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Food requirements of grey partridge *Perdix perdix* chicks

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Experimental investigations showed that during the first 10 days of their life partridge *Perdix perdix* chicks grew most vigorously on a high protein value diet composed largely of insects. They grew less quickly on rearing crumbs and were unable to survive when fed entirely on seeds. We determined the daily uptake of food and, from carcass analysis, the proportion assimilated. From this information the average daily food requirement in terms of the dry weight of insects was calculated as 0.80 g on day 2 and 1.95 g on day 9. We calculated the number of individual insects of various groups required daily, if feeding was restricted to one group, and the amount of habitat that would need to be searched if insects were taken randomly. Resistance to chilling was shown to be correlated with weight and not with age. Thus shortage of insect food in the first few days of life would extend the period when the chicks are particularly vulnerable to lower temperatures and rain, effects that have also been demonstrated in other studies.

Key words: chilling, diet, insects, nutrition, partridge chicks, Perdix perdix

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Foreword *by G.R. Potts*

In every field of ecology, there are one or two pieces of work that are regarded as milestones in our understanding of the subject. They are innovative and set in motion a cascade of work that progresses for decades afterwards. The work reported in this paper is one such milestone. Its completion led to decades of work on grey partridge ecology both in the UK by The Game Conservancy Trust and by others throughout Western Europe, the then Eastern Block and North America. It led to an appreciation of the importance of the correct chick diet and the role of insects in the diet. From this developed research that led to our understanding of the indirect effects of pesticides operating through the disruption of food chains and the ecology of insects and weeds in agricultural ecosystems, particularly cereal crops. Even today it continues to generate important new research.At the time (i.e. the mid-1960s) the work was not accepted for publication for reasons that are best lost in the mists of time. Its publication now is long overdue but at least the record is straight.

In the grey partridge *Perdix perdix* mortality of the young chicks is the key factor influencing variations in the size of the September population (Blank, Southwood & Cross 1967, Potts 1986). Many observations have demonstrated that insects are a major component of chick food during this period (Ford, Chitty & Middleton 1938, Oko 1964, Southwood & Cross 1969, Potts 1970, Green 1984, Rands 1985, Potts 1986, Pulliainen 1986, Helenius, Tuomola & Nummi 1995, Itämies, Putaala, Pirinen & Hissa 1996, Pulliainen 1996).

The present work was undertaken (i) to determine the effect of diet on the chick's growth and resistance to chilling, and (ii) to estimate the quantity of insect food required in the first 10 days of the chick's life. Brief outlines of the findings are given by Southwood (1968) and Potts (1986), both of whom provide illustrations of chicks raised with different diets. Potts (1986) also reported further research showing that growth rates of chicks increased as the proportion of insects in the diet increased. More recently Liukkonen, Putaala & Hissa (1996) have carried out rather similar experiments on diet and resistance to chilling and, although the diets differed in detail, they obtained essentially similar results; whilst Warner, Darda & Baker (1982) did so with pheasants. Borg & Toft (1999) found that partridge chicks did not grow normally when fed the aphid *Rhopalosiphum padi* alone; their chicks grew better on locusts and best on a diet containing both types of insect. The sulphur-amino acids may be particularly important in relation to feather growth (Cross 1966, Wise 1982, Potts 1986), and insects provide a rich source.

If the requirements for insect food are known these may be related to the insect populations in the field. Stiven (1961), in a study of the blue grouse *Dendragapus obscurus fuliginosus* on Vancouver Island, also attempted to relate the food requirements of a game-bird chick to that actually available. However, he did not make a direct assessment of the chick's requirements but assumed a similarity with the basic energetics of the domestic poultry chick, which are well established (Ewing 1951, Titus 1961).

This approach necessitates the gross analysis of insects as a food source, together with feeding trials and associated experiments to assess their relative value for growing chicks. Few studies have been made in this area of work. McHargue (1917) assessed the value of insect protein for poultry, and Brownlee (1939) made a less detailed study on domestic hen chicks allowed free access to insects in the field.

In fast growing animals the limiting factor in a given diet is normally the protein level and the efficiency with which proteins can be broken down and resynthesised into new tissue. In the present study, therefore, most attention was paid to this aspect of nutrition, considerations such as vitamin and mineral contents being outside the scope of the investigation. (However, careful observations were made at all times for signs of deficiency symptoms). The experimental diets were chosen on this basis, one having a high level of protein and the other a low level. Details of the diets are given below.

Methods

Feeding trials on partridge chicks were carried out in two consecutive years (1963 and 1964) and with two diets in each year, one low protein value diet and one high protein value diet, abbreviated to 'LPV diet' and 'HPV diet' in reference to their relative protein levels. In the first year it was intended to demonstrate directly that the chicks would not grow on a diet of natural vegetable material alone (this being the only alternative to an insect diet in the wild) and that they could be reared satisfactorily on a predominantly insect diet. Therefore the differences between the diets were initially maximal. An attempt was also made to establish the total calorific intake (by comparing the energy value of the food to that of the droppings) and to correlate this with the increases in body weight of the chicks.

The investigation in the second year was in three parts: (i) rearing trials from which data on weight gain and digestibility of the various food components were derived; (ii) slaughter experiments in which the relative contributions of the main chemical components (protein, fat and carbohydrate) to the total body weight gain over a period were investigated for both diets; (iii) chilling experiments in which the ability of chicks to resist low temperature stress was recorded. The results from parts (i) and (ii) were used to determine the utilisation of the diets.

The experiments in both years were accompanied by standard analyses of foodstuffs (particularly insect species collected from the partridge chicks' natural habitat) for fat, nitrogen (protein) and ash content, along with sundry determinations of calorific values and, in the arthropods, cuticle weights.

Rearing trials

The partridge chicks were supplied from the late Lord Rank's estate in Hampshire. They had hatched from eggs that had been collected from wild nests by the gamekeepers and placed in an incubator. Within a few hours of hatching and drying they were transported by road to the Imperial College Field Station, Silwood Park, Ascot, where they were divided into two batches (of 17 and 23 in year one, and 20 each in year two), individually weighed and placed in two separate brooders of the Glevum type.

The floors of both chambers in the brooders were covered with polythene sheets throughout the experiments, overlain by squares of wire netting. The purpose of the polythene was to simplify collection of food and droppings and to maintain a reasonable degree of hygiene.

Water was supplied from small gravity feed troughs, and suitably graded limestone grit was supplied with each feed. Daily records were kept of body weight in both diet groups. In the second year individual chicks were recognised by a system of marking the toes with ink.

The diets chosen for comparison were 1) *Tenebrio molitor* larvae and small amounts of mixed insects (collected from grassland) with mixed seed in the first year, and with manufacturers' rearing crumbs in the second year, giving a high protein value (HPV) diet, and 2) mixed seeds or mixed seeds with rearing crumbs in the first year, and rearing crumbs alone in the second year, to give a low protein value (LPV) diet. In the second year's trials, on day 7, *T. molitor* larvae alone were fed to the HPV group of chicks; this 'pure' diet period, although relatively short, enabled a more accurate measure of the digestibility of the insect material to be made. The mixture of seeds consisted of various grasses, e.g. *Lolium* spp. (60% by weight), clover *Trifolium medium* and *T. repens* and kale *Brassica oleracea acephala* (30%) and chopped beans *Phaseolus vulgaris* and peas *Pisum sativum* (10%).

The diet of mixed seed alone was tried only in the first year and, since it proved unpalatable (the chicks not feeding), commercial rearing crumbs intended for partridge chick rearing, were added after the third day. This met the nutritional requirements of the experiment by having a much lower protein content than the *T. molitor* larvae (22% of dry weight as opposed to 41%; see Tables 4 and 5). Both seeds and crumbs were moistened with sufficient water to cause them to adhere loosely.

Determination of digestibility

Every morning all debris on the floor of the brooders was collected. In the first year, food remains and droppings were separated from the grit, as far as this was possible, and placed in separate containers. These were weighed and samples of about 2 g were dried and reweighed, so enabling the total dry weight to be calculated. With the HPV diet, food remains were further subdivided into insect remains and seeds or crumbs (see below). Each sample was then combusted in a calorimeter (described in the methods of chemical analysis below) to determine the difference in energy value, weight for weight, between the food supplied and the droppings collected, i.e. the energy intake of the chicks as a group.

The procedure described above gave rise to practical difficulties in sorting and analysis; therefore a considerably modified form was adopted for the second year's experiments. Here only easily recognisable insect remains in the HPV diet were separated; everything else, grit included, was collected together, dried, ground and weighed. Grit contamination was estimated by ashing small samples of this material. After the weights of ash in the diet and that in the material collected from the chambers were subtracted, the amount of food retained by the chick could be calculated. Since birds eliminate most of their metabolic nitrogen as uric acid intimately mixed with faeces, direct comparison of food eaten to droppings voided gives the apparent digestibility of the diet concerned. The presence of uneaten food, mixed with the droppings, confuses the calculation, thus care was taken not to excessively overfeed so that minimal amounts of uneaten food remained. The values for absorption achieved on days of complete, or near complete, consumption were taken as the apparent digestibility of that particular diet.

Chick carcass analysis

The procedures used in this work were based on those of Maynard & Loosli (1956). Carcass analysis of vertebrates for the comparison of diets poses great problems of sampling error, as it is rarely possible to examine large enough numbers. In this study two individuals were killed on day 7 and two on day 10.

The four chicks were enclosed in polythene bags, weighed and then frozen for six hours over solid carbon dioxide. When solid, they were broken up by hammering, refrozen for a further 12 hours, and dried *in vacuo* over phosphorus pentoxide. Each chick was then reweighed (the loss from the initial weight gave the water content), and ground in a mechanical mill. Subsequent methods of chemical analysis are described below.

Chilling experiments

Selected chicks (all of the same age) were weighed and then transported in an insulated box to a cold room (temperature controlled at 10°C) where they were transferred to special cages constructed from paper honeycomb, which allowed free access of air from all directions. These cages were kept in the same area of the room, but at such a distance from each other as to avoid any possible effect on the ambient temperature.

Chicks exposed to such temperatures go through a series of well defined stages, up to (presumed) eventual

Table 1. Number of partridge chicks (N) and their average weights (AW) in the first and second rearing trials during which they were fed either a low protein value (LPV) or a high protein value (HPV) diet.

	First trial				Second trial			
	LPV		HPV		LPV		HPV	
Age in days	N	AW (g) ± 2 SE	N	AW (g) ± 2 SE	N	AW (g) ± 2 SE	N	AW (g) ± 2 SE
1	17	8.5 ± 0.4	23	8.5 ± 0.3	18	9.3 ± 0.3	11	8.7 ± 0.5
2	17	8.1 ± 0.6	23	8.3 ± 0.6	18	9.9 ± 0.3	11	8.6 ± 0.5
3	16	8.0 ± 1.0	22	11.1 ± 0.7	18	10.6 ± 0.4	11	10.2 ± 0.5
4	13	9.3 ± 0.8	21	12.9 ± 1.4	18	11.4 ± 0.5	11	11.7 ± 0.5
5	13	11.7 ± 0.9	20	14.7 ± 1.3	18	12.8 ± 0.6	11	12.7 ± 0.9
6	13	12.3 ± 0.7	17	17.0 ± 2.2	18	14.2 ± 0.6	11	14.9 ± 1.1
7	13	13.7 ± 0.8	14	19.6 ± 1.0	18	15.2 ± 0.8	11	17.4 ± 1.3
8	13	13.7 ± 0.8	14	19.6 ± 1.9	17	15.2 ± 0.8	10	17.4 ± 1.3
9	13	15.5 ± 1.2	13	25.2 ± 2.0	17	18.5 ± 1.2	10	23.0 ± 2.2
10	11	16.7 ± 1.4	13	27.7 ± 2.4	17	20.4 ± 1.2	10	26.0 ± 2.3

death, established in preliminary tests and generally similar to those described for the domestic hen chick by Sturkie (1954). In fact no chick was taken beyond the point of incapacitation where the bird was unable to move in a co-ordinated fashion (tested by removing it with a gloved hand from its cage and placing it on a flat surface). After exposure, the chicks were removed to a warm box heated by a low power electric bulb. The times taken to chill, recover and recommence feeding were noted.

Standard chemical analyses used in the study

All materials analysed during the course of the investigation were freeze dried as a preliminary step, this being preferable to oven drying when fat content and calorific value are to be determined. If delay was likely before analysis, samples were stored in a desiccator over phosphorus pentoxide.

Nitrogen determinations were performed using a micro-Kjeldahl method based on that of Chibnall, Rees & Williams (1943), but the quantities of reagents were scaled down and selenium dioxide substituted for sodium selenite as catalyst, and Conway micro-diffusion unit was used for the titration. The average nitrogen content of protein was assumed to be 16%, so that N x 6.25 was taken as the gross protein content.

Fat and oil content were estimated by extraction with diethyl ether in a soxhlet or, for very small samples, a micro-soxhlet apparatus. Ash was estimated by incinerating a weighed sample of the material, at 500°C for 12 hours, in a muffle furnace. Calorific values were determined in a Gallenkamp ballistic bomb calorimeter, the instrument having been calibrated with samples of benzoic acid of known weight. The cuticle weight of insect material examined was taken as that part not dissolved after four hours in hot 3N sodium hydroxide.

Results

Growth

Growth was measured quantitatively in terms of weight and the daily average weight is given in Table 1. Some initial weight loss always occurred, presumably whilst the chicks were learning to feed and the remains of the yolk were being absorbed. In the first year's trial the low protein value (LPV) diet for days 1-3 consisted of a seed mixture but, as there had been no weight increase and four chicks had died, commercial rearing crumbs were fed on day 4. This led to feeding and an increase in weight. Although chicks were chosen at random, in the second trial, the LPV diet chicks were, on average, heavier at the outset. The average percentage daily weight increase (over days 2-10) was higher in both years

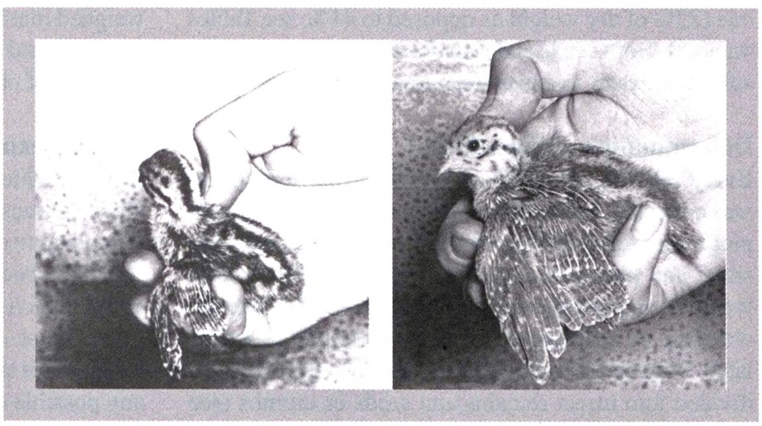

Figure 1. Two-week-old partridge chicks fed a low protein diet (left) or a high protein diet (right).

(14.5 and 13.1%, respectively) on the HPV diet than on the LPV diet (8.7 and 9.1%). These growth rates resulted in striking differences in weight and plumage (Fig. 1; see also Southwood (1968: Plate 8) and Potts (1986: Plate VII). It is interesting, in view of the results of Borg & Toft (1999), that when the chicks were fed a mixture of insects (in year 1) they obtained a greater weight by day 7 than when fed on one insect type, *T. molitor* larvae (in year 2). The weights of the chicks on similar diets are very comparable in the two studies.

In both years some chicks were lost through an enteric disease, in the first year both batches were equally affected. In the second trial only some chicks on the HPV diet were affected but, as these chicks were individually marked, their weights were excluded from the records.

Digestibility of the experimental diets

The attempts made in the first year of trials to establish the calorific intake on the test diets were greatly complicated by the effects of grit contamination, both accidentally mixed with the food and droppings on the floor of the brooders, and passing through the gut from the gizzard. The approximate figures for calorific intake and apparent digestibility were derived from the first year's data and these were used as a basis for calculating feeding rates in the second year's trials, and for providing general information on maximum possible intake of *T. molitor* larvae for each age.

The apparent digestibility for day 7 in the second year (the period of 'pure' diet on the HPV diet) was found to be 75% on the high protein diet and 65% on the low protein diet.

The composition of the chicks' carcasses is given in Table 2. If the percentage compositions are applied to the average weight of chicks of this age, the average composition by weight may be calculated (Table 3). The greatest difference between the two diets is in the increase in the fat content: 1.5% of the dry weight gain on the LPV diet and 26% of the gain on the HPV diet. Protein constituted 46% and 60%, respectively, of the dry weight gains.

Table 2. Composition of individual partridge chicks seven or 10 days old and fed either a low protein value (LPV) or a high protein value (HPV) diet as determined from carcass analysis.

	LPV		HPV	
Composition	7 days old	10 days old	7 days old	10 days old
Fresh weight (g)	13.5	19.0	14.5	23.0
Dry weight (g)	3.4	4.8	3.6	6.0
% water	75.0	75.0	75.0	74.0
% protein	54.1	51.8	53.4	55.3
% fat	13.1	10.3	16.2	18.8
% ash	9.5	13.6	10.8	11.3
% other	23.3	24.3	29.5	14.6
J x $10^3 g^{-1}$	20.6	18.1	21.0	22.3
Total J x 10^3	70.1	86.5	75.6	134.4

Chilling experiment

As described above, selected chicks from both groups were subjected to an ambient temperature of 10ºC until there was an obvious disorganisation of movement accompanied by the cessation of shivering. The sequence of events observed closely paralleled those for the domestic poultry chick described by Sturkie (1954), who stated that respiratory failure and death usually followed within 30 minutes of the cessation of shivering.

In healthy fed chicks, differences in resistance were related to weight rather than to age or diet (Fig. 2), although all three are inter-related (see Table 1). The correlation between weight (x) and resistance to chilling (y) is highly significant ($r = 0.95$, $P < 0.001$) and the regression is of the form $y = 22.57 + 3.9x$. The recovery times were inversely related to the resistance times, but the range of variation between light and heavy chicks was smaller. It would appear that the larger fat reserves noted in the HPV diet chicks (see Table 3) did not significantly increase their ability to withstand low temperature when compared with an LPV diet chick of similar weight.

Table 3. Composition expressed as average weight (AW; in g) for 7- and 10-day-old partridge chicks fed either a low protein value (LPV) or a high protein value (HPV) diet, and the weight gain according to individual components of the diet as calculated from data in Tables 1 and 2.

	Diet					
	LPV			HPV		
Composition	AW Day 7 (g)	AW Day 10 (g)	Weight gain (g)	AW Day 7 (g)	AW Day 10 (g)	Weight gain (g)
Fresh weight	15.2	20.4	5.2	17.4	26.0	8.6
Dry weight	3.8	5.1	1.3	4.4	6.5	2.1
Water	11.4	15.3	3.9	13.10	19.5	6.4
Protein	2.05	2.65	0.6	2.33	3.58	1.25
Fat	0.49	0.51	0.02	0.70	1.24	0.54
Ash	0.38	0.71	0.33	0.48	0.72	0.24
Other components	0.87	1.22	0.35	0.88	0.95	0.07

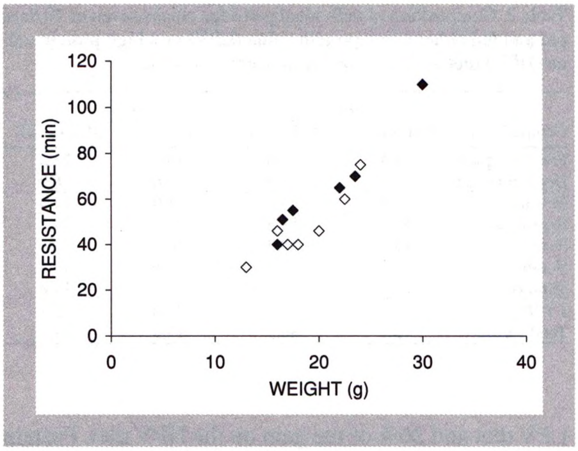

Figure 2. Relation between the resistance of young partridge chicks to chilling at 10°C and their weight for chicks fed either an LPV diet (◇) or an HPV diet (◆).

Analysis of insect material

In the results of the analysis of various arthropod species (Table 4) all the values represent the averages of several samples, most of which were taken from different populations.

The main point of interest from Table 4 is the small variation between groups investigated, in both protein content (40-58% dry weight which agrees with the determinations of Rock & King (1966)) and ash content (3.1-4.1% dry weight). Water content is also fairly constant at 61-75%, except in lepidopterous and Symphyta larvae which contain 80% water. Fat content, however, shows considerable variation: *T. molitor* larvae contain 31%, while at the other extreme, the Formicidae (*Myrmica* and *Lasius* workers) contain an average of only 4%. The calorific value shows a marked relationship to the quantity of fat present.

The weight of the cuticle was determined in six insect species or stages, i.e. *T. molitor* adult, *T. molitor* larva, *Pieris brassicae* larva, *Schistocerca gregaria* adult, pentatomid adult and muscid adult, and was found to range from 4.3% of the dry weight in the large white caterpillar *Pieris brassicae* to 16% in a pentatomid (Heteroptera), the average being slightly under 10%. Since insect cuticle contains a proportion of chitin in combination with proteins, the nitrogen content of this material has to be allowed for in the estimates of crude protein made from the analyses mentioned above. A figure of 2-3% was found to be the probable error from this source; suitable corrections for it were applied in the rearing trials and subsequent computations.

Of the amino acids considered essential for the poultry chick (Titus 1961), all but tryptophane could be recognised in paper chromatograms of insects, and this failure was probably due to its destruction during acid hydrolysis rather than to its complete absence. In addition other non-essential amino acids were recognised, no gross differences being noted between the patterns produced by different taxonomic groups, except for the presence of quantities of hydroxy-proline in spiders.

Analysis of other food material

Other food materials were: commercial rearing crumbs, mixed wild grass seed and fresh clover leaves and buds. The results of the analyses as percentage dry weight are summarised in Table 5, and agree closely with published values for similar materials. They show that, although the protein content of rearing crumbs is higher than that of vegetable foods, the properties of the other dry weight constituents are similar. Greenstuffs have, of course, a much higher water content.

Table 4. Contents of water, crude protein, fat and ash for various orders and species of insects and spiders. Water content is given as % live weight, whereas all other contents are given as % dry weight. Crude protein values are not corrected for the error due to nitrogen in chitin (of the order of 2-3%).

		Contents in %				
Order	Species	Water	Crude protein	Fat	Ash	Calorific value J x 10^3g^{-1}
Collembola	*Sminthurus*	70	58	9.0	3.1	21.4
Coleoptera	*Tenebrio molitor*	67	-	7.8	3.2	21.0
	Mixed spp.	68	50	7.6	3.2	21.4
Coloptera larvae	*T. molitor*	64	41	31.0	3.5	27.6
Coloptera larvae	*T. molitor* (fat extracted)	-	-	0	-	18.1
	Coccinelid	43	20.0	3.4	-	
Diptera	Muscid	73	58	10.4	3.3	22.5
Heteroptera	Mixed	72	51	11.0	3.4	21.4
Homoptera	Mixed	65	49	10.0	-	21.4
Hymenoptera	Parasitic	70	46	-	3.8	-
	Formicidae	68	55	6.1	4.0	20.2
Hymenoptera larvae	Symphyta	80	46	16.8	3.1	23.9
Lepidoptera	*Pieris brassicae* larvae	80	45	17.7	2.8	23.7
Orthoptera	Tettigoniid	70	55	8.4	4.1	21.0
Araneida	Mixed	68	-	-	-	-
Mixed insects	Mixed	64	53	10.5	3.3	24.0

Table 5. Contents of water, protein, fat and ash of three categories of non-arthropod partridge food with experimental value obtained in this study compared with the manufacturers' specifications, or with 'average values' given by Titus (1961). Water content is given as % live weight, whereas the other contents are given as % dry weight.

	Food category					
	Rearing crumbs		Mixed grass seeds		Clover leaves and buds	
Content	Experiment	Manufacturer	Experiment	Titus	Experiment	Titus
Water %	7.1	-	12.0	11.2	80.5	84.3
Protein %	21.6	23.0	12.5	12.2	17.0	19.3
Fat (Oil) %	3.4	3.5	3.4	3.4	5.4	4.3
Ash %	6.1	4.5	2.0	2.7	10.5	11.8
Rest %	68.9	69.0	82.1	81.1	67.1	64.6

Discussion of the experimental results

The rearing trials and the carcass analysis demonstrate the faster growth rate of the chicks on the HPV diet. This increased growth rate is ecologically beneficial as resistance to low temperature increases quickly with increasing body weight (see Fig. 2). The similarity of the times recorded for both experimental diets, weight for weight, suggests that this relationship is almost certainly due to the feathering rate.

Sturkie (1954) stated that in birds resistance to chilling increases progressively with the development of juvenile plumage, temperature control not being effective until this has been completed. Liukkonen et al. (1996) also demonstrated a close relationship between weight and cooling speed in partridge chicks.

In the wild state this relationship between cold susceptibility and feathering is of significance: any deficiencies in either the quality or quantity of the available protein will lead to a slower growth rate of the juvenile plumage, thereby lengthening a critical period when chilling could be a major cause of death.

Although the composition of the experimental diets differs from natural foodstuffs, these observations show that insect material, being the only significant source of protein in the wild, leads to a rapid growth rate and hence resistance to chilling. Partridge chick survival in the wild is correlated positively with air temperature, and negatively with rainfall (Green 1984, Panek 1992), and also with diet composition, the percentages of caterpillars and small beetles being important (Potts & Aebischer 1991).

Conclusions on the food requirements of the partridge chick

The food requirements of an animal, expressed in terms of energy, depend upon its size and activity, the stage of its development and the type and quantity of the diet. The relationship between these factors has been thoroughly investigated for poultry and the basic constants in the equations determined (Titus 1961). These values were used by Stiven (1961) to determine the theoretical energy requirements of the blue grouse. The theoretical total energy requirements of both diet groups in our study can be found from these equations, using the average weights for days 7, 8, 9 and 10. These are summarised in Table 6, where they are compared with a direct assessment of each group's actual energy intake and the known gains in body composition, expressed as calorific values, as determined in the carcass analyses. The measure of agreement indicates that these equations, derived for poultry, are approximately correct for partridge chicks and, along with the information obtained on the digestibility of insect materials and the rate of tissue synthesis, it is possible to use them to calculate approximate levels of growth. *T. molitor* larvae are not an ideal choice to represent insects generally; therefore in order to draw conclusions relevant to field conditions, estimates of dietary requirements were based on the average insect ('mixed insects' in Table 4).

If the level of growth is taken as that necessary to achieve a weight of 20 g on day 10, the earliest at which chicks can first attempt flight (G.R. Potts, pers. comm.), then the food requirements in terms of dry weight of aver-

Table 6. Average weight (AW; in g) and energy requirements per day (in Joule x $10^3 day^{-1}$) for partridge chicks expressed as an average for day 7-10 and determined by calculation and experimentation.

			Energy requirements (J x $10^3 day^{-1}$)		
Diet	AW (g)	Calculated or experimental	Activity + resting + growth metabolism ($Jx10^3 day^{-1}$)	Net growth ($Jx10^3 day^{-1}$)	Total metabolisable ($Jx10^3 day^{-1}$)
LPV	17.1	Calculated	22.6	5.0	27.6
		Experimental	29.3	5.0	29.3
HPV	20.3	Calculated	33.4	18.4	51.8
		Experimental	31.4	18.4	50.0

Table 7. Daily weight (in g) of chicks, basic energy requirements (in Joule x 10^3), food intake needed and total weight gain (in g) of chicks fed a 'mixed' insect diet.

Day	Daily weight (g)	'Basic' energy requirements ($Jx10^3$)	Dry weight food needed (g)	Dry weight protein gain (g)	Total dry weight gain (g)	Total fresh weight gain (g)
2	9.0	11.3	0.80	0.08	0.08	0.5
3	9.5	11.9	0.85	0.08	0.08	0.5
4	10.0	12.6	1.05	0.17	0.17	1.0
5	11.0	13.8	1.28	0.25	0.25	1.5
6	12.5	15.7	1.48	0.29	0.29	1.8
7	14.3	17.9	1.59	0.28	0.28	1.7
8	16.0	20.0	1.80	0.33	0.33	2.0
9	18.0	22.6	1.95	0.33	0.33	2.0
10	20.0					

age insects can be calculated (Table 7). The calculated amounts can be regarded as virtually minimal, at least for the older chicks as they would not allow any deposition of fat, and a weight of 20 g at 10 days is less than that achieved by the insect-fed chicks in the present trials (see Table 1).

We determined the average dry weight per individual of various groups of insects found in partridge habitat (Cross 1966). For the groups that are important components of the chicks' diet the values were: Homoptera 0.44 mg, Heteroptera 0.83 mg, Coleoptera 0.30 mg, and larvae of Symphyta and Lepidoptera 9.20 mg. Any chick will take a mixture of types, but the numbers involved if the diet was restricted to one order of insects are given in Table 8. That these figures are high in relation to the maximum numbers of insects found in chick crops (462; Ford et al. 1938), or remains in faecal pellets (1,195; Itämies et al. 1996), indicates that larger items are selected, and highlights the significance of the larvae of Lepidoptera and Symphyta (Potts 1970, 1986, Potts & Aebischer 1991). They also suggest that an estimate of a requirement of 2,000-3,000 insects per day (Southwood 1963, Helenius et al. 1995) is not unreasonable in the absence of larger prey. This would imply a feeding rate of about three insects per minute in a 15 hour day, but such a rate is probably not achievable, providing further support for the emphasis on the importance of larger prey items (Potts 1986).

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Table 8. Number of individual insects of various orders required to meet the chick's daily food requirements on days 2 and 9.

Order	Day 2	Day 9
Homoptera	1818	4431
Heteroptera	964	2349
Coleoptera	2666	6500
Lepidoptera & Symphyta larvae	87	212

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