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Diet and survival of capercaillie *Tetrao urogallus* chicks in Scotland

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The diet of young capercaillie *Tetrao urogallus* chicks in Scotland was assessed from analysis of their faeces, collected at the roost sites of broods with radio-marked mothers. Lepidoptera larvae were their main invertebrate food and bilberry *Vaccinium myrtillus* their main plant food. The concentration of larval remains in the chicks' droppings was correlated with the abundance of larvae found by sweep netting in nearby vegetation. Broods of chicks with the greatest concentration of larval remains in their droppings survived best. Sweep netting for larvae in a semi-natural pine forest in June 1991-1996 showed that larval size, abundance and timing differed among years, and that the sites with the most larvae also differed from year to year. In the same forest, we estimated capercaillie breeding success from hens and chicks found during dog counts. The average number of young per hen in July was correlated with the size, rather than the abundance, of larvae in mid June.

Key words: capercaillie, chick diet, faecal analysis, chick survival, geometrid larvae, sweep netting, Tetrao urogallus

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Capercaillie *Tetrao urogallus* became extinct in Scotland in the late 1700s, but were successfully reintroduced in 1837-38 (Lever 1977). Since the mid 1970s, their range and number have declined greatly (Moss 1994) and by 1992-93 only 2,000-3,000 birds remained (Catt, Baines, Picozzi, Moss & Summers 1998). Poor chick survival may have contributed to the decline (Moss 1994, Moss & Picozzi 1994, R. Moss, N. Picozzi, R.W. Summers & D. Baines, unpubl. data) but the food and habitat requirements of broods are poorly understood. There has been no previous study of the diet of capercaillie chicks in Scotland. However, Scandinavian studies have indicated the importance of invertebrates, especially lepidoptera larvae, in the chicks' diet (Rajala 1959, Cramp & Simmons 1980, Kastdalen & Wegge 1985, 1991, Sjöberg 1996).

Here we document the diet of nine broods of capercaillie and test the following predictions: 1) broods which eat more larvae survive better; 2) the number of larvae caught in sweep nets in brood habitats reflects the number eaten, and 3) hens rear more chicks in years when more larvae are caught in sweep nets.

Study areas

We studied hens in commercial plantations and semi-natural coniferous woodlands in northeast and cen-

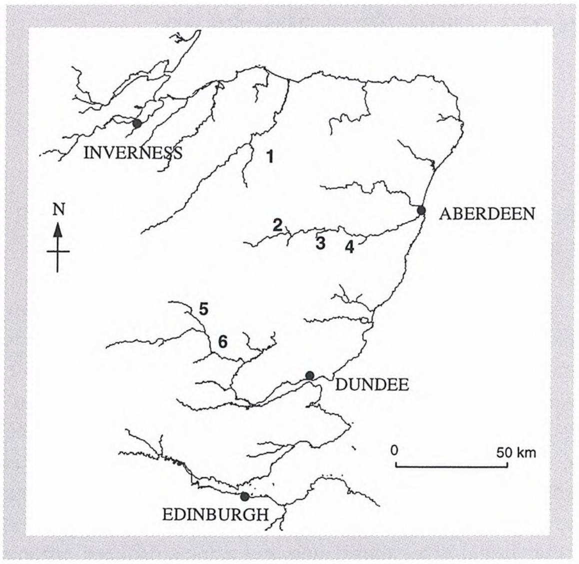

Figure 1. Locations of the six study areas in Scotland; 1 - Glenlivet, 2 - Coilacriech, 3 - Glen Tanar, 4 - Finzean, 5 - Dunkeld, 6 - Drumbuich.

tral Scotland (Fig. 1). The landscape comprised a heterogeneous mixture of forest stands separated by moorland and farmland, broadly coarse-grained at the hectare scale and fine-grained at the km^2 scale. In some places, gamekeepers killed predators such as carrion crows *Corvus corone* and red foxes *Vulpes vulpes*.

Glenlivet, Moray was 2 km^2 of largely pole stage forest, containing a mixture of species with lodgepole pine *Pinus contorta* on the highest ground, and Scots pine *P. sylvestris*, larch *Larix kaemferi* and Sitka spruce *Picea sitchensis* on the lower slopes. Most of the vegetation under the trees had been shaded out, but the rides (narrow corridors with no trees) between forest compartments were well-vegetated, with dwarf shrubs in the drier parts and patches of grass and rush on wet ground. Broods were always found in the rides. There was no effective predator control.

Coilacriech, Upper Deeside, Aberdeenshire included about 1 km^2 of old, native pines on a steep, bouldery slope to the north of the river Dee. To the south of the river, there was about 1 km^2 of birch *Betula* spp. and thicket and pole stage Scots pines. The ground vegetation, predominantly heather *Calluna vulgaris* with some bilberry *Vaccinium myrtillus*, was moderately grazed by red deer *Cervus elaphus*. There was some predator control, less effective than at Glen Tanar.

Glen Tanar, Deeside, Aberdeenshire lay to the south of the river Dee and comprised 12 km^2 of mature and regenerating semi-natural Scots pine of all ages. The ground vegetation was dominated by long, often rank, heather intermixed with patches of bilberry and cowberry *V. vitis-idaea*. Effective predator control meant that crows and signs of foxes were seldom seen during the capercaillie breeding season.

Finzean, Lower Deeside, Aberdeenshire lay on a 3 km^2 hill. There were open semi-natural mature Scots pines on the south-facing slope, and plantations of pine, larch and Sitka and Norway spruce *P. abies* on the east- and north-facing slopes. An extensive block of restock lay across the well-vegetated northern slope. It separated pole stage pine and larch, with a ground layer of dwarf shrubs, at the top of the hill from a mixture of mature spruce and pine, with a predominantly grassy ground layer, at the foot of the hill. Predator control was largely ineffective.

The nine broods hatched in pinewoods at Glen Tanar, Coilacriech and Finzean (see Table 1) all fed in the more open parts of the forest, where the field layer of heather and bilberry was well developed. At Finzean, one of the two broods also fed in a flushed site of rank heather and rushes in a clearing, and both visited the restock.

Dunkeld, Newtyle Hill, Perthshire was a steep south-facing 1 km^2 hillside, partly afforested with pole stage Sitka spruce. In small clearings (0.5 ha or less) hardwoods were being established in growth tubes. Outside the plantation were stands of mature birch and damp rushy flushes. Where trees were absent, the ground vegetation was dominated by grass and forbs, but from July extensive dense patches of bracken *Pteridium aquilinum* covered the slope. In both years (see Table 1) the hen nested in the spruce plantation with little or no ground cover. In 1994, the newly hatched brood immediately left the plantation for the birch wood. In 1995, the brood remained within the plantation until the chicks were three weeks old, and then moved out to the birch wood. There was no predator control.

Drumbuich, Perthshire comprised 2 km^2 of restocks, thicket and pole stage plantations of pine, larch, Douglas fir *Pseudotsuga menziesii*, Sitka and Norway spruce (Picozzi, Moss & Catt 1996). A varied ground vegetation was present in the restocked sites and rides. The brood (see Table 1) was located twice in dense vegetation in a restock and once in a well-vegetated ride that ran through dense plantations with little ground vegetation. There was some predator control, less effective than at Glen Tanar.

Methods

Capture, marking and tracking

Most of the studied hens had been caught in hand nets in late July and early August as well-grown poults. They were found by trained pointer and setter dogs and marked with 18-g radio transmitters that hung loosely around the neck and had a life of 12-18 months. We recaptured the hens when they were in moult a year later and had moved up to 20 km during natal dispersal (N. Picozzi, R. Moss & D.C. Catt, unpubl. data). We replaced their transmitters with sets that weighed 28 g (about 2% of a hen's body weight) and had an expected life of 2-3 years. In addition, two adult hens were caught and marked, one on a lek, the other on a nest.

Hens with chicks had home ranges of 10-60 ha (N. Picozzi, R. Moss & D.C. Catt, unpubl. data). We tracked them until the chicks were 4-6 weeks old or all had died. We avoided flushing the hens during this period and so were not always certain exactly when chicks died.

Collecting chick droppings

Shortly after dark, the roosting radio-tagged hen and her brood were located approximately by walking around her. Three pairs of canes were then aligned with her radio signal at 120° intervals and approximately 25 m from her. The following morning, after the brood had moved, we located the roost site at the intersection of the projections along the pairs of canes. The chicks' droppings were very dark with white caps and resembled those of a passerine. We noted the number of distinct groups at the roost site as an indication of the number of chicks still alive, and stored them all together as a single sample in 70% alcohol.

We followed a different procedure at Glenlivet, which could not be visited at night. Here, the hen was located by day and chicks were caught and put in a sweep net for a few minutes until each had produced a dropping.

Analysing droppings

The droppings in each sample were teased apart and carefully washed together in a 210 mμ sieve. The retained material was stored in 70% alcohol. A subsample of 0.2 ml of well-settled material was drawn into a wide-mouthed syringe and transferred to a shallow Petri dish. We identified key fragments of the main invertebrate types (usually order, but sometimes family or species) by comparison with plates in Moreby (1988) and with slides made of specimens from brood locations. The number of each type of invertebrate in each subsample was estimated by dividing the number of relevant mandibles by 2, legs by 6 and so on, and each expressed as number.ml^{-1}. The total area of plant material in the sample was measured against a 1 mm^2 grid placed beneath the Petri dish. The areas of fragments of heather, bilberry, conifer needles, ferns and the glumes of rush, sedge and grass, were also measured separately.

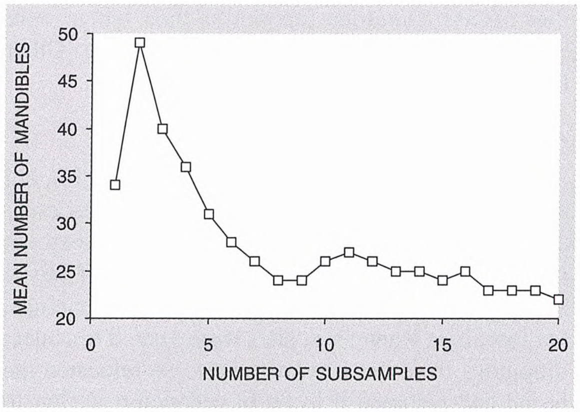

Figure 2. Running mean of the number of lepidoptera mandibles in 20 subsamples from the roost droppings of capercaillie in Glen Tanar.

For most purposes, we expressed the invertebrate content of the diet as the estimated number.ml^{-1} of settled material from a sieved sample of droppings. Preliminary trials indicated that six 0.2 ml subsamples were enough to give consistent results for the main key fragments (Fig. 2). We routinely examined 6-10 subsamples. An invertebrate index, given by the number of invertebrates.cm^{-2} of plant material, was used to illustrate the relative amounts of invertebrate and plant material in each sample.

Feeding trials with bantam chicks less than 14 days old checked the relationship between the number of invertebrates eaten and the number estimated from fragments in the droppings. One worker fed the chicks with a known number of invertebrates in addition to their usual pelleted food, and collected the droppings for 48 hours after the feeding; other workers analysed the droppings without knowing the diet. Lepidoptera larvae were fed in every trial, in combination with one or two of the following invertebrate types often found in capercaillie chick droppings: click beetles (Elaterid), weevils (e.g. Curculionid), small ants (Formicidae), wood ants *Formica* spp., spiders (Araneae), harvestmen (Opiliones) and house flies *Musca domestica* (chosen as their wings were sometimes found in capercaillie droppings). Other Diptera, such as midges, are more fragile.

Collecting invertebrates

Sweep netting has many biases (De Long 1932), but remains convenient for sampling invertebrates, especially larvae, in the field layer. We took sweep net samples to determine whether the number of larvae in them reflected numbers in the chicks' droppings. On mornings when roost sites were visited to collect droppings from the previous night, we relocated the brood and assumed it to be in vegetation similar to that in which the chicks had fed the previous evening. A standard 25 sweeps was taken selectively through each distinct vegetation type, mainly heather- or bilberry-dominated dwarf shrubs, close to the brood but without disturbing it. The net was 45 cm in diameter and each sweep at least 1 m apart. Invertebrates >1 mm were saved for later identification. Sweeps over wet vegetation captured fewer invertebrates and so, if the vegetation was wet, we took sweep net samples the following day, if dry.

In 1991-1996, we also sampled invertebrates by sweep-netting along 11 fixed transects in parts of Glen Tanar where sample counts of capercaillie broods were made each year in July and August using trained dogs (Moss & Oswald 1985). We counted the number of larvae obtained per transect and estimated their volume by displacement of water in a narrow measuring cylinder. Three of the sample sites were in unenclosed forest grazed by red deer, eight were inside a fence and much less heavily grazed. We made 25 sweeps in patches of bilberry along each transect. Bilberry was selected because the heather was tall and springy and more difficult to sample for invertebrates using a net. Most chicks hatched in the first few days of June and samples were taken once a week over three or four weeks, until the number of larvae was negligible. The dates were 1-4, 8-11, 15-18 June (20 June in 1991) and 21-24 June (samples in 1994-1996 only). In 1991 and 1996, we abandoned the first sample because the vegetation was too wet for reliable sampling, although enough larvae were collected in week 1, 1991 to estimate their size (volume/number).

Numerical analyses

Of 31 hens marked as poults in or near Glen Tanar from 1991-1995, at least 16 reached potential breeding age at one year (four radios failed). In addition, three hens were marked elsewhere, two as adults and one as a poult. Data on the food of chicks were obtained for nine broods of seven hens at six widely separated sites (above) in four different years. The chicks of three other broods died before droppings could be collected (see Table 1). This was too small a sample to control for site and year differences, but inspection of the data showed no obvious individual hen effect. We therefore treat each brood as independent, and the conclusions as preliminary.

The number of invertebrates.ml^{-1} of droppings, and the number and volume of larvae per 25 net sweeps, each had a skewed distribution with many small values and a few large ones. They were approximately normalised by ln(number + 0.1), ln(number + 1) and ln(volume + 1), respectively. Size (volume/number of larvae per transect) was normally distributed. Most analyses were done with SAS (1990) procedures.

Recovery of invertebrates from feeding trials with bantam chicks was analysed by stepwise logistic regressions (SAS LOGISTIC procedure). Potential explanatory variables included each separate trial

Table 1. Number of days at least one chick survived and age of hen (years in parentheses, u = age unknown).

Location	1991	1992	1993	1994	1995
Glen Tanar					
Hen 1	-	-	-	R (3)	< 4 (4)
Hen 2	-	-	11* (1)	58* (2)	-
Finzean					
Hen 1	-	-	-	6 (2)	> 60* (3)
Hen 2	-	-	5 (1)	33* (2)	-
Coilacriech					
Hen 1	R (1)	10* (2)	-	-	-
Hen 2	-	-	-	-	< 4 (1)
Drumbuich	-	-	-	6* (2)	-
Dunkeld	-	-	-	> 60* (u)	38* (u)
Glenlivet	-	-	19* (u)	-	-

R Nest robbed during incubation
* Chick droppings collected from this brood

and, for items other than larvae, the proportion of larvae recovered in each trial.

Results

Mortality

A nest at Glen Tanar and one at Coilacriech were robbed by predators during incubation (Table 1). The brood hen at Glenlivet was killed by a predator when her still-dependent chicks were 19 days old and the Drumbuich hen died after flying into a deer fence when her chicks were six days of age. Clearly, predation was a cause of egg and chick loss, but we do not know what role it played in the loss of chicks whose mother was still alive.

Diet of chicks

Preliminary inspection of the data showed that the numbers of invertebrates in the droppings of chicks in their first three days, while they still had yolk sacs, were lower than in their droppings from four days of age. We therefore used data for chicks between four and 40 days of age for subsequent analyses. When analysing data in relation to time, chick age and date were each used as explanatory variables in separate analyses. Each led to identical conclusions and so we give only the analyses using chick age (SAS GLM models with brood as class variable in all cases). The GLM analyses each provided: 1) an intercept, 2) a common slope estimating the rate at which the concentration of invertebrates in the chicks' droppings changed with age, and 3) a set of 'brood terms', which indicated the mean number of invertebrates in each brood's droppings, relative to the intercept and corrected for chick age.

Changes in diet with chick age

The estimated number of invertebrates.ml^{-1} of droppings showed no change with chick age in the nine broods between four and 20 days ($F_{1,22} = 0.09$, $P = 0.77$). However, the relative amounts of larvae, and of invertebrates other than larvae, did change (Fig. 3). Concentrations of larvae probably declined with chick age ($F_{1,22} = 3.63$, $P = 0.07$) while invertebrates other than larvae increased ($F_{1,22} = 9.69$, $P = 0.005$); the slopes of the two regressions differed significantly (respectively -0.098 ± 0.051 SEM and 0.070 ± 0.023; $t = 4.25$, $P < 0.001$). In particular, there was an increase in spiders ($F_{1,22} = 6.44$, $P = 0.019$) and, probably, ants with age ($F_{1,22} = 3.66$, $P = 0.069$). We infer

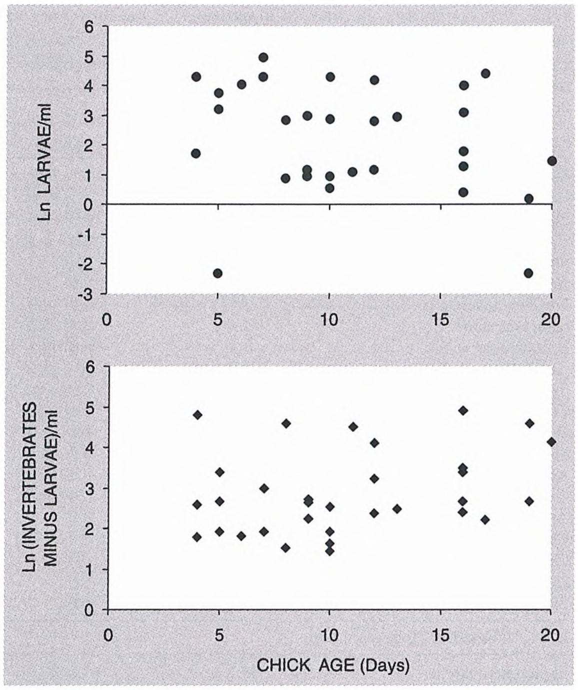

Figure 3. Estimated number of larvae, and of invertebrates minus larvae, in dropping of chicks 4-20 days of age.

that, as the preferred larvae pupated and declined in availability (see below) during the chicks' first 20 days, they ate proportionately fewer larvae and more of other invertebrates (Table 2). In the longer term (4-40 days) the number of invertebrates.ml^{-1} of droppings declined ($F_{1,35} = 56.3$, $P \leq 0.0001$) as the chicks turned increasingly to plant food (Fig. 4).

Bilberry and heather leaves and shoots were the main plant remains identified in chick droppings from places where these foods were readily available (Table 3). Older chicks ate fruiting heads of monocotyledons, notably sedges *Carex* spp., as they ripened in late June and July. At Dunkeld, where dwarf shrubs were scarce and heavily grazed, bracken fronds and sedge heads formed a large part of the diet, as did Sitka spruce needles, especially in 1995, when the brood spent their first three weeks in the forest. The tender new spruce shoots lay in profusion on the forest floor after strong winds broke them from the canopy. Most of the remaining material appeared to be forbs, which were too well digested to identify further. There were no clear trends in the use of any particular plant with chick age, other than more use of fruiting heads of monocotyledons by older chicks, and a significant increase of unidentified material as vegetation became increasingly well digested ($F_{1,37} = 5.67$, $P = 0.023$).

Table 2. Invertebrates, in order of abundance, in the droppings of broods of capercaillie chicks up to and greater than 20 days old. The results are based on brood medians, so that the value for each item given is the median of brood medians. Items present, but with a median of ≤ 0.01, are denoted by T. Items are adult unless specified.

Items, no.ml^{-1} broods ≤ 20 days (N = 9)		
Invertebrates	Median	Range
Lepidoptera larvae	17.3	2.1-76.7
Formicidae	1.8	0.2-17.6
Elateridae	0.8	0.0- 7.5
Opiliones	0.8	0.0- 6.3
Staphylinidae	0.7	0.0- 1.3
Araneae	0.6	0.0- 1.2
Lochmaea saturalis	0.4	0.0- 2.9
Ichneumonidae	0.4	0.0- 5.6
Unidentified	0.3	0.0- 4.4
Carabidae	0.3	0.0- 1.9
Symphyta larvae	0.3	0.0- 0.6
Curculionidae etc.	0.1	0.0-63.8
Diptera	0.1	0.0- 1.3
Scarabidae	0.0	0.0- 1.9
Acaridae	0.0	0.0- 1.9
Cicadellidae	0.0	0.0- 0.6
Aphididae	T	0.0
Chrysomelidae	T	0.0
Tipulidae	T	0.0
Hemiptera	T	0.0
Symphyta	T	0.0
Items, % broods ≤ 20 days (N = 9)		
Lepidoptera larvae	68.7	1.9-90.4
Opiliones	3.9	0.0- 6.4
Formicidae	2.8	1.5-19.9
Ichneumonidae	1.7	0.0- 5.8
Elateridae	1.5	0.0-18.6
Staphylinidae	1.2	0.0- 2.3
Araneae	0.6	0.0- 8.0
Diptera	0.4	0.0- 5.9
Carabidae	0.4	0.0- 3.7
Unidentified	0.0	0.0- 9.9
Curculionidae etc.	0.0	0.0-58.2
Lochmaea saturalis	0.0	0.0-21.3
Acaridae	0.0	0.0- 3.0
Symphyta larvae	0.0	0.0- 1.5
Scarabidae	0.0	0.0- 1.3
Cicadellidae	0.0	0.0- 0.4
Aphididae	T	0.0
Chrysomelidae	T	0.0
Tipulidae	T	0.0
Hemiptera	T	0.0
Symphyta	T	0.0

Items, no.ml^{-1} broods > 20 days (N = 5)		
Invertebrates	Median	Range
Opiliones	2.5	0.8- 9.7
Lepidoptera larvae	2.2	0.8-10.0
Formicidae	0.8	0.0- 5.8
Diptera	0.6	0.0- 0.9
Elateridae	0.6	0.0- 0.8
Unidentified	0.6	0.0- 0.8
Araneae	0.0	0.0- 0.9
Hemiptera	0.0	0.0- 0.3
Symphyta	0.0	0.0- 0.3
Curculionidae etc.	0.0	0.0- 0.3
Aphididae	T	0.0
Carabidae	T	0.0
Chrysomelidae	T	0.0
Cicadellidae	T	0.0
Tipulidae	T	0.0
Lochmaea saturalis	T	0.0
Ichneumonidae	T	0.0
Symphyta larvae	T	0.0
Scarabidae	T	0.0
Staphylinidae	T	0.0
Acaridae	T	0.0
Items, % broods >20 days (N = 5)		
Opiliones	22.2	10.0-60.3
Lepidoptera larvae	21.7	14.3-41.0
Formicidae	15.6	0.0-33.3
Unidentified	4.4	0.0-11.1
Diptera	2.2	0.0- 4.5
Elateridae	2.2	0.0-14.3
Araneae	0.0	0.0- 3.8
Acaridae	0.0	0.0-16.7
Curculionidae etc.	0.0	0.0- 1.3
Aphididae	T	0.0
Carabidae	T	0.0
Chrysomelidae	T	0.0
Cicadellidae	T	0.0
Tipulidae	T	0.0
Lochmaea saturalis	T	0.0
Hemiptera	T	0.0
Ichneumonidae	T	0.0
Symphyta	T	0.0
Symphyta larvae	T	0.0
Scarabidae	T	0.0
Staphylinidae	T	0.0

Differences among broods

The GLM analyses identified significant differences between the diets of the different broods over both 4-20 days and 4-40 days for the total number of invertebrates, larvae alone and invertebrates less larvae, and for ants, spiders and beetles (Table 4). The effect for beetles was due largely to many weevils eaten in the spruce plantation by the Dunkeld brood in 1995.

Diet of chicks in relation to sweep net samples

The number of larvae.ml^{-1} of chick droppings from roosts was compared with the number from sweep-netting at brood sites (Fig. 5). This comparison was done separately for sweeps through heather and through bilberry (there were insufficient data for

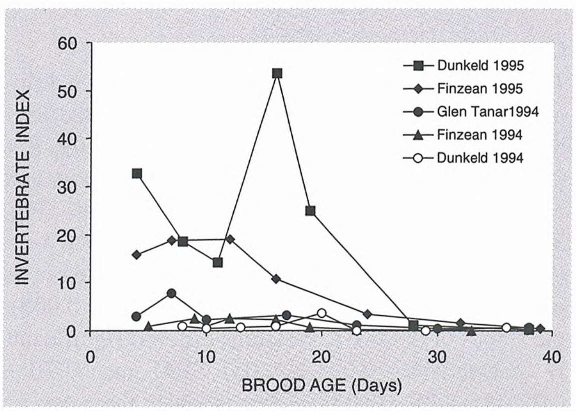

Figure 4. Invertebrate index (number of invertebrates/plant area) for five capercaillie broods 4-40 days old.

Table 3. Vegetation (median % area) in droppings of capercaillie chicks up to and older than 20 days of age.

Plant items	Finzean 1993	Finzean 1994	Finzean 1995	Glen Tanar 1993	Glen Tanar 1994	Glenlivet 1993	Dunkeld 1994	Dunkeld 1995	Overall Median
Broods ≤ 20 Days									
V. myrtillus	13	50	78	41	48	25	3	0	33
C. vulgaris	0	0	15	30	9	23	0	0	4
Carex spp.	0	2	0	0	0	0	3	0	0
P. aquilinum	0	0	0	0	0	0	10	0	0
Dryopteris spp.	0	0	0	0	0	0	0	0	0
P. sitchensis	0	0	0	0	0	0	0	63	0
Other*	87	29	9	29	43	19	55	37	33
Broods > 20 Days									
V. myrtillus	-	21	32	-	47	-	0	0	21
C. vulgaris	-	0	35	-	0	-	0	0	0
Carex spp.	-	27	0	-	1	-	18	12	12
P. aquilinum	-	0	0	-	0	-	0	4	0
Dryopteris spp.	-	0	0	-	0	-	0	13	0
P. sitchensis	-	0	0	-	0	-	0	0	0
Other*	-	53	33	-	52	-	62	73	53

* Other items were largely unidentified

analysis from other vegetation types). Data were available from five broods. Analyses of covariance using log-transformed data showed no significant brood effect so each sample was treated as independent. There were significant positive correlations between the number of larvae in the droppings and numbers on both heather (Spearman r = 0.68, P = 0.0009) and bilberry (Spearman r = 0.66, P = 0.005). Interpreting this result was complicated by the fact that the number of larvae eaten and the number taken in sweep nets both fell through June as the chicks grew older. However, partial Spearman correlations controlling for the effect of chick age gave much the same results (heather, r = 0.68, P = 0.001; bilberry, r = 0.66, P = 0.008). It seems reasonable to conclude that the number of larvae taken in sweep nets is related to the number taken by the chicks. Other invertebrates showed no such correlations. Although there was much variation between broods, larvae represented a median value of 69% (range 2-90%) of all the items identified in the first 20 days, and of 22% (range 10-60%) thereafter (see Table 2). Most larvae in sweep nets were those of geometrid moths, notably the winter moth *Operophtera brumata* and July highflyer *Hydriomena furcata*. Also caught in small numbers were the larvae of microlepidoptera, noctuids and sawfly *Symphyta* spp.

Table 4. Statistics (SAS GLM) for differences among nine capercaillie broods in the number and type of invertebrates in their faeces.

Item	Broods 4-20 days old $F_{8,22}$	Broods 4-20 days old P	Broods 4-40 days old $F_{8,35}$	Broods 4-40 days old P
Total invertebrates	10.33	≤0.0001	6.07	≤0.0001
Larvae	5.14	0.001	6.22	≤0.0001
Invertebrates ÷ larvae	14.18	≤0.0001	5.34	0.0002
Ants	2.50	0.042	2.14	0.058
Spiders	3.81	0.006	3.55	0.004
Beetles	10.85	≤0.0001	5.11	0.0003

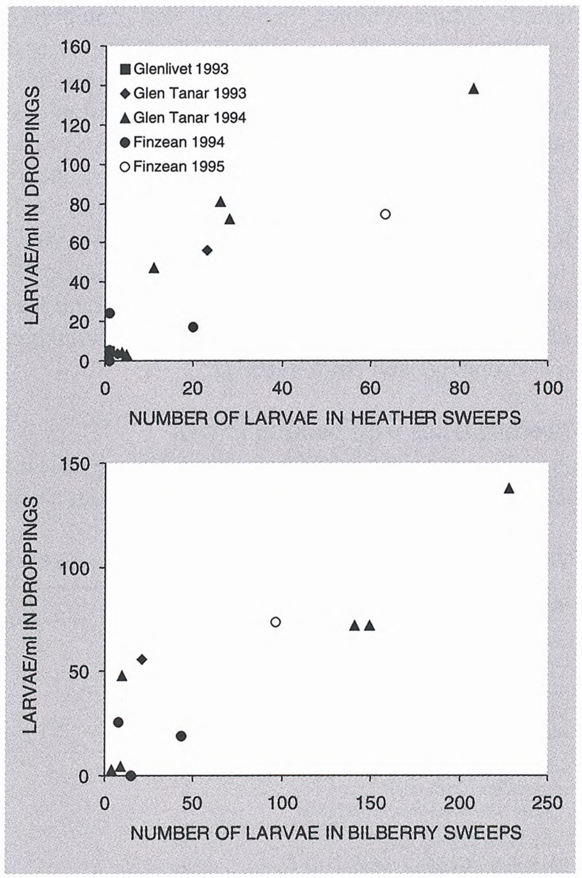

Figure 5. Estimated number of larvae in chick droppings from 4-20 days and the number in sweep net samples through heather and bilberry at the brood site.

Table 5. Invertebrate concentrations (GLM brood terms) controlled for chick age.

Brood	Broods 4 - 20 days old			Broods 4 - 40 days old		
	All invertebrates	Larvae	Other invertebrates	All invertebrates	Larvae	Other invertebrates
Glen Tanar 1994[Ψ]	1.21	2.34	-0.14	1.21	2.05	0.27
Finzean 1995[Ψ]	1.23	2.07	1.59	1.13	1.79	1.38
Drumbuich*	0.73	1.18	0.99	0.34	1.13	0.44
Dunkeld 1994[Ψ]	-0.07	0.43	0.36	0.11	0.25	0.47
Glen Tanar 1993	0.14	0.17	1.24	-0.05	0.11	0.94
Finzean 1994	0.00	0.00	0.00	0.00	0.00	0.00
Dunkeld 1995	1.39	-0.82	2.86	1.34	-0.39	2.48
Glenlivet*	-0.80	-0.94	0.89	-0.60	-1.01	1.09
Coilacriech	-0.27	-3.00	0.04	-0.46	-3.06	-0.26

[Ψ] At least one chick survived >50 days
* Hen died when chicks were small

Chick diet and survival

The brood terms from analyses of covariance (SAS GLM procedure, see Table 5) indicated the relative number of invertebrates in each brood's droppings, corrected for the age of chicks. In three of the nine broods, at least one chick survived more than 50 days. Droppings from these three broods contained more larvae than droppings from the six failed broods (Mann-Whitney one-tailed test comparing GLM brood terms, $U_{3,6} = 1$, $P = 0.024$). However, two of the nine brood hens with dependent chicks died. When these two broods were removed from the analysis, the result remained significant ($U_{3,4} = 0$, $P = 0.028$). Alternatively, one can assume that the chicks would have survived had the hens not died ($U_{4,5} = 3$, $P = 0.056$). The results were the same for the periods 4-20 days and 4-40 days. These results emphasise the importance of larvae in the diet of chicks. There was no association between total invertebrate numbers. ml^{-1} droppings and chick survival.

Feeding trials with bantam chicks

A stepwise logistic regression showed no significant differences in the recovery rate for larvae from chick faeces among the 12 trials, except for one low result (1/10, Wald $\chi^2 = 5.72$, $P = 0.012$, Table 6). Individual trials were never selected by the regression procedure within other invertebrate types. However, there were differences between the rate of recovery for similar types, such as weevils vs click beetles (Fisher exact $P = 0.038$) and wood ants vs small ants (Fisher exact $P = 0.01$). In practice it was seldom possible to distinguish between the different families of ants in the capercaillie chick droppings and so, in Table 6, a combined recovery rate is also shown.

The main conclusion from these trials was that Diptera, and probably spiders and harvestmen, were likely to be under-represented by analyses of fragments in chick droppings, and beetles may have been over-represented. We chose not to calculate 'conversion factors' (Green 1984) because recovery rates were likely to vary with invertebrate species and size, time of passage through the gut, chick age and diet. Instead, we draw conclusions which do not depend upon an accurate knowledge of the chicks' diet.

Abundance and size of larvae in Glen Tanar

The abundance of larvae in Glen Tanar in the six

Table 6. Percentage recovery of invertebrates in bantam chick faeces.

Item	No of trials	No of items	Recovery %	95% CL
Larvae (Lepidoptera, Symphyta)	12	108	55	45-64
Larvae* (Lepidoptera, Symphyta)	11	98	59	49-68
Small ants (Formicidae)	3	30	53	36-70
Wood ants (Formicidae)	2	20	95	73-99
All ants (Formicidae)	5	50	70	55-82
Spiders (Araneae)	3	24	21	9-41
Harvestmen (Opiliones)	1	10	30	10-62
Spiders and harvestmen (Arachnida)	4	34	24	10-44
Click beetles (Elateridae)	3	22	73	51-87
Weevils (eg. Curculionidae)	2	14	100	-
'Beetles' (Coleoptera)	5	36	81	64-91
Houseflies (Muscidae)	2	20	5	1-28

*Excludes one trial with abnormally low recovery rate.

years 1991-1996 was indicated by sweep net samples along 11 permanent transects. Geometrids accounted for most of the larvae and analyses including all larvae gave results similar to those for geometrids alone, except that the variance was increased by a very occasional large noctuid. Accordingly, results below refer only to geometrids, all species combined each year.

In 1992 and 1993, the number and volume of geometrids were greatest at the start of the month, before most chicks had hatched, and declined rapidly towards mid June (Fig. 6), when most chicks were 1-2 weeks old. In 1994, numbers remained high until mid June, although the larvae were smaller than in previous years. The 1995 and 1996 seasons were also prolonged.

Analyses of variance (SAS GLM) accounted for variations in larval number, volume and size (R^2 = 0.86, 0.82 and 0.74, respectively) in terms of year, sampling period, and sample location, and there were significant interactions for year*period and year*location (Table 7). Other interactions were not significant. Hence larval abundance differed among years, sampling periods and sample locations, its timing differed among years, and the relative abundance at different sample sites changed from year to year. Larval size differed between years and sampling periods, but not between locations.

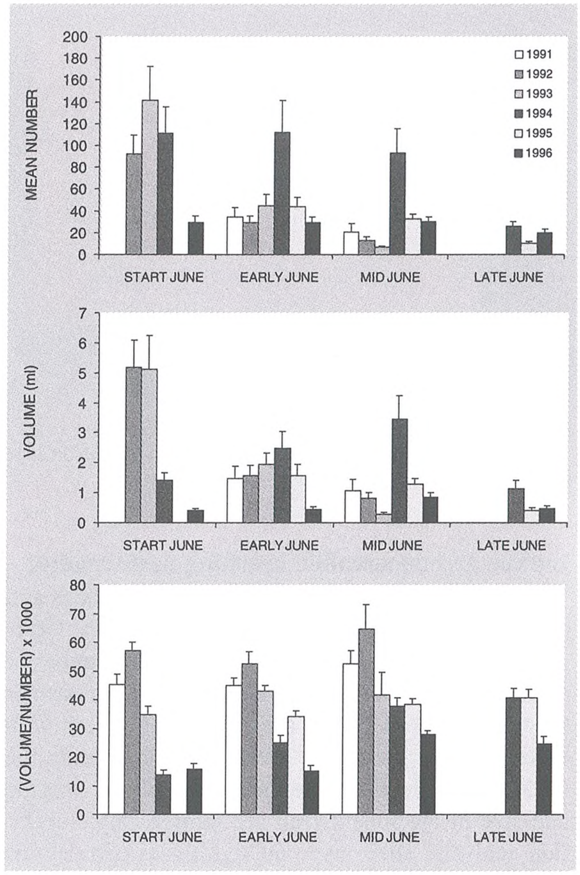

Figure 6. Mean number, volume and size (+ 1 SE) of geometrid larvae in Glen Tanar in June 1991-1996. Missing column means that no sample was obtained.

We checked whether larval abundance was related to the level of deer grazing on the host plants of lepidopteran larvae, as reported by Baines, Sage & Baines (1994), who had Glen Tanar as their study site 8. We did this by comparing three 'grazed' transects, outside a deer fence, with eight 'control' transects inside it. An analysis of variance for larval numbers (as in the previous paragraph, but substituting 'grazed' or 'control' for location), showed no significant effect of grazing ($F_{1,183}$ = 0.38, P = 0.64), but a significant grazing*year interaction ($F_{1,183}$ = 2.93, P = 0.014). In 1992, there were significantly fewer larvae on the grazed sites (t = 2.39, P = 0.018), but in 1994 there were significantly more (t = 2.39, P = 0.018). Overall, there were three years with more larvae on control sites and three with more on the grazed sites. One result in each direction was significant. Similar analyses with larval volume and size showed no significant grazing effect, nor grazing*year interaction.

Table 7. Statistics from analysis of variance (SAS GLM) for the number, volume and size (volume/number) of geometrid larvae in Glen Tanar at 11 sampling locations over three or four weeks in June 1991-1996. All main effects (year, sampling period and location) and their interactions were first entered into each analysis. The insignificant location effect for size was then dropped to give the results below.

Larvae	Year	Sampling period	Sampling location
Number	$F_{5,129} = 21.6$, $P \leq 0.0001$	$F_{5,129} = 78.2$, $P \leq 0.0001$	$F_{10,129} = 12.7$, $P \leq 0.0001$
Volume	$F_{5,129} = 22.5$, $P \leq 0.0001$	$F_{3,129} = 22.7$, $P \leq 0.0001$	$F_{10,129} = 12.0$, $P \leq 0.0001$
Size	$F_{5,139} = 50.9$, $P \leq 0.0001$	$F_{3,139} = 13.9$, $P \leq 0.0001$	
	Year*period	Year*location	
Number	$F_{10,129} = 16.2$, $P \leq 0.0001$	$F_{50,129} = 2.92$, $P \leq 0.0001$	
Volume	$F_{10,129} = 18.6$, $P \leq 0.0001$	$F_{50,129} = 1.93$, $P \leq 0.0001$	
Size	$F_{11,139} = 1.73$, $P = 0.072$	$F_{60,139} = 1.42$, $P = 0.05$	

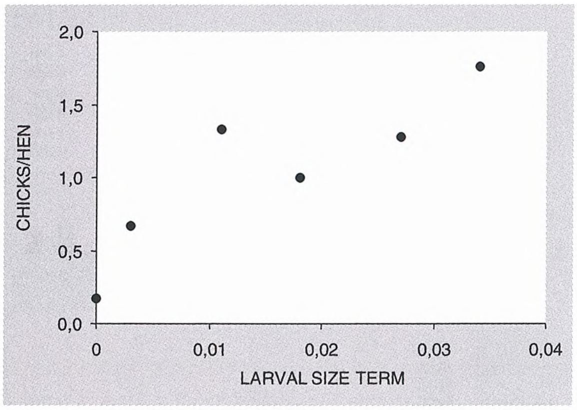

Figure 7. Mean number of chicks per hen in Glen Tanar in July 1991-1996 and size of geometrid larvae in brood habitats in June (year term from GLM analysis).

Larvae and capercaillie breeding performance

The breeding performance of the sample of hens and chicks counted with dogs in Glen Tanar in July 1991-1996 was expressed in three ways: 1) the number of chicks per hen, 2) brood size (number of chicks per successful brood), and 3) the proportion of hens with chicks. These measures were compared with the GLM year effects for geometrid numbers, volume and size in the June sweep net samples, by correlation analysis. There were no significant correlations between any of the measures of breeding performance and the number or volume of larvae, but the mean number of chicks per hen in July was correlated with the size of larvae each year (r = 0.88, P = 0.02, Fig. 7).

Most chicks hatch in the first week of June and have yolk sacs for 4-5 days. Hence, larvae are likely to be most important to them in the second and third weeks of June, when the second and third sweep net samples were taken (Table 8). The best single correlates, using data from weeks 2 and 3 separately, were between the mean brood size in July and, respectively, the size of geometrid larvae in weeks 2 (P = 0.011) and 3 (P = 0.057), and between the number of chicks per hen in July and the size of larvae in week 3 (P = 0.032).

Multiple regressions tested whether size and number of larvae together explained significantly more of the variation in breeding performance than size alone; R^2 values were increased, but not significantly so. For example, the annual GLM term for size explained most of the variation in the number of chicks per hen (R^2 = 0.77), increasing by 0.14 (R^2 = 0.91) when the number term was included (P = 0.12).

Discussion

Chick food

Plant material

Where available, bilberry leaves were usually the main identified plant food for young chicks (see Table 3). The 'other' material in Table 3 included annual forbs, which were too well digested to identify further. Our faecal analyses probably underestimated the proportion of such highly digestible foods in the diet. We did not examine poults' droppings, but it was apparent from their purple colour and loose texture that berries were taken as they became available. Heather and the fruiting heads of sedges, rushes and grasses were also eaten, as were substantial amounts of Sitka spruce, forbs and bracken at Dunkeld, where bilberry was scarce. The importance of bilberry in this limited sample is consistent with studies in Bavaria (Storch 1993, 1994) and Norway (Spidsø & Stuen 1988). It is also an important food plant for geometrid larvae in June. Nonetheless, other

Table 8. Correlations (Pearson) between measures of breeding performance and the number, volume and size of geometrid larvae in Glen Tanar, 1991-1996.

Larvae in sweep samples in June	Breeding performance in July: Mean chicks/hen (all hens seen)	Mean brood size (successful hens)	Proportion of hens with chicks
Week 2			
Number	0.01	-0.17	0.31
Volume	0.60	0.65	0.59
Size	0.67	0.91**	0.32
Week 3			
Number	0.02	-0.60	0.36
Volume	0.31	-0.28	0.59
Size	0.85*	0.80*	0.53

* P < 0.05, ** P < 0.01

plants, such as forbs and sedges, might provide adequate substitutes. Sedges featured largely in the diet of moulting adult cocks in a plantation forest in Perthshire (Picozzi et al. 1996) and, in the Pyrenees, capercaillie broods often frequented forb-rich grassy meadows with no bilberry (Menoni 1991).

Invertebrates

Results based on analyses of droppings may be biased in favour of invertebrates with parts resistant to digestion. In the trials with bantam chicks (see Table 5), spiders and flies were underrepresented in droppings and beetles probably overrepresented. Even so, it is clear from Table 2 that larvae were usually the main invertebrates in the diet of capercaillie chicks.

Previous studies of the crop contents of capercaillie chicks (Cramp & Simmons 1980, Spidsø, Kastdalen, Stuen & Wegge 1984) also stressed the importance of invertebrates, notably larvae, in the diet of young chicks for their first month or so. In Norway, Kastdalen & Wegge (1985, 1991) showed that chicks ate a large proportion of arthropods (up to two-thirds by volume), including ants, spiders, beetles, and especially the larvae of moths and sawflies. The diet of older chicks comprised largely plant material, especially bilberry leaves and berries. Ants were the most numerous invertebrate seen to be eaten in another Norwegian study using captive chicks imprinted on observers but foraging in the wild (Spidsø & Stuen 1988). We noted a significant increase in ants and spiders in the droppings as larvae decreased over the first 20 days, and Storch (1994) points out that, in the central European literature, ants are frequently assumed to be important in brood habitat.

Predictions

We tested three predictions:

1) that broods which eat more larvae survive better. The observation that the droppings of the broods which survived best had the most larvae in them agreed with this. The small sample came from several different areas and years and so we regard this confirmation as tentative;
2) that the number of larvae caught in sweep nets reflects the number eaten. This was also confirmed: the concentration of larvae in chicks' droppings was correlated with the number in sweep net samples from nearby vegetation;
3) that hens rear more chicks in years when more larvae are caught in sweep nets. This prediction, however, was not sustained. Larval abundance (number or volume) was not significantly correlated with any of the three measures of breeding success. Unexpectedly, larval size was correlated with breeding success. In Norway, Kastdalen & Wegge (1991) also found no correlation between breeding performance and larval abundance from four years' data, but they did not consider size. Big larvae may have been easier to find and provided more sustenance for less effort than small larvae. It is not clear to what extent annual variations in larval size were due to size variations within species, or to variations in the proportions of species of different size. Our result is not dissimilar to the findings of Hill (1985) for pheasant chicks to 12 days of age: chick survival was greatest for those broods which had ingested the highest biomass of insects.

By the third week of June, most chicks in Glen Tanar were 2-3 weeks old and the invertebrate content of their droppings was still high. Their total requirement for invertebrate food was probably increasing because they were growing rapidly, but the proportion of larvae in their diet declined as did the number caught in sweep nets. Hence the availability of larvae in the third week of June could be critical if chicks depended largely on larvae. Alternatively, other invertebrates might provide a substitute. The main prey of two broods, at Glenlivet and at Dunkeld (in 1995), were beetles: click beetles and heather beetles *Lochmaea saturalis* at Glenlivet, weevils at Dunkeld. Neither brood survived, although the Glenlivet brood might have done so had the hen not been killed, as she had reared a brood successfully in the same habitat the previous year (D. Dugan, pers. comm.).

Breeding success of capercaillie at Glen Tanar was poor throughout this study, never exceeding 1.4 chicks per hen in August. In an earlier, 9-year study at Glen Tanar, Moss & Oswald (1985) recorded an average breeding success of 2.3 chicks per hen (range: 1.4-3.4). They found an inverse correlation between breeding success and the number of days with rain in the first 10 days of June and suggested that wet conditions might inhibit the chicks' foraging. In 1991-1997, capercaillie breeding success in 14 Scottish forests was related to rainfall in mid June (D. Baines, R. Moss & D. Dugan, unpubl. data).

Capercaillie chicks eat more arthropods for longer than any other tetraonid chick (Savory 1989), possibly because they have to support the fastest growth rate of all. Baines, Wilson & Beeley (1996) indicated that the timing of capercaillie hatching roughly coincided with peak biomass of larvae in Scotland (see their Fig. 1). Similarly, the hatching of great tits *Parus major* and blue tits *P. caeruleus* in Wytham Wood near Oxford was timed such that they could take advantage of peak populations of larvae (largely winter moth, as for capercaillie in Glen Tanar) on the oak trees (Perrins 1991, Noordwijk, McCleery & Perrins 1995). Whereas our evidence largely supports such a suggestion for capercaillie, it is certainly not the whole story, since prediction 3) was falsified. Also, larval abundance declined rapidly after the beginning of June (see Fig. 6), and breeding success at Glen Tanar was related to larval size (see Fig. 7) rather than abundance.

Baines et al. (1996) suggested that deer grazing, by reducing ground vegetation, may also reduce numbers of larvae, the main food of capercaillie chicks, and so reduce their breeding success. Their study was done in 1991 and 1992 and included Glen Tanar as one of their eight study areas. They concluded, from sweep-netting, that lepidopterous larvae were less numerous on grazed sites than on controls. Our data for 1991-1992 confirm this (combined P from t-tests < 0.05). However, over the full six years of our study, there was no significant effect of grazing on larval numbers. Rather, there was a significant year*treatment interaction, such that grazed areas had more larvae in three years (1992 significant) and controls had more in three (1994 significant). Perhaps the effect of grazing on capercaillie chick diet is non-linear. Grazing may affect the number of larvae present positively or negatively while increasing their availability (Atlegrim & Sjöberg 1995). A reasonable working hypothesis is that moderate grazing provides capercaillie chicks with the highest intake of larvae per unit effort.

Baines et al. (1996) concluded that spring numbers of lepidopterous larvae increased sevenfold from west (Argyll) to east (Deeside) Scotland in 1991-1992. Their samples comprised 6×125 sweeps, three sets in grazed and three in ungrazed sites, in each forest each year. They were taken in a three week period from mid May to early June, when larval numbers exhibited least variation (D. Baines, pers. com.), and the data for the two years were combined. We did not sample in May since capercaillie chicks hatch in early to mid June. Nonetheless, the rapid week-to-week changes in larval abundance through June in Glen Tanar suggest that one sample per forest per year may not be sufficient to distinguish within and between-forest variations. Thus, the magnitude and direction of any west to east cline in larval abundance across Scotland could vary from year to year. Furthermore, our data suggest that, for capercaillie chicks, larval size is at least as important as number. Hence, further work on geographical variations in larval size and abundance is necessary in view of its implications for the breeding performance and distribution of woodland grouse.

Conclusions

Larvae, especially of winter moth, were the main invertebrate food of capercaillie chicks and chicks which ate more larvae survived better. But, despite abundant larvae in some years, breeding was poor throughout the study. Factors other than larval abundance seemed to be important. These included the size of larvae and perhaps the availability of other invertebrate foods.

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