invertebrate taxa (e.g.Kastdalen & Wegge 1984, Picozzi & Hepburn 1984, Baines et al. 1994), lepidopteran larvae may be of particular importance (Spidsö & Stuen 1988), as they are particularly rich in proteins and easy to prey upon. Bilberry is commonly associated with occurrence of lepidopteran larvae (Wegge et al. 2005, Lakka & Kouki 2009). Furthermore, bilberry is the dominant type of ground vegetation in the so-called *Oxalis-Myrtillus* forest-site type (Hyvämäki 2002), which is traditionally considered the most important brood habitat type in Finland (Rajala 1966, Lindén & Rajala 1981). During the second half of the 20th century, however, the total coverage of bilberry should have decreased by about 50% (Reinikainen et al. 2000). Our results therefore suggest that in addition to increased predation (effect on nest success; Ludwig 2007) and weather and climate change (effects on brood survival; Ludwig et al. 2006), declines in bilberry cover may have contributed to the long-term decline in reproductive success observed in Finnish black grouse populations (Ludwig 2007).

In addition to bilberry cover, the daily brood survival was affected by interactions of chick body mass, temperature and hatching date; in particular by the interactions temperature*hatching date and temperature*chick body mass. The respective models with main effects only were not included in the set

of selected models, which suggests that the effects occur only by means of interactions. Averaged parameter estimates of main effects, as estimated from interaction models, are commonly difficult to interpret, especially the direction of the effect. The visualisations of the interactions (see Figs. 2 and 3) shed more light on how the covariates interact. Both interactions suggest that daily survival rates increase with temperature. However, the benefits of increased temperatures are more pronounced when hatching early (see Fig. 2). This is likely due to the development of temperature patterns in early summer: while the mean temperatures of the 10 day post-hatching periods tend to increase from early to late hatchers, the variance of experienced temperatures decreases rapidly (Ludwig et al. 2006). Our results therefore strengthen the view that early hatching is more risky than late hatching. This is especially true under the scenario of the concurrent climate change. Due to the advancement of spring phenology, black grouse have advanced reproduction and increasingly hatch earlier. Since early summer has not advanced, i.e. has not become warmer, chicks increasingly hatch into unfavourable and more variable conditions (Ludwig et al. 2006). Also, hens that lay too early may produce a poor quality of eggs, because they lay before their diet allows them to optimise the egg quality (Moss et al. 1981). Later hatchers, on the other hand, are likely to face warmer temperatures with less pronounced daily fluctuations, hence the interaction between temperature and hatching date. In a study of black grouse in the Swiss Alps, Zbinden & Salvioni (2004) found that if the mean temperature of the first five days after hatching falls below a threshold of about 11.5°C, the probability of brood loss increases significantly. In the Alps, this does not occur before the beginning of July (when chicks hatch in the Alps), but in central Finland it happens already by about mid June, or even earlier (when chicks hatch in central Finland). A similar threshold level could be functional in our study population (see Figs. 2 and 3).

Cold temperatures may act as a double jeopardy for newly hatched chicks. First, after having used the nutrients of the egg yolk sack the energy requirement of grouse chicks are particularly high at the age of 4-8 days (Lindén 1981b), and the chicks rely entirely on protein rich insect food (Baines et al. 1994, Wegge et al. 2005) before gradually shifting towards a more plant dominated diet from the age of 2-3 weeks onwards. Cold temperatures in early summer may well affect the availability of insect food. Secondly, the thermoregulatory capacity fully develops only at the age of approximately three weeks (Hissa et al. 1983). Before that, and especially before becoming fledglings, excessive heat loss is likely to be lethal. That is, when temperatures are cold and acquiring food is particularly important, chicks need to trade-off between getting warmed up by the mother and foraging.

The interaction between temperature and the chick's body mass is more complicated (see Fig. 3). Heavy chicks seem to be less successful at very low temperatures, but their survival prospects improve at a faster rate when temperature increases. Already at rather low temperatures (11-12 °C), large chicks gain advantage, and do consistently better than light chicks at more elevated temperatures. The mechanism of this interaction is less clear. Large chicks should be more resistant to hypothermia, but on the other hand, they might be more prone to food shortage, due to increased metabolic demands. It seems clear, however, that under normal conditions heavy chicks do better than the lighter chicks.

The remaining variables included in at least one selected model (see Table 2) are likely to be of lower importance. Their averaged Akaike weights are relatively low, and the confidence intervals of their main effects all include zero. Furthermore, all of them were included in a model along with bilberry cover, suggesting that their inclusion may be due to bilberry cover. However, among these less important variables, the effect of drainage may be worth further discussion. For the same study population, we have recently demonstrated a negative effect of drainage upon nesting success, especially at high predator densities (Ludwig 2007). Furthermore, using nationwide data, drainage has been shown to affect annual reproductive output in forest grouse in southern and central, but not in northern Finland (Ludwig et al. 2008). In the present study, however, the effect of drainage on early brood survival was surprisingly positive. That is, the mechanisms by which drainage affects nesting and early brood success differ from each other. While drained areas may suffer from increased nest predation when predators are abundant, this is not the case for chicks after they hatched. Another likely and often speculated direct negative effect of drainage is drowning. Before chicks fledge at the age of about one week, crossing ditches may be lethal unless they are dry. Although we do not have local data on water levels in the ditches during the post-hatching

period, we may say from observations that 2003 (with a high mortality) was rather dry and the majority of ditches were dry. On the other hand, the two last years (2004 and 2005 with a lower mortality) were wetter and many ditches contained water. Drowning therefore did not seem to be a problem in our case. The observed slight, but positive effect, is likely to be microhabitat and/or food related. Fertilisation of drained areas, a common practice in Finland, may have positive effects on the growth of bilberry, at least at a local scale (Helle & Ludwig 2003). We found a negative, but non-significant, relationship (P = 0.13) between the proportion of brood locations occupying un-drained sites and bilberry cover, i.e. drained areas had a somewhat higher cover of bilberry. This may, to some extent, explain the weak positive effect of drainage. Considering the rather low weight of the variable, as well as recent results on the population level (Ludwig et al. 2008) and on individual nesting success (Ludwig 2007), nevertheless, suggest that on the long term, drainage does have overall detrimental effects on breeding success.

Among the variables not included in any of our alternative models, predator track density is the most peculiar one. Predator track density did not seem to affect chick survival, be it as a main effect or as an interaction with other variables, despite the fact that successful and unsuccessful broods differed in terms of mean predator track density (see Table 1). However, it needs to be noted that the two years with moderate to high predator track densities (2003-2004) were also clearly colder than the year with a low predator track density (2005). For the same population of black grouse, predator track density was the single most important variable in determining spatial and temporal variation in nesting success (Ludwig et al., submitted). Mammal predation has been shown to be a major source of early chick mortality in capercaillie (Kastdalen & Wegge 1991) and willow ptarmigan (Steen et al. 1988) in Norway, and in sharp-tailed grouse in Alberta, Canada (Manzer 2004). Predation by raptors, on the other hand, was significant for early chick survival in red grouse (Thirgood et al. 2000) and ruffed grouse (Larson et al. 2001). For black grouse, however, there is little information about predation patterns during early life. A number of raptor species are known to prey upon black grouse chicks in Finland, but the predation occurs at later chick stages (Reif et al. 2004, R. Tornberg, pers. comm.). This and our results suggest that black grouse chicks are relatively safe from predation during the first 10 days after hatching. Black grouse chicks hatch more or less synchronously (within 12-24 hours), and after hatching is completed, the chicks may remain in the nest for a couple of hours before leaving. The risk of complete brood loss due to predation is therefore likely to be highest during this period, but that did not seem to be an issue in our study.

Targeting of management practices to relieve mortality at key stages is commonly given a high priority in declining populations of grouse. That is, management at a local scale should focus on retaining, restoring or even creating suitable brood habitat. As mentioned earlier, abundance of bilberry has significantly decreased during the past decades as a result of intensified timber production (Reinikainen et al. 2000). In terms of early survival, management targets favouring an increase in the local coverage of bilberry should be considered. Predator control to improve juvenile survival is commonly advocated (Hudson 1986, Larson et al. 2001), but in the scenario we present, there would probably be no significant benefit for early juvenile survival.

Little can be done about the effect of temperature. Our results on brood survival of individual hens are in accordance with our recent results on the population level mentioned above (Ludwig et al. 2006). No management practice can possibly improve weather conditions, but the weather conditions experienced by the chicks could be used as a management tool. We have shown (Ludwig et al. 2006) that spring temperatures can be used as proxy for the timing of hatching. By doing so, one could estimate local hatching times and hence evaluate early-life conditions, such as temperature and precipitation. Whenever post-hatch conditions are below the threshold, a bad breeding output is to be expected. In order to avoid exacerbation of juvenile mortality in such years, hunting should be reduced, or hunting should not occur at all.

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