Does timing of breeding and subsequent hatching in boreal forest grouse match the phenology of insect food for the chicks?

Per Wegge[1,*], Truls Vesterås[1] & Jørund Rolstad[2]

[1] *Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway (*e-mail: per.wegge@umb.no)*
[2] *Norwegian Forest and Landscape Institute, P.O. Box 115, NO-1432 Ås, Norway*

During the first few weeks of life, chicks of the capercaillie (*Tetrao urogallus*) and black grouse (*T. tetrix*) subsist mainly on insects, of which lepidopteran and hymenopteran larvae are the main components. We studied the breeding phenology of these two species and examined how the timing of breeding was related to the temporal distribution of their larval food source. During a five-year survey, capercaillie mated and hatched consistently four to six days before black grouse. Depending on the vegetation type, the number of larvae (≥ 2 mm in length) increased between five and ten times within 10 days, and hatching coincided roughly with the peaks in larval numbers. Due to body growth, however, larval abundance in terms of volume was reached later and occurred 8–9 and 13–14 days after the mean hatching dates in the two species, respectively. Slightly later development of Hymenoptera as compared with that of Lepidoptera contributed in extending the period of high larval abundances for more than one week. The timing of breeding of the two species appears, therefore, to match the temporal distribution of insect food for the fast-growing chicks as they hatch several days before the peak in larval volumes. In one year, when mating was advanced, presumably due to exceptionally warm weather before mating (yet the temporal abundance of larvae was unchanged), breeding success was higher than in years when mating occurred later.

Introduction

Grouse chicks require protein-rich and easily digestible food after hatching (Savory 1989). In the boreal forests of Eurasia, invertebrates dominate the chicks' diet during their first two and four weeks of life in black grouse (*Tetrao tetrix*) and the larger capercaillie (*T. urogallus*), respectively (Fig. 1; Wegge & Kastdalen 2008). Lepidopteran larvae, especially geometrids, constitute the main source of food for these birds (Kastdalen & Wegge 1985, Atlegrim 1991, Atlegrim & Sjöberg 1995, Picozzi *et al*. 1999, Wegge & Kastdalen 2008).

Both black grouse and capercaillie are lekking species, with matings taking place during a
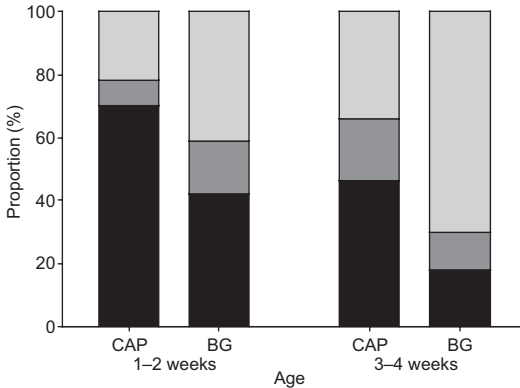
Fig. 1. Proportion of larvae (black), other insects (dark grey), and plants (light grey) in the diets of capercaillie and black grouse chicks at Varaldskogen in southeast Norway during the first weeks after hatching (adapted from Wegge & Kastdalen 2008).

few days in early spring, when most vegetation is still in the dormant stage. Thus, most broods hatch within a short time-span of less than 10 days. Already more than 70 years ago, Lack (1933) proposed the idea that birds time their breeding so that hatching coincides with maximum availability of food for the chicks. If so, it must be adaptive, because most birds in northern latitudes initiate breeding before they have cues to predict the temporal variation in chick food. This is particularly the case with larger birds with long incubation time, like forest grouse.

Studies on the relationship between breeding and chick food have mainly dealt with passerines, especially tits (*Parus* spp.) (Perrins 1991, van Noordwijk *et al.* 1995). From the boreal region, only Atlegrim (1991) and Wegge and Kastdalen (2008) reported how the larval food source develops and varies during the period when grouse chicks depend on this source of food. In Scotland and England, Baines *et al.* (1996) compared the hatching dates of capercaillie and black grouse with the availability of larval food and concluded that since they peaked at the same time, the time of breeding was adapted to chick food. However, they did not discuss the phenology in detail, i.e. taking into account that larval biomass varies with the unit of measurement (number, weight, volume). Additionally, the chicks' intake of food — including insect larvae — increases rapidly

with age due to their very high growth rate. In this study, we measured the phenology and composition of the larval food source, which we then relate to the mating and hatching dates of black grouse and capercaillie hens. The main objective was to determine the exact times of mating and hatching, and to discuss if timing of the latter was optimal with respect to the abundance of insect food for the young chicks.

Material and methods

Study area

The ca. 100 km^2 Varaldskogen study area (60°09′N, 12°30′E) in southeast Norway lies in the mid-boreal sub-zone (Ahti *et al.* 1968) and is typical of intensively managed conifer forests in Fennoscandia. Mixed Norway spruce (*Picea abies*) and Scots pine (*Pinus silvestris*), interspersed with birch (*Betula* spp.) and aspen (*Populus tremula*) cover the landscape, with ca. 75% of the semi-natural, mature conifer forests now replaced by younger plantations. Ground vegetation is dominated by ericaceous shrubs and dwarf birch (*B. nana*) at poorer sites and along oligotrophic bogs. Bilberry (*Vaccinium myrtillus*), the main host plant of lepidopteran larvae (Atlegrim 1991), is the dominant shrub in these semi-natural, mature forests. The fauna is typical of boreal forests, with a high density of moose (*Alces alces*), fewer roe deer (*Capreolus capreolus*), and medium to high abundances of grouse predators like red fox (*Vulpes vulpes*), pine marten (*Martes martes*), and goshawk (*Accipiter gentilis*). Following a recent decline of black grouse, capercaillie and black grouse were nearly equally abundant in 2008 at spring densities of two to three birds per km^2 (P. Wegge & J. Rolstad unpubl. data).

Timing of breeding

Capercaillie and black grouse populations have been monitored at Varaldskogen since 1979. During five years (1981, 1983, 1984, 2007 and 2008) sufficient data were collected to reliably estimate and compare the timing of breeding

and hatching, combining the following three methods: (1) monitoring of radio-tagged hens, (2) observations of hens at leks, and (3) ageing of chicks in young broods.

Radio-tagged birds

Mating data were mostly derived from the monitoring of radio-tagged hens. We experienced that birds that were captured while on leks mated and hatched some days later than undisturbed hens. Therefore, we included only hens that had been captured and tagged on the leks in previous years, thus all were > 1 year of age. If mating was not directly observed, we defined the date of mating of these hens as the last date that they visited the lek. The radio-tagged hens were monitored regularly during incubation until hatching. For hens that lost their eggs to predators, we calculated hatching dates by assuming incubation period to be the same as for the successful hens.

Observations at leks

In 2007–2008, we monitored several radio-tagged black grouse hens, but had no radio-tagged capercaillie hens to compare with. During these years, we defined the mating date in capercaillie as the date of peak attendance of hens, including observed matings. We then added the average number of days from mating to hatching recorded among previously radio-tagged hens ($n = 9$) to determine their hatching dates. In capercaillie, most hens mated within two or three days, whereas in black grouse, mating was less synchronized and hens mated over a longer period of time (Kruijt & Hogan 1967, and Results). Thus, estimates of mating peaks from lek observations are rather reliable in capercaillie. Owing to the more variable visitation pattern of black grouse hens, we did not use lek observations to estimate mating peaks in this species.

Ageing of chicks

In 1983 and 1984, information on hatching dates was supplemented by ageing chicks in unmarked, young broods that were encountered during brood sampling. Age was estimated from the development and moulting pattern of feathers derived from chicks in broods of known age (Kastdalen 1986), and from a growth curve of capercaillie chicks provided by Spidsø and Stuen (1991). The dates of hatching of these unmarked broods were estimated by backdating from the date when they were encountered during fieldwork.

For each year, the dates of mating and hatching were determined as the means of the independent sampling methods described above. Our radio-tagged hens consisted of only adult birds. These adult birds might have mated earlier than yearlings, thus biasing the estimates of mating (and hatching) dates forward. However, in capercaillie there was no difference in mating dates based on radio-tagged hens and observations of lek attendance, and in black grouse there was no difference in hatching dates based on radio-tagged hens and aged broods (Wilcoxon signed-rank tests: $p \geq 0.19$, both).

Sampling of larvae

In 2007 and 2008, larval food items were sampled by sweep-netting at five fixed stations, spaced > 500 m apart, in mature, semi-natural forests — two in the common *Vaccinium*-rich, mixed conifer forest (VM) and one in each of the three other vegetation types (Table 1). These forests are dominated by bilberry, the main foraging habitats of both capercaillie and black grouse broods during the first three to five weeks after hatching (Wegge & Kastdalen 2008). A net with a diameter of 36-cm attached on a 2.0-m-long pole was swept rapidly through the field-layer vegetation (for details, *see* Wegge & Kastdalen 2008). During each sampling occasion, 10 sweeps were made two times at each station. The locations of sweep-netting within each vegetation type were selectively chosen to consist mainly of bilberry.

In 2008, sampling was performed every 3–5 days, beginning approximately two weeks before hatching of black grouse and ending 3.5 weeks post hatch. In the field, we placed all larvae from each sampling occasion in glass vials containing 70% alcohol. In the laboratory, we identified the

larvae to Lepidoptera or Hymenoptera taxa, and counted them according to different size classes as follows: 2–5 mm (small), 5–12 mm (medium) and > 12 mm (large). We determined the volume of larvae from each sample by measuring the liquid displacement when put in a finely graduated cylinder filled with 70% alcohol. In 2007, we sampled larvae by the same method and at the same stations, but less frequently at intervals of 7–10 days. Only the total number of larvae was recorded in 2007. Using the same method, larvae were also sampled in 1983 and 1984 (Wegge & Kastdalen 2008), but at different locations.

Analyses

To achieve normality, periods for hen lek attendance were square-root transformed prior to *t*-tests. Since number of group sizes differed, a general linear model (GLM) was used for comparing larval distributions on vegetation types. Before the GLM analyses, we tested for equal variance with Levene's test. When comparing abundances of each larval group among vegetation types, we used Tukey's post-hoc test.

Results

Breeding phenology

Capercaillie bred consistently three to four days earlier and hatched five to six days earlier than black grouse (Table 2). Radio-tagged hens of both species mated and hatched within periods of less than one week. There was a tendency for shorter lek visitation by individual capercaillie hens (2.9 days *versus* 4.7 days in black grouse, on average), but the difference was not statistically significant ($t_{19} = 1.18$, $p = 0.14$). However, the period with hens present at the leks was longer in black grouse (7.1 ± 1.1 SD days) than in capercaillie (4.1 ± 0.7 SD days) ($t_{29} = 2.52$, $p < 0.01$), implying that mating was less synchronous in black grouse.

In 2008, the year when larvae were measured most intensively, we monitored two black grouse leks daily for a period of 16 days. During this year, seven radio-tagged hens from the previous year visited the leks over a period of nine days in total (mean = 4.9 days per hen). The earliest and latest matings of these hens were spaced four days apart. Nests of four of the hens were depredated, and one of them laid a second, successful

Table 1. The four vegetation types sampled for larval abundances at Varaldskogen during 2007 and 2008.

Acronym	Vegetation type*	Description
VM	*Vaccinium*-rich, mixed conifer forest (*Vaccinio-Pinetum*)	Mixed conifer forest of Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*), with birch (*Betula* spp.) interspersed. The field layer consists of a dense mixture of bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*) and crowberry (*Empetrum nigrum*), with bog whortleberry (*Vaccinium uliginosum*) at moist sites and heather (*Calluna vulgaris*) at dry sites.
VS	*Vaccinium* spruce forest (*Eu-Piceetum myrtilletosum*)	Spruce-dominated forest with aspen (*Populus tremula*) and birch interspersed at more productive sites. Field layer dominated by bilberry.
VB	*Vaccinium* bog forest (*Oxycocco-Pinetum vaccinietosum*)	Pine-forested bogs with occasional spruce in lower strata. A transition zone between poorer, heather/bog cottongrass (*Eriophorum angustifolium*)-dominated bogs and *Vaccinium*-rich, mixed conifer forest (VM). Field layer dominated by a mixture of bilberry, cowberry, bog whortleberry and dwarf birch (*Betula nana*).
SS	Spruce swamp forest (*Chamaemoro-Piceetum*)	Poorly drained *Vaccinium* spruce forest (VS), with some birch. Field layer dominated by open-growing bilberry, cloudberry (*Rubus chamaemorus*), mosses, horsetails (*Equisetum* spp.), and small ferns.

* Classification according to Kielland-Lund (1981).

clutch. The three successful first-nesters hatched their eggs 41, 42, and 43 days after mating.

Within species, the peak dates of breeding varied little among years, except for 2007 when both species mated about one week earlier than in other years (Table 2). In this year, average April temperatures were 7.8 °C, which was 2.4 °C higher than the mean of the other four years.

Larval development

During 2008, depending on vegetation type, the number of lepidopteran larvae (≥ 2 mm in size) increased 5–10-fold within 10 days, peaking 3–4 days before the mean hatching date in black grouse. Their numbers then declined at a slightly lower rate (Fig. 2a). The pattern was similar in the four vegetation types, but abundances in terms of numbers of individuals differed among them ($F_{3,49} = 3.98$, $p = 0.015$), with *Vaccinium* spruce (VS) showing higher larval densities than *Vaccinium* mixed (VM) (Tukey's post hoc: $p = 0.013$). More than 80% of the Lepidoptera larvae were geometrids.

Of the total number of larvae collected, roughly 25% were sawflies (Hymenoptera). They fluctuated somewhat differently from that of the lepidopteran larvae: they peaked ca. 12 days later and maintained their high level for longer (> 10 days) before declining. This is illustrated in Fig. 2b, which shows the number of large-sized (> 12 mm) larvae of the two main groups. As for Lepidoptera, the number of sawfly larvae differed between vegetation types ($F_{3,49} = 4.23$, $p = 0.011$) and tended to be more numerous in *Vaccinium* mixed (VM) than in spruce swamp (SS) (Tukey: $p = 0.070$) (Table 3). There were no statistical differences between the vegetation types in terms of total number ($F_{3,49} = 0.20$, $p = 0.89$) or total volume ($F_{3,49} = 0.49$, $p = 0.75$) when the two groups of larvae were combined.

Timing of hatching and temporal distribution of larvae

During the season, larvae grew in size. Hence, while the total number of larvae peaked a few days before hatching, the total volume peaked about one week after they hatched in 2008 (Fig. 3a), because medium and large sized larvae then made up a larger fraction of the samples. A high volume of larvae ($> 65\%$ of the maximum value) was maintained for about two weeks, from about five days before to 10 days after hatching in black grouse. The abundance of larvae declined rapidly thereafter, reaching a low level of $< 10\%$ of the peak abundance within 10 days.

Due to infrequent sampling in 2007, data do not portray the phenology of larvae as well as for 2008. Nevertheless, hatching of both species occurred about five days earlier in 2007 (Fig. 3b) than in the more normal year 2008, whereas the larval peak advanced little, or not at all. Hence,

Table 2. Breeding phenology of capercaillie and black grouse at Varaldskogen, Norway.

| | | Capercaillie | | | | | Black grouse | | | |
| | | Mating date | | Hatching date | | | Mating date | | Hatching date | |
	N^1	Mean	Range[2]	Mean	Range[2]	N^3	Mean	Range[2]	Mean	Range[2]
1981	6/4	27 Apr	24–29 Apr	5 Jun	3–9 Jun	5/0	2 May	30 Apr–3 May	11 Jun	10–14 Jun
1983	6/4	28 Apr	27–30 Apr	7 Jun	4–9 Jun	3/8	1 May	28 Apr–4 May	12 Jun	11–15 Jun
1984	6/4	26 Apr	25–27 Apr	4 Jun	3–6 Jun	2/6	29 Apr	27 Apr–3 May	9 Jun	7–14 Jun
2007	0/3	20 Apr	19–21 Apr	29 May	28–30 May	5/0	23 Apr	22–26 Apr	3 Jun	1–5 Jun
2008	0/3	24 Apr	24–25 Apr	2 Jun	2–3 Jun	7/0	27 Apr	24–30 Apr	8 Jun	7–9 Jun
Means		25 Apr		3 Jun			29 Apr		9 Jun	

[1] Number of radio-tagged hens/number of leks with number of visiting hens recorded (*see* text).
[2] The maximum range of dates from the different methods employed (*see* text).
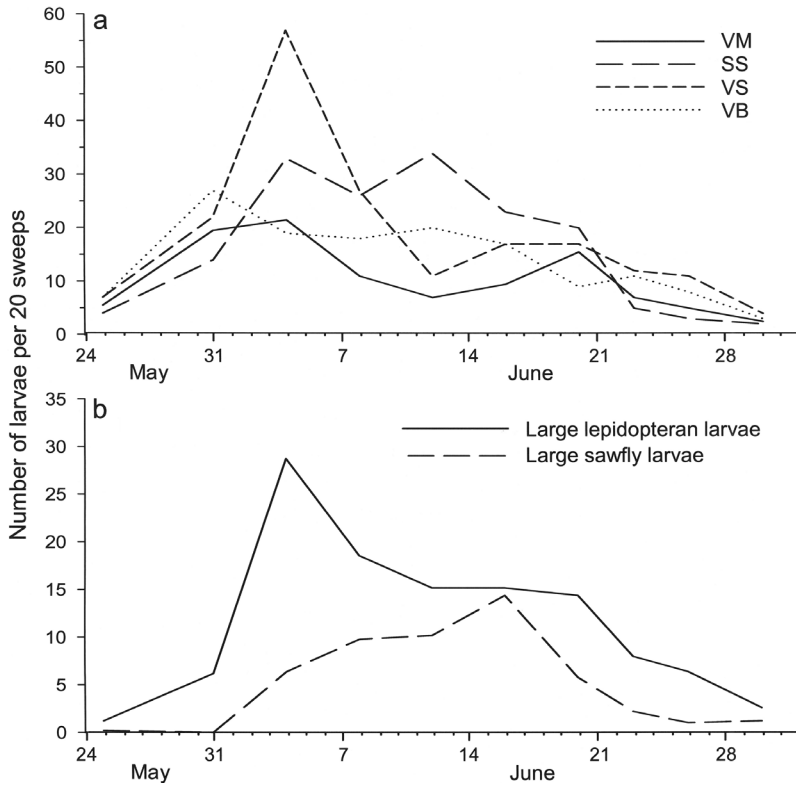[3] Number of radio-tagged hens/number of aged broods (*see* text).

Fig. 2. Temporal distribution of larvae at bilberry-dominated sites in different vegetation types at Varaldskogen, southeast Norway, in 2008. — **a**: Total number of Lepidoptera larvae in *Vaccinium*-rich, mixed conifer forest (VM), spruce swamp forest (SS), *Vaccinium* spruce forest (VS), and *Vaccinium* bog forest (VB). — **b**: Total number of large (≥ 12 mm) Lepidoptera and Hymenoptera larvae (means of the four vegetation types).

in 2007 the time interval between hatching and peak larval abundance (volume) was extended by about one week.

Discussion

Capercaillie consistently mated and hatched before black grouse. This is probably an adaptation; chicks of the larger capercaillie need more time to grow to be physiologically mature for winter as compared with black grouse chicks. This is probably also the reason for the longer time that capercaillie chicks subsist on insect food, which is highly nutritious, easily digestible, and contains the amino acids cysteine and methionine that are essential for growth (Wise 1985), thus facilitating the exceptionally high growth rate of young capercaillie chicks (Lindén 1981).

Grouse chicks are born with a yolk sac, which provides nourishment during the first few days post hatch (Marcström 1960, Romanoff

Table 3. Number of larvae per 20 sweeps in bilberry shrubs in different vegetation types at Varaldskogen, Norway, from 25 May to 30 June 2008. Two samples (each consisting of ten sweeps) were collected at fixed stations in each vegetation type every 3–5 days; total number of samples in VS, VB and SS = 22, in VM = 44.

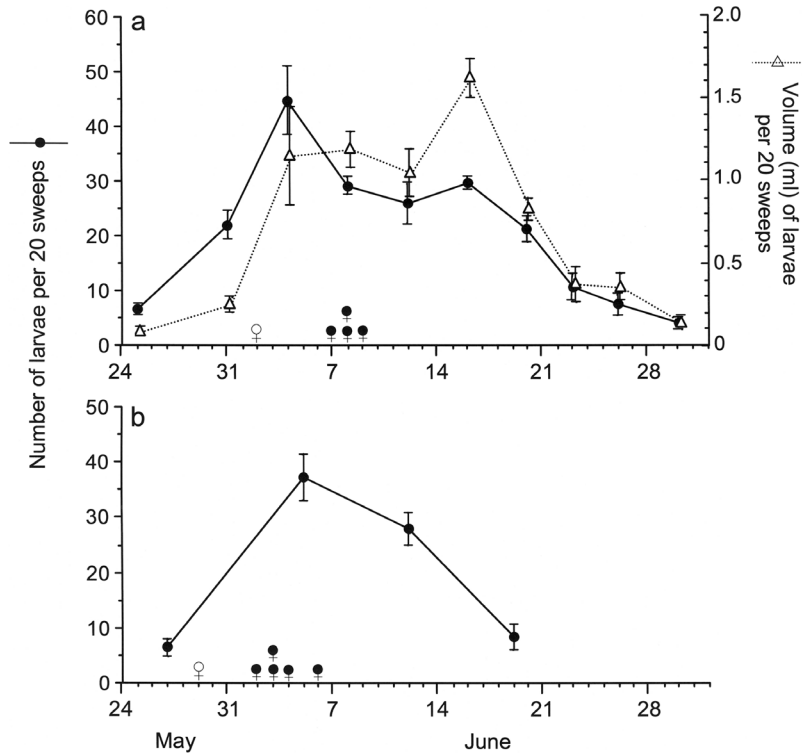| Vegetation type	Lepidoptera		Hymenoptera		Total larvae	
	Mean	SE	Mean	SE	Mean	SE
Vaccinium mixed forest (VM)	10.3	0.08	8.9	0.11	19.2	0.14
Vaccinium spruce forest (VS)	8.5	0.48	3.9	0.13	22.4	0.22
Vaccinium bog forest (VB)	13.9	0.23	6.8	0.20	20.7	0.21
Spruce swamp forest (SS)	16.4	0.40	2.5	0.10	18.9	0.37

Fig. 3. Temporal distribution of larvae (Lepidoptera and Hymenoptera combined), hatching dates of radio-tagged black grouse hens (filled symbols), and estimated mean hatching date of capercaillie (open symbols) at Varaldskogen, southeast Norway. — **a**: Total number and volume of larvae (mean ± SE) and hatching dates in 2008. — **b**: Total number of larvae (mean ± SE) and hatching dates in 2007.

1960). After hatching, insect food — mainly larvae — dominates the diets of black grouse and capercaillie chicks for periods of about two and four weeks, respectively (Wegge & Kastdalen 2008). During this period, daily food intake increases exponentially with the growth in body size (Moss & Hanssen 1980, Lindén 1981). Thus, the intake of larvae also increases markedly, peaking 2–3 weeks post hatch in capercaillie and about 2 weeks post hatch in black grouse (Wegge & Kastdalen 2008). Optimal hatching date is therefore not at the time of maximum larval abundances, as concluded by Baines *et al.* (1996), but some days earlier.

Mating and hatching extend over a longer period in black grouse than in capercaillie. The extended "plateau" of larval abundances — mainly due to sawfly larvae — means that larvae are available for a longer period of time after the start of the hatching period in black grouse, thus providing easily digestible and rich food also for late hatchers. Capercaillie hatches about one week before black grouse, and because mating is generally more synchronized in this species (Höglund & Alatalo 1995), most capercaillie

chicks are also born during a shorter time interval than black grouse chicks. Since capercaillie chicks eat proportionally more larvae than black grouse chicks and do so for a longer period of time (Wegge & Kastdalen 2008), capercaillie breeding success is likely to be more sensitive to variation in the abundance of larval food. From a study in Scotland, Picozzi *et al.* (1999) reported that geometrid larvae were an important part of the diet of young capercaillie chicks. Their data indicated a positive relationship between breeding success and the abundance of large-sized larvae, rather than the total number of larvae.

The abundance of larvae increased 5-10 times in the course of ca. 10 days. In terms of numbers, they started to decrease shortly after this peak, reaching the initial low level about three weeks later. The peak in volume was reached some days later than the peak in numbers, and high volumes were maintained for more than one week before declining. The somewhat later development of sawfly larvae, which made up about a quarter of the total number of larvae, contributed in extending the period when the volume of larvae was quite high. Although the increase in larval size

is mainly due to more body fluids, a chick probably derives more nourishment from ingesting a large-sized larva as compared with a small one. Volume is therefore a more appropriate measure of food biomass than numbers. Also, chicks probably forage more efficiently on larger-sized larvae, as they are more easily detected during feeding bouts.

The abundance of larvae declined rapidly after reaching their peaks. Although the period of high abundance was maintained and extended for several days, due partly to sawfly larvae irrupting a bit later than Lepidoptera larvae, the composite larval food supply declined during the period when chicks of both species increase their daily uptake of this food. With capercaillie chicks depending on animal food for a longer period than black grouse, they should therefore also hatch earlier, which they did. The reason for proportionally less animal food in the diets of the chicks of the two species as they grew older is probably the result of trade-off selective pressures: as availability of the larval food source declined as they entered the pupal stage, the energetic cost of searching for larvae increased, leading eventually to a no net gain situation. During the same period, the chicks develop ceacal intestines, which effectively digest plant material (Moss & Hanssen 1980, Savory 1989), and the chicks are then able to eat successively more of such food.

The two groups of larvae differed somewhat in their habitat affinities. Among geometrids, highest abundances were recorded in the spruce-dominated VS and SS forest types, while among sawflies the mixed conifer VM type contained the highest numbers. The latter is a drier, more open, and less productive forest type than spruce forests. From north-central Sweden, Atlegrim (1991) reported a similar distribution pattern. He also showed that Lepidoptera larvae reached their peaks later in bilberry that grows in open, sunny sites compared to shady habitats — comparable to our mixed (VM and VB) and spruce-dominated (VS and SS) types, respectively. While other studies have reported pronounced variation among vegetation types in their abundances of lepidopteran larvae (Stuen & Spidsø 1988, Atlegrim 1991), total abundances did not vary among the four vegetation types examined here. The most

likely explanation is that our vegetation types are closely related ecologically, and that within these, we sampled larvae selectively in more or less homogeneous layers of bilberry shrubs.

In 2008, black grouse hatched after the peak in larval numbers but before the peak in volume. Although sampling was less intensive and data therefore not as clear in 2007, the same pattern might have occurred that year. In both years, capercaillie hatched several days before the peaks in larval volumes. In 1983 and 1984, when larvae had been sampled in the same study area, albeit at different locations and including other vegetation types, larval abundances peaked exceptionally late in 1983, after a very slow build-up phase. Hatching then occurred three to four weeks before the peak in larval volume. The following year was more "normal"; the larvae developed rapidly and peaked earlier, and black grouse and capercaillie hatched at or shortly before the peak, respectively (Wegge & Kastdalen 2008). Kastdalen (1986) speculated that the unusually slow development of larvae in 1983 might have been due to a different composition of the larval guild. Assuming that our results from 2008 reflect general differences among larval groups, later-developing sawfly larvae might have dominated instead of geometrids in 1983. Different temperature regimes might also have slowed down the development of larvae in 1983; 20 May to 7 June — the period when larvae usually irrupt — was quite cold in 1983 with 5 °C lower temperatures, on average, than in 1984.

In recent years, concerns have been raised that global warming may lead to a mismatch between time of breeding and availability of insect food for newly hatched chicks (e.g. Visser *et al.* 2004), and several studies have examined this, mainly in relation to the reproduction of passerines. Based on time series data on mating in black grouse and temperature records in Finland, Ludwig *et al.* (2006) predicted that with warmer springs and associated earlier breeding, the adapted match with optimal food at hatching may be disrupted, leading to poorer chick survival. Although the question of the effects of climate change is outside the scope of this paper, our results indicate that the relationship is quite complex. In our study area, an exceptionally

warm period in mid-April led to mating (and subsequent hatching) taking place about one week earlier in 2007 than in the more normal year 2008. On the other hand, the temporal distribution of larvae was about the same, as were the May–June temperatures. In 2007, breeding success was higher — not lower — than in 2008 (Wegge 2008). Thus, it did not support the hypothesis of a negative effect on reproduction due to earlier breeding.

The timing of avian breeding and the temporal distribution of larvae are governed by different environmental conditions at different time periods in early spring (Visser *et al.* 2006). Hence, these do not shift synchronously from year to year. Negative effects on breeding success are therefore likely to occur in years when temperatures advance mating but not larvae irruption — or *vice versa*. In the Finnish study, such mismatching might have occurred, since April temperatures were reported to have increased markedly but June temperatures had not (Ludwig *et al.* 2006). In our "mismatch" year of 2007, when mating time but not larvae abundance advanced, breeding success of both species was the highest ever recorded during 30 years in the study area (Wegge 2008). Thus, the temporal match between timing of hatching and the availability of larvae food is only one of several factors determining the breeding performance of these species.

Acknowledgements

References

Ahti, T. Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — *Annales Botanici Fennici* 5: 169–211.

Atlegrim, O. 1991: *Interactions between the bilberry (Vac-*

cinium myrtillus) and a guild of insect larvae in a boreal coniferous forest. — Ph.D. thesis, Department of Wildlife Ecology, Swedish University of Agricultural Sciences, Umeå, Sweden.

Atlegrim, O. & Sjöberg, K. 1995: Lepidoptera larvae as food for capercaillie chick (*Tetrao urogallus*): a field experiment. — *Scandinavian Journal of Forest Research* 10: 278–283.

Baines, D., Wilson, I. A. & Beeley, G. 1996: Timing of breeding in black grouse *Tetrao tetrix* and capercaillie *Tetrao urogallus* and distribution of insect food for the chicks. — *Ibis* 138: 181–187.

Höglund, J. & Alatalo, R. V. 1995: *Leks*. — Monographs in Behavior and Ecology, Princeton University Press, New Jersey.

Kastdalen, L. 1986: *Storfugl- og orrfuglkyllingers nærings-valg i Sør-Øst Norge*. — M.Sc. thesis, University of Oslo, Norway.

Kastdalen, L. & Wegge, P. 1985: Animal food in capercaillie and black grouse chicks in SE Norway. — *International Grouse Symposium* 3: 499–513.

Kielland-Lund, J. 1981: Die Waldgesellschaften SO-Norwegens. — *Phytocoenologia* 9: 53–250.

Kruijt, J. P. & Hogan, J. A. 1967: Social behaviour on the lek in black grouse. — *Ardea* 55: 203–240.

Lack, D. 1933: Nesting conditions as a factor controlling breeding time in birds. — *Proceedings of the Zoological Society of London* 104: 231–237.

Lindén, H. 1981: Growth rates and early energy requirements of captive juvenile capercaillie, *Tetrao urogallus*. — *Finnish Game Research* 39: 53–67.

Ludwig, G. X., Alatalo, R. V., Helle, P., Lindén, H., Lindström, J. & Siitari, H. 2006: Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. — *Proceedings of the Royal Society London B* 273: 2009–2016.

Marcström, V. 1960: Studies on the physiological and ecological background to the reproduction in capercaillie *Tetrao urogallus* Lin. — *Viltrevy* 4: 311–342.

Moss, R. & Hanssen, I. 1980: Grouse nutrition. — *Nutrition Abstracts and Reviews B* 50: 555–567.

Perrins, C. M. 1991: Tits and their caterpillar food supply. — *Ibis* 133: 49–54.

Picozzi, N., Moss, R. & Kortland, K. 1999: Diet and survival of capercaillie *Tetrao urogallus* chicks in Scotland. — *Wildlife Biology* 5: 11–23.

Romanoff, A. L. 1960: *The avian embryo*. — Macmillan, New York.

Savory, C. J. 1989: The importance of invertebrate food to chicks of gallinaceous species. — *Proceedings of the Nutrition Society* 48: 113–133.

Spidsø, T. K. & Stuen, O. H. 1991: Age determination of young capercaillie *Tetrao urogallus* chicks. — *Fauna Norvegica C* 14: 29–32.

Stuen, O. H. & Spidsø, T. K. 1988: Invertebrate abundance in different forest habitats as animal food available to capercaillie (*Tetrao urogallus*) chicks. — *Scandinavian Journal of Forest Research* 3: 527–532.

van Noordwijk, A. J., McCleery, R. & Perrins, C. 1995: Selection for the timing of great tit breeding in relation

to caterpillar growth and temperature. — *Journal of Animal Ecology* 64: 451–458.

Visser, M. E., Both, C. & Lambrechts, M. M. 2004: Global climate change leads to mistimed avian reproduction. — *Advances in Ecological Research* 35: 89–110.

Visser, M. E., Holleman, L. J. M. & Gienapp, P. 2006: Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. — *Oecologia* 147: 164–172.

Wegge, P. 2008: Still high density of grouse at Varaldskogen. — *KJFF Nytt* 34: 7.

Wegge, P. & Kastdalen, L. 2008: Habitat and diet of young grouse broods: resource partitioning between capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*) in boreal forests. — *Journal of Ornithology* 149: 237–244.

Wise, D. R. 1985: Nutrition of wild red grouse (*Lagopus lagopus scoticus*). — *International Grouse Symposium* 3: 122–130.