

Feeding of hand-reared grey partridge *Perdix perdix* chicks - importance of invertebrates

Tuija Liukkonen-Anttila, Ahti Putaala & Raimo Hissa

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Survival of hand-reared gamebirds is reported to be poor after release into the wild. One reason for the high mortality is assumed to be nutritional maladaptation of hand-reared birds to natural foods. In captivity, birds are usually fed commercial poultry foods, which are originally meant for chickens. We carried out a feeding trial to examine the importance of invertebrates and animal protein on the growth and development of temperature regulation in grey partridge *Perdix perdix* chicks. Three diet groups were established: invertebrate-rich, low-invertebrate, and fish groups. Invertebrate food consisted of fly (*Calliphora*) larvae and ant (Formicoidea) pupae, and the fish diet of fresh vendace *Coregonus albula* and smelt *Osmerus eperlanus*. Each diet group was provided with *ad libitum* plant food. Chicks were weighed every third day, their primaries were measured, and their cooling rate at 0°C was recorded. Chicks fed an invertebrate-rich diet were heavier than the other chicks, and their primaries developed earlier than the other chicks' feathers. Chicks fed a low-invertebrate or a fish diet cooled faster than chicks fed an invertebrate-rich diet. A wild brood was captured and 7-day-old wild chicks were examined as a reference group for the captive chicks. Results obtained from these chicks are in agreement with the results obtained from the chicks fed an invertebrate-rich diet. In conclusion, invertebrates are not replaceable by a fish diet like the one used in our study during the growth period of hand-reared grey partridges. Invertebrates should be included in the diet of hand-reared grey partridge chicks during their first weeks of life.

Key words: body mass, chicks, grey partridge, invertebrates, Perdix perdix, primaries, temperature regulation

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Hand-rearing and releasing of gamebirds have become very popular in the struggle to strengthen natural populations. However, most releasing programmes have failed, because the birds died soon after the release into the wild (Panek 1988, Schroth 1991, Putaala & Hissa 1998). Several galliform species, when hand-reared, differ from their wild counterparts in many morphological and physiological aspects (Moss 1972, Putaala & Hissa 1995, Liukkonen-Anttila, Saartoala & Hissa 2000). These differences may at least partly be explained by the commercial poultry foods used in hand-rearing. These foods are usually manufactured for chickens. They are based on a variety of cereals and a source of animal protein (fish/meat-powder), are high-digestible, and have a relatively low fibre and a high protein content. Although adult grey partridges *Perdix perdix* feed mainly on plant food, chicks feed almost entirely on invertebrates during their first 2-3 weeks of life (Green 1984, Potts 1986, Panek 1992), and switch to a plant diet only gradually (Dahlgren 1987, Itämies, Putaala, Pirinen & Hissa 1996).

Commercial poultry foods are relatively cheap and easy to serve for a large flock of hand-reared birds. However, galliform birds fed with these low-fibre food-stuffs have shorter intestines and lighter gizzards than wild birds (Moss 1972, Putaala & Hissa 1995, Liukkonen-Anttila et al. 2000). The gut morphology may affect the quality of hand-reared birds and their survival if they are reared for release into the wild. However, collecting large amounts of natural food, such as invertebrates for chicks, is time-consuming and may be prohibitively expensive.

In this study we examined the impact of invertebrates and animal protein on growth and development of temperature regulation of grey partridge chicks. The control of body temperature of newly hatched chicks is poorly developed, partly because the plumage and insulation are incompletely developed (Hissa, Saarela, Rintamäki, Lindén & Hohtola 1983, Marjoniemi, Hohtola, Putaala & Hissa 1995). As chicks grow, their ability to produce heat and their insulation improve (Spiers, McNabb & McNabb 1974, Ricklefs 1979, Marjoniemi et al. 1995).

We also wanted to study whether the animal protein from invertebrates could be replaced by easily served and relatively cheap fish meals for captive-reared chicks. Further, we studied the effects of fish meals on growth, development of temperature regulation, and development of wing primaries. Fish protein is rich in cysteine and methionine compared with invertebrates or green plant material (Anon. 1970). These amino acids are essential for the growth of the plumage (Bagliacca,

Chiarcossi & Mori 1985). A preliminary report has been presented elsewhere (Liukkonen, Putaala & Hissa 1996).

Material and methods

Birds

Grey partridges, captive for several generations, were housed in outdoor aviaries at the Zoological Gardens, University of Oulu, Finland. Eggs collected from 22 pairs were artificially incubated. Air temperature in the incubator was set at 37.8°C and relative humidity (RH) at 55-60%. Two days before the estimated hatching, the RH was raised to 80%. On the hatching day chicks were moved to open wooden boxes of 1 m² with 10 chicks in each box (it is not possible to rear grey partridge chicks in individual cages). The boxes were placed under a 250 W lamp hanging 70 cm above the floor. The housing conditions (light, temperature, humidity) were similar for each box. At the age of three weeks the chicks were transferred to outdoor aviaries of 20 m².

In addition to hand-reared chicks one wild brood of known hatch date was captured for comparison with captive-bred birds. Wild radio-tagged male and female birds, with a brood of twelve chicks were captured from their roosting site at Tyrnävä (64°50'N, 25°37'E) using the method described by Kenward, Robertson, Coates, Marström & Karlbom (1993). These birds were housed indoors as described for hand-reared chicks. Parents were kept in a separate box next to the chicks. The chicks and their parents were kept for two days, and after measurements of body mass, primary length and cooling rate at the age of seven days they were released back into the wild.

Feeding experiments

Hand-reared grey partridge chicks were randomly allocated to one of three diet groups, and individually marked with colour rings. The 20 chicks used in each group were fed an invertebrate-rich diet, a low-invertebrate diet, or a fish diet. Siblings may have ended up in the same diet group.

Chicks were fed three times a day: 08:30-09:30, 14:00-15:00 and 20:00-21:00. Invertebrate food consisted of larvae of *Calliphora* (Diptera), ant (Formicoidea) pupae and a variety of insects found in the plant material provided. Food was divided onto several plates to avoid competition between chicks. The fish diet consisted of fresh, fine-chopped smelt *Osmerus eperlanus* and vendace *Coregonus albula*. The quantities of invertebrates and fish supplied are given in Table 1. The amount of invertebrates given to chicks at the age of

Table 1. Amounts of invertebrates and fish (in g fresh weight) supplied to each of the three diet groups of grey partridge chicks at the age of 1-14 and 14-21 days.

Diet group	Age	
	1-14 days ¹	14-21 days ²
Invertebrate-rich	6 g/chick	15 g/chick
Low-invertebrate	1.5 g/chick	9 g/chick
Fish	6 g/chick	15 g/chick

¹ Based on Dahlgren (1987);

² Based on experimental experience.

1-14 days was based on Dahlgren (1987). To determine the amount of invertebrates that chicks should be given at the age of 14-21 days, we weighed the food left by chicks on the plates between feedings 1-14 days old, and estimated the adequate amount based on this. Plant material was given *ad libitum*, and it consisted of fresh green leaves and flowers of *Stellaria media*, *Polygonum* sp., *Rumex acetosa*, *R. acetosella*, *R. longifolia* and *Chenopodium album*, as well as seeds of *Galeopsis* sp., *Fallopia convolvulus*, *Polygonum* sp. and *C. album*. Each diet group had *ad libitum* access to water and grit. During the first week the chicks were provided with Terramycin (Pfizer) in the water against microbial diseases, and at the age of seven days charcoal powder was added to the food to prevent diarrhea. Wild chicks were fed plant material, and commercial chicken food (Poikas-Herkku, Raisio, Finland) which contained 19% crude-protein, 6.1% crude-fibre and 5.1% crude-fat. From the age of 21 days, all chicks were fed the same diet, consisting of plant material, commercial chicken food and grains of oats *Avena sativa*.

Measurements

All chicks were weighed every third day (to the nearest 0.1 gram) before the morning feeding until the age of 28 days, and again at the age of 56 days (eight weeks) and 91 days (13 weeks). The chicks used in the cooling rate measurements, were also weighed on the morning of the experiment day as were the wild chicks.

Primary growth and cooling rate of seven randomly chosen (but the same throughout the trial) chicks from each diet group were measured. Primaries of the left wing were measured every third day (to the nearest 0.1 mm) according to the method described by Zwickel & Lance (1966), with the wing not flattened. The last measurements were carried out at the ages of eight and 13 weeks. Primary feather 1 (P1) is the innermost (closest to the body) and P10 the outermost of the primaries. Primary lengths of wild chicks were examined at the age of seven days.

The cooling rate of chicks was measured at the ages of 1, 7, 11, 15, 18 and 21 days, and the body temper-

ature of the chicks was continuously monitored at 0°C as in Marjoniemi et al. (1995). It was recorded for 20 minutes or until it had dropped to +25°C in 1-day-old chicks, to +30°C in 7- and 11-day-old chicks, to +33°C in 15-day-old chicks and to +35°C in 18-day-old chicks. At the age of 21 days the body temperature was expected to remain above +35°C for 20 minutes in every chick. The cooling rate of wild chicks was examined at the age of seven days.

Statistical analysis

Statistical analysis was conducted using the statistical software package SPSS 8.0. Body mass of chicks in separate boxes at the hatching day was tested with one-way ANOVA. Body mass during the feeding trial (1-21 days) was tested using a repeated-measures analysis of variance (ANOVAR). The set of measurements in each rearing box was the within-subject factor, and diet group was the between-subject factor. Firstly, ANOVAR reveals whether the response (the form of the curve) in the set of measurements is similar in each treatment. Secondly, ANOVAR gives a straight answer to the question, whether the treatment had an impact on the individuals of separate groups. Tukey's test ($P < 0.05$) was used for paired comparisons. Days 24-28 were excluded from the statistical analysis, because the chicks were fed the same diet from the age of 21 days. Differences in body mass at the age of eight and 13 weeks were analysed using one-way ANOVA, followed by Tukey's test.

Differences in the length of the primaries and the cooling rate during the feeding trial (1-21 days) between diet groups were analysed using the ANOVAR, again with

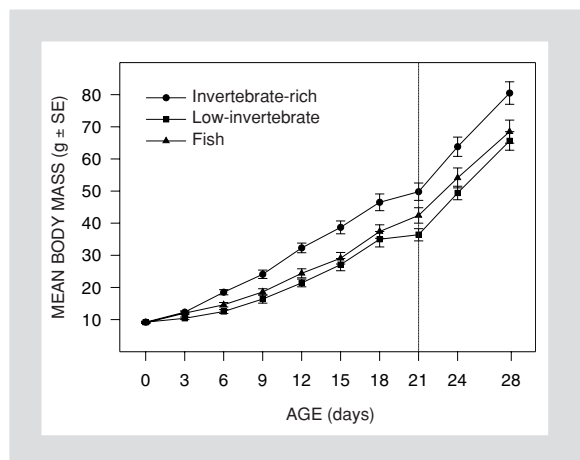


Figure 1. Mean body mass ($g \pm SE$) of hand-reared grey partridge chicks fed three different diets. On the x-axis, 0 = hatching day. For each group of chicks, $N = 20$. The vertical line indicates the end of the feeding trial.

Table 2. Mean body mass (g ± SE) of the grey partridge chicks in each of the diet groups at hatching and at the age of 1, 8 and 13 weeks. At hatching and at the age of 8 and 13 weeks: N = 20 in each diet group; at the age of one week: N = 7 in each diet group; in the wild chicks N = 12.

Diet group	Age of chicks			
	Hatch day (g ± SE)	1 week (g ± SE)	8 weeks (g ± SE)	13 weeks (g ± SE)
Invertebrate-rich	9.2 ± 0.2	17.4 ± 1.2	258.7 ± 4.9	374.3 ± 5.8
Low-invertebrate	9.2 ± 0.3	12.9 ± 0.9	234.8 ± 9.6	363.2 ± 5.3
Fish	9.1 ± 0.2	15.6 ± 0.9	230.3 ± 8.9	362.9 ± 5.7
Wild		16.4 ± 0.5		

Results

the set of measurements in each rearing box as the within-subject factor, and diet group as the between-subject factor. Paired comparisons were conducted using Tukey's test. Primary measurements at the age of 24 and 28 days were excluded because the developmental stages of primaries varied greatly between diet groups. Primary lengths at the age of eight and 13 weeks were tested using one-way ANOVA, followed by Tukey's test. Wild chicks were excluded from the statistical analyses.

Body mass

The mean body mass of newly hatched chicks was 9.2 ± 0.1 g (Fig. 1, Table 2). There was no statistical difference between chicks in different boxes ($F_{5,54} = 0.186$, $P = 0.966$).

The body mass increased differently in chicks from different diet groups ($F_{14,21} = 12.830$, $P < 0.001$; see Fig. 1), and the diet had an impact on body mass ($F_{2,3} = 54.447$, $P = 0.004$). Chicks fed an invertebrate-rich diet were significantly heavier than chicks fed a low-

Table 3. Mean lengths of the primaries P1-P10 (mm ± SE) of grey partridge chicks according to diet group and age in days (7-91). Empty cells indicate that the feathers were not comparable due to different developmental stages, and 0 indicates that the feathers were not yet growing.

Diet	Day	Primary									
		P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
Invertebrate-rich											
	7	7.3 ± 1.0	7.6 ± 0.5	7.6 ± 1.2	5.9 ± 1.5	6.8 ± 1.3	6.3 ± 1.1	6.8 ± 0.2	1.4 ± 0.7	0	0
	9	18.4 ± 1.6	23.8 ± 1.1	21.4 ± 0.7	14.5 ± 2.0	15.9 ± 1.5	15.9 ± 0.9	12.1 ± 0.9	3.3 ± 1.0	0	0
	12	31.4 ± 1.3	34.2 ± 1.6	33.1 ± 1.4	31.5 ± 1.7	29.8 ± 1.4	27.4 ± 1.7	20.5 ± 1.9	5.2 ± 1.3	0	0
	15	37.4 ± 1.4	39.1 ± 1.7	40.9 ± 1.7	42.6 ± 1.9	39.9 ± 2.3	38.0 ± 2.1	30.4 ± 1.9	10.2 ± 1.2	0	0
	18	43.0 ± 1.3	46.8 ± 1.3	50.2 ± 2.2	51.4 ± 2.2	48.0 ± 2.6	45.6 ± 2.8	45.7 ± 1.9	16.4 ± 2.2	0	0
	21	46.4 ± 1.2	49.9 ± 1.4	54.6 ± 1.6	57.8 ± 2.2	56.8 ± 2.0	52.4 ± 2.3	54.1 ± 2.7	24.7 ± 2.0	0	0
	24	-	-	-	-	-	-	-	-	0	0
	28	-	-	-	-	-	-	-	-	0	0
	56	-	-	-	-	-	-	-	-	78.8 ± 2.3	71.3 ± 1.6
	91	-	-	-	-	-	-	-	-	-	95.8 ± 4.1
Low-invertebrate											
	7	5.1 ± 0.4	4.0 ± 1.1	6.6 ± 0.9	5.4 ± 1.2	4.4 ± 0.9	4.5 ± 1.3	2.7 ± 0.8	0	0	0
	9	11.0 ± 1.0	12.1 ± 1.0	12.2 ± 0.9	12.1 ± 0.7	11.5 ± 1.4	13.3 ± 0.6	8.9 ± 0.7	0	0	0
	12	18.8 ± 1.7	19.9 ± 1.4	21.3 ± 2.0	24.0 ± 1.9	22.6 ± 2.2	20.9 ± 1.3	17.3 ± 1.2	1.1 ± 0.4	0	0
	15	25.8 ± 2.0	27.6 ± 2.5	33.8 ± 2.2	29.7 ± 2.1	29.3 ± 1.5	26.7 ± 1.8	23.2 ± 1.5	2.4 ± 0.9	0	0
	18	38.7 ± 1.6	36.8 ± 0.9	42.3 ± 2.5	40.9 ± 2.1	40.0 ± 1.6	36.4 ± 1.6	36.6 ± 1.7	5.9 ± 1.9	0	0
	21	42.4 ± 1.5	44.5 ± 1.8	46.1 ± 2.1	48.2 ± 1.6	47.8 ± 1.5	42.4 ± 2.3	45.4 ± 1.8	10.6 ± 2.5	0	0
	24	-	-	-	-	-	-	-	-	0	0
	28	-	-	-	-	-	-	-	-	0	0
	56	-	-	-	-	-	-	-	-	77.6 ± 1.5	54.9 ± 6.1
	91	-	-	-	-	-	-	-	-	-	98.3 ± 1.9
Fish											
	7	4.1 ± 0.9	4.5 ± 0.9	3.1 ± 1.0	4.5 ± 0.9	3.9 ± 0.1	3.8 ± 0.8	3.5 ± 0.8	0	0	0
	9	7.4 ± 0.8	7.5 ± 0.7	8.1 ± 0.5	6.4 ± 0.3	8.8 ± 0.8	6.6 ± 0.4	8.2 ± 0.6	0	0	0
	12	15.6 ± 0.7	14.5 ± 0.9	13.8 ± 1.3	18.5 ± 2.1	17.9 ± 1.8	15.4 ± 1.8	12.8 ± 1.0	1.2 ± 0.8	0	0
	15	32.6 ± 1.4	26.0 ± 1.1	30.7 ± 1.9	27.1 ± 1.6	28.6 ± 1.5	25.8 ± 2.5	23.9 ± 1.5	5.1 ± 0.9	0	0
	18	31.7 ± 1.5	35.7 ± 2.7	36.2 ± 2.0	38.6 ± 1.4	35.5 ± 1.8	34.0 ± 2.3	38.5 ± 2.0	9.4 ± 1.3	0	0
	21	35.1 ± 1.4	39.2 ± 1.3	43.4 ± 1.8	45.1 ± 1.0	45.9 ± 1.9	44.2 ± 1.6	46.2 ± 1.8	15.2 ± 1.3	0	0
	24	-	-	-	-	-	-	-	-	0	0
	28	-	-	-	-	-	-	-	-	0	0
	56	-	-	-	-	-	-	-	-	76.8 ± 2.8	65.5 ± 1.8
	91	-	-	-	-	-	-	-	-	-	96.4 ± 1.0
Wild											
	7	12.4 ± 0.4	13.5 ± 0.6	12.5 ± 0.6	11.3 ± 0.6	10.6 ± 0.3	9.6 ± 0.3	7.9 ± 0.3	0	0	0

Table 4. P-values of Tukey's test following ANOVA for comparison of primary (P1-P8) lengths of grey partridge chicks belonging to the diet groups: 1 = invertebrate-rich; 2 = low-invertebrate; 3 = fish.

Age	Diet	Primary no							
		P1	P2	P3	P4	P5	P6	P7	P8
Day 7	1-2	0.107	0.000	0.407	0.352	0.000	0.007	0.002	0.008
	1-3	0.048	0.001	0.014	0.049	0.000	0.002	0.003	0.008
	2-3	0.537	0.092	0.027	0.160	0.007	0.073	0.110	1.000
Day 9	1-2	0.016	0.001	0.002	0.022	0.002	0.018	0.003	0.000
	1-3	0.005	0.000	0.001	0.001	0.001	0.000	0.002	0.000
	2-3	0.093	0.011	0.021	0.001	0.008	0.001	0.186	1.000
Day 12	1-2	0.001	0.001	0.023	0.028	0.001	0.000	0.002	0.000
	1-3	0.001	0.000	0.005	0.005	0.000	0.000	0.000	0.000
	2-3	0.056	0.009	0.062	0.052	0.002	0.000	0.001	0.940
Day 15	1-2	0.004	0.003	0.067	0.003	0.007	0.003	0.002	0.000
	1-3	0.056	0.002	0.022	0.002	0.005	0.002	0.003	0.002
	2-3	0.017	0.368	0.275	0.153	0.780	0.594	0.647	0.011
Day 18	1-2	0.175	0.036	0.006	0.000	0.022	0.007	0.001	0.000
	1-3	0.012	0.026	0.001	0.000	0.006	0.004	0.003	0.000
	2-3	0.041	0.827	0.011	0.013	0.094	0.199	0.139	0.001
Day 21	1-2	0.227	0.037	0.002	0.001	0.004	0.000	0.000	0.000
	1-3	0.218	0.005	0.001	0.000	0.002	0.001	0.000	0.000
	2-3	0.999	0.039	0.053	0.024	0.185	0.043	0.021	0.002

invertebrate diet, from the age of three days until the age of 21 days ($P = 0.001-0.037$), and significantly heavier than chicks fed a fish diet, from the age of six days until the age of 18 days ($P = 0.001-0.039$). The difference between chicks fed a low-invertebrate and a fish diet was significant at the age of three days ($P = 0.046$), and almost significant at the age of 18 days ($P = 0.054$). Otherwise, no difference was found in body mass between

chicks fed a low-invertebrate and a fish diet ($P = 0.098-0.682$).

At the age of one week wild chicks had a similar body mass to chicks fed an invertebrate-rich or fish diet (see Table 2). At the age of eight weeks chicks still differed from each other in body mass ($F_{2,57} = 3.595$, $P = 0.034$; see Table 2). Chicks fed an invertebrate-rich diet were heavier than chicks fed a fish diet ($P = 0.039$). Chicks fed a low-invertebrate diet did not differ from those fed

an invertebrate-rich ($P = 0.106$) nor from those fed a fish ($P = 0.920$) diet. At the age of 13 weeks the body mass of chicks was similar in each group ($F_{2,57} = 1.338$, $P = 0.270$).

Primary development

The development of primaries was different in the different diet groups ($F_{10,15} = 3.468-231.027$, $P = 0.001-0.015$). During the feeding trial the diet had a clear impact on the growth of the primaries P1-P8 ($F_{2,3} = 95.472-1805.149$, $P < 0.001 - P = 0.002$). Data on primary lengths are given in Table 3 and test statistics of paired comparisons in Table 4. Wild chicks seemed to have longer primaries than hand-reared chicks of any of the diet groups at the age of seven days. P9 and P10 primaries were not measurable during the feeding trial.

Chicks fed an invertebrate-rich diet had fully developed primaries earlier than the chicks of the other diet groups. Chicks fed an invertebrate-rich

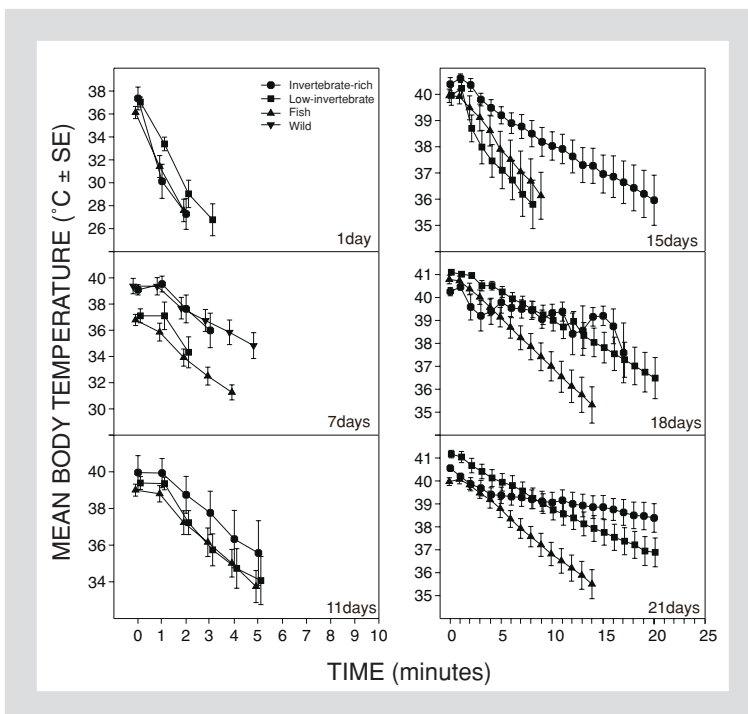


Figure 2. Cooling rates of hand-reared grey partridge chicks fed three different diets at the ages of 1, 7, 11, 15, 18, 21 days and for 7-day-old wild chicks at an ambient temperature of 0°C. For each group $N = 7$.

diet had at least five, and chicks fed a low-invertebrate or a fish diet three completely developed juvenile primary feathers at the age of 28 days. At the age of eight weeks chicks fed different diets did not differ from each other neither in the length of P9 ($F_{2,5} = 0.731$, $P = 0.551$) nor in the length of P10 ($F_{2,5} = 7.582$, $P = 0.076$). All chicks had a fully developed P10 at the age of 13 weeks, and at this age the length of P10 did not differ ($F_{2,5} = 1.340$, $P = 0.384$) for chicks fed different diets.

Cooling rate

The chicks' responses to cooling varied during the feeding trial. At the ages of one ($F_{4,6} = 2.114$, $P = 0.197$; Fig. 2) and 15 days ($F_{16,24} = 0.997$, $P = 0.490$) the response was similar in each group. At the ages of seven ($F_{4,6} = 10.928$, $P = 0.006$), 11 ($F_{10,15} = 4.413$, $P = 0.005$), 18 ($F_{28,42} = 5.193$, $P < 0.001$) and 21 days ($F_{28,42} = 11.149$, $P < 0.001$) the chicks responded differently.

During the first day chicks did not differ from each other in cooling rate ($F_{2,3} = 0.935$, $P = 0.483$). However, diet had an impact on the cooling rate at the ages of seven and 11 days ($F_{2,3} = 183.581$, $P = 0.001$ and $F_{2,3} = 25.843$, $P = 0.013$, respectively). Chicks fed an invertebrate-rich diet had a lower cooling rate than chicks fed a low-invertebrate ($P = 0.002-0.024$) or a fish ($P = 0.002-0.008$) diet. The difference between chicks fed a low-insect or a fish diet was not significant ($P = 0.056-0.966$). The cooling rate of wild chicks was similar to that of the chicks fed an invertebrate-rich diet (see Fig. 2). Diet had no impact on the cooling rate at the age of 15 days ($F_{2,3} = 0.975$, $P = 0.472$), but the chicks fed an invertebrate-rich diet could stay longer in the experiment.

At the age of 18 days the cooling rate differed between diet groups ($F_{2,3} = 9.713$, $P = 0.049$). The cooling rate in chicks fed an invertebrate-rich diet varied greatly (see Fig. 2). It did not differ from the cooling rate of chicks fed a low-invertebrate diet ($P = 0.080-0.999$), except for three minutes at the beginning of the experiment ($P = 0.015-0.028$). There was no difference between chicks fed an invertebrate-rich and a fish diet in the cooling rate ($P = 0.071-0.682$), except at the end of the experiment when the body temperature of chicks fed an invertebrate-rich diet increased ($P = 0.025$). Chicks fed a low-invertebrate diet had a similar cooling rate to chicks fed a fish diet ($P = 0.092 - 0.254$).

At the age of 21 days the cooling rate was influenced by the diet ($F_{2,3} = 9.901$, $P = 0.048$). Chicks fed an invertebrate-rich diet could keep their body temperature relatively stable (see Fig. 2). Chicks fed an inver-

tebrate-rich diet had a similar cooling rate to chicks fed a low-invertebrate ($P = 0.059 - 0.997$) or a fish diet ($P = 0.068-0.964$). Only in the last minutes of the experiment did chicks fed a low-invertebrate or a fish diet cool faster than chicks fed an invertebrate-rich diet ($P = 0.002-0.034$). Furthermore, the initial body temperature of chicks fed a fish diet was lower than that of chicks fed a low-invertebrate diet ($P = 0.013$).

Discussion

Body mass and growth of grey partridge chicks

Our results on the influence of invertebrates on the growth of grey partridge chicks are in agreement with Potts (1986) and Dahlgren (1987), who suggested that the growth of grey partridge chicks is clearly facilitated by invertebrate food, as the chicks fed an invertebrate-rich diet grew faster than other chicks. In our experiment, chicks fed a fish diet tended to be heavier than chicks fed a low-invertebrate diet, but the difference was not significant, and wild 1-week-old chicks had a similar body mass to chicks fed an invertebrate-rich diet.

Although all the birds were fed a commercial diet from the age of 21 days and onwards, the chicks fed an invertebrate-rich diet were still heavier at the age of eight weeks. The body mass of chicks fed a low-invertebrate diet and a fish diet increased relatively quickly after changing to the commercial diet. At the age of 13 weeks chicks from different diet groups did not differ anymore from each other in body mass. The high-digestible energy-rich commercial poultry food may have enabled this rate of growth. According to Dahlgren (1987) grey partridge chicks fed a low-insect diet until the age of 63 days are lighter than chicks fed an insect-rich diet even in the next breeding season. Grey partridge chicks do not grow as fast on grains and weed seeds as on invertebrate food, not even when protein-rich clover *Trifolium* sp. is added to the diet (Potts 1986). On low-insect diet the chicks are more vulnerable to the effects of pesticides (Dahlgren 1987). Sage grouse *Centrocercus urophasianus* chicks survive without insect food at the age of three weeks, but their growth rate is lower than in chicks fed insects (Johnson & Boyce 1990).

Grey partridge chicks fed a low-invertebrate or a fish diet in the current study were lighter than grey partridge chicks fed commercial foods (Marjoniemi et al. 1995). Moss, Watson, Parr, Trenholm & Marquiss (1993) also noticed that red grouse *Lagopus lagopus scoticus* chicks fed commercial poultry food grew faster than wild chicks. Survival of heavy chicks is assumed to be

better than that of lighter chicks. Heavier wild chicks reach their flying ability earlier - approximately at the age of 10 days - than lighter chicks (Potts 1986), which facilitates their survival. However, high adult body mass of hand-reared birds resulting from the commercial poultry food has negative effects on the flying ability (Putala, Oksa, Rintamäki & Hissa 1997). In our study, birds fed an invertebrate-rich diet started to make attempts to fly some days before other chicks, typically at the age of 10 days (T. Liukkonen-Anttila, A. Putala & R. Hissa, unpubl. data), and all chicks could fly at the age of 14 days. It is also noteworthy that the chicks fed an invertebrate-rich diet rested most of the time, whereas the chicks fed a low-invertebrate diet seemed to search for food all day long, although their access to plant food was unlimited.

Development of the primaries

Wild 7-day-old chicks seemed to have longer primaries than hand-reared chicks. The well-balanced natural invertebrate diet probably facilitated the growth of primaries and flight ability. An invertebrate-rich diet also facilitated both the growth (length) and the development (moult schedule) of primaries in comparison to low-invertebrate or fish diet. At the ages of 24 and 28 days the moulting stage differed noticeable between groups. Chicks fed an invertebrate-rich diet had post-juvenile feathers growing, most probably due to their high-protein diet. Chicks fed a low-invertebrate diet moulted their P1 primaries later than chicks fed an invertebrate-rich diet. And finally, in chicks fed a fish diet P1 was fully developed markedly later than in chicks belonging to the other diet groups. It has also been shown that during the first five weeks of life, food with a high protein content affected the plumage development in the ring-necked pheasant *Phasianus colchicus*; for instance the development of tail feathers was enhanced (Woodard, Vohra & Snyder 1977).

At the age of four weeks grey partridge chicks grow fast and they start to moult their juvenile wing feathers for post-juvenile feathers. The daily combined requirement for methionine and cysteine is 0,6% per kilo food in pheasants and quails *Coturnix coturnix* (National Research Council 1984). Poor appetite and/or slow/poor growth are symptoms of amino acid or protein deficiency under which growth of feathers may be disturbed and the primaries may be ragged instead of normally flat (National Research Council 1984). In our study, the bursting of feathers from the sheath was abnormal in the chicks fed a fish diet, i.e. the offscaling of the sheath was delayed.

According to McCabe & Hawkins (1946) the juve-

nile P1 primary feather in the grey partridge is replaced at the age of ca 3.5 weeks. Our results from chicks fed an invertebrate-rich diet are in agreement with this. In the fish-fed group replacement of the primaries started at ca four weeks of age and even later in the group fed a low-invertebrate diet. Of the birds fed an invertebrate-rich diet a few had changed their P2s before they were four weeks old. In the wild, moulting probably happens faster than in captivity (McCabe & Hawkins 1946). The primaries of all the birds used in our study were equally developed when the chicks reached the age of 13 weeks. Compensatory growth enabled the chicks fed a low-invertebrate or a fish diet to 'catch up' with the chicks fed an invertebrate-rich diet when they started to feed on the commercial poultry food. Again, this may have been a result of the high protein content of these foods.

Diet group differences in cooling rate

Newly hatched grey partridge chicks are not able to maintain a constant body temperature and their level of body temperature may be several degrees (°C) lower than in adult birds, which is typical for all galliform chicks (Spiers et al. 1974, Aulie 1976b, Myhre & Steen 1979, Hissa et al. 1983, Jurkschat, Burmeister & Nichelmann 1989, Gdowska, Górecki & Weiner 1993). However, the behavioural temperature regulation is well developed in precocial chicks. The development of physiological temperature regulation in growing chicks is linked to the increase in body mass and development of plumage as well as improved capacity for heat production (Spiers et al. 1974). In newly hatched precocial galliform chicks, the heat production occurs primarily in leg muscles (Whittow & Tazawa 1991). However, pectoral muscles grow fast and take part in heat production in the form of shivering at the age of a few days (Aulie 1976a). Marjoniemi et al. (1995) reported shivering in 5-day-old grey partridge chicks. In our study shivering was obvious at the age of seven days and was noticed when we held the chicks in our hands after the experiment.

The chicks were not fed during their first day, because they could rely on the nutrient reserves of the yolk sack. As expected, no difference was seen in the cooling rate at this age. At the age of seven days the cooling rate of wild chicks and chicks fed an invertebrate-rich diet was similar, which probably resulted from their developmental stage due to versatile animal proteins in their foods. Also the slower cooling of the chicks fed an invertebrate-rich diet at the ages of 11, 18 and 21 days was a result of the heavier body mass and better insulation. Most probably this was the case also in the 15-day-old chicks, as the chicks fed an invertebrate-rich diet were able to keep their body temperature

above the critical level longer than the other chicks. The inadequate protein quality of the food may have resulted in a poor temperature regulation ability in chicks fed a low-invertebrate and a fish diet. As shown, chicks fed a fish diet had the weakest ability for temperature regulation.

Nutrient requirements of growing chicks

According to Hermes, Woodard, Vohra & Snyder (1984) the diet of the red-legged partridge *Alectoris rufa* does not have to include animal protein, if sufficient quantities of minerals and vitamins are included. This result was obtained in a feeding trial with birds fed either plant food or a combined plant-fish diet (fish content 5%). However, from insects chicks get protein, phosphorous and B₁₂-vitamin (Savory 1974), which are essential for growth. Methionine and cysteine concentrations are, in general, higher in invertebrates and fish proteins than in plant proteins (Anon. 1970). The amount of these amino acids in different foods affects the amount of food that chicks have to ingest to meet their amino acid requirements, and to achieve normal growth rate. Methionine and cysteine affect the development of the plumage (Bagliacca et al. 1985, Potts 1986). The feather proteins need more cysteine to develop than other tissues (Murphy & King 1982, Murphy, King, Taruscio & Geupel 1990). The amount of cysteine may also affect the quality of the feathers, i.e. how much rubbing or twisting they can tolerate (Murphy & King 1982).

Is a fish diet suitable for feeding of hand-reared grey partridge chicks?

Among the chicks fed a fish diet in our study feather-picking occurred at the age of three weeks. The term 'cannibalism' is widely used to describe this behaviour, although it literally means killing and eating conspecifics. It is possible that the diet somehow triggered this behaviour (Anon. 1994) since we did not notice this behaviour in the two other diet groups.

Fish contains a high level of important proteins and a wide variety of amino acids which are essential for growth. Although the protein content, as well as the contents of methionine and cysteine in these proteins, are higher in fish than in insect or plant proteins, the disparities in amino acid compositions make it impossible to replace the invertebrate-proteins with fish protein. In addition, fish meals may not have been palatable, as the chicks did not eat all the fish available.

In the light of our study it appears that invertebrates are not replaceable by fish - at least not the fish used in our study - in the diet of growing hand-reared grey partridges. Body mass gain was low, cooling rate was

high and primary growth poor in fish-fed chicks. However, commercial poultry foods are easy to use and well-balanced in nutrients. Chicks grow fast on commercial diets, but these foods may affect the gut disadvantageously. Adaptation of the gastro-intestinal tract to use high-digestible low-fibre commercial food may take several weeks, even months, and cause problems in the utilisation of natural foods after the release into the wild. Therefore, it would be beneficial to feed the grey partridge chicks a diet supplemented with invertebrates during their first weeks of life.

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