The importance of invertebrate food to chicks of gallinaceous species

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In the wild, the precocious young of gallinaceous birds are omnivorous, and proportions of plant and animal food in their diets vary greatly between and within species (Cramp & Simmons, 1980; Johnsgard, 1983). The animal food consists almost entirely of invertebrates (mainly arthropods), and the purpose of the present paper is to examine factors that cause its consumption to vary, and its importance relative to plant food in terms of meeting nutritional requirements for growth and survival.

A search of the literature revealed detailed quantitative information on the diets of twenty-one species of Galliformes, in two families (Tetraonidae and Phasianidae), in their first month or two of life. Most of the published accounts referred to in Table 1 allowed mean percentages of invertebrate food (IF), based on volumes or dry weights of crop contents, or in a few cases on analyses of faecal droppings, to be assigned to one of four categories (>90%, 50–90%, 10–50% or <10%) in each of three age-classes (weeks 1 and 2, 3 and 4, and 5–8). A check on how representative crop contents are of the alimentary tract as a whole was made by Savory (1974) by comparing proportions of plant and animal material in crops and gizzards of (the same) four red grouse (*Lagopus lagopus scoticus*) chicks; IF accounted for 3·4% dry weight of crop contents and 3·0% of gizzard contents, so it is assumed that any separation of material in the crop is negligible. In the few cases based on faecal analyses, values were either corrected to allow for measured differences in digestion between food items (Green, 1984; Hill, 1985), or a check was made that proportions of plant and animal material in faecal remains did compare well with those in crop contents (Savory *et al.* 1978), or plant remains were almost totally absent (Picozzi & Hepburn, 1986). With six of the twenty-one species in Table 1, categories were assigned either wholly or partly on the basis of written descriptions in Cramp & Simmons (1980) or Johnsgard (1983) that were sufficiently explicit for quantitative estimates of consumption of IF to be made.

In the first 2 weeks of life, sixteen of the twenty-one species were recorded as eating either 50–90 or >90% IF, and only two, red grouse and Caucasian snowcock (*Tetraogallus caucasicus*), as not eating >10% (Table 1). In the second 2 weeks, only eight species ate >50% and six species <10%, and in the second month of life, fifteen species were recorded with <10% and only two, lesser prairie chicken (*Tympanuchus cupido*) and sharp-tailed grouse (*Tympanuchus phasianellus*), continued to eat >50%. As a general rule, therefore, consumption of IF is highest in the first 2 weeks and declines thereafter, and, at any given age, variation in this consumption appears to be greater between than within species. Conclusions based on knowledge of proportions of different dietary constituents alone must necessarily be qualified, since ultimately growth depends on total intake of each constituent. In none of the accounts referred to in Table 1, however, were estimates made of food consumption of wild chicks at any age.

Reasons for variation in consumption of IF with age

Few studies have measured invertebrate abundance in habitats occupied by broods of gallinaceous chicks at different dates, so it is not easy to relate changes in consumption of IF to changes in availability. Nevertheless, there is evidence that where chicks specialize in eating abundant types of insect whose availability is restricted in time, such as red

Table 1. *Recorded mean percentages of invertebrate food (in categories A, B, C, D*) in diets of wild chicks of twenty-one gallinaceous species at three different ages*

Species	Common name	Age			References
		Weeks 1 and 2	Weeks 3 and 4	Weeks 5–8	
Tetraonidae					
Centrocercus urophasianus	Sage grouse	B,C	C	C,D	Patterson (1952), Klebenow & Gray (1968), Peterson (1970)
Dendragapus obscurus	Blue grouse	A,B	B,C	C,D	Beer (1943), King (1968)
Dendragapus canadensis	Spruce grouse	A	C	D	Pendergast & Boag (1970)
Dendragapus falcipennis†	Sharp-winged grouse	B	C	D	Dementiev & Gladkov (1967)
Lagopus l. lagopus	Willow ptarmigan	B,C	C,D	D	Lid & Meidell (1933), Spidso (1980), Williams et al. (1980)
Lagopus l. scoticus	Red grouse	D	D	D	Savory (1977)
Lagopus mutus	Rock ptarmigan	C,D	C,D	D	Weeden (1969), Gardarsson & Moss (1970), Theberge & West (1973)
Lagopus leucurus†	White-tailed ptarmigan	B	C	D	May (1970)
Tetrao urogallus	Capercaillie	B	B,C	C	Rajala (1959), Penttinen (1974), Kastdalen & Wegge (1986)
Tetrao tetrix	Black grouse	A,B	C	D	Kastdalen & Wegge (1986), Picozzi & Hepburn (1986)
Tetrao mlokosiewizci†	Caucasian black grouse	A	B	C	Dementiev & Gladkov (1967)
Bonasa umbellus	Ruffed grouse	A,B	C	C,D	Bump et al. (1947), Stewart (1956), King (1969)
Bonasa bonasia†	Hazel grouse	A	B	C	Donaurov (1947)
Tympanuchus cupido	Pinnated grouse/Prairie chicken	A	A	A	Davis et al. (1980)
Tympanuchus phasianellus	Sharp-tailed grouse	A	A,B	B,C	Kobriger (1965), Pepper (1972)
Phasianidae					
Alectoris chukar†	Chukar partridge	C	D	D	Georgiev (1963), Potts (1980)
Alectoris rufa	Red-legged partridge	C	D	D	Green (1984)
Perdix perdix	Grey partridge	A,B	C	D	Ford et al. (1938), Green (1984)
Phasianus colchicus	Pheasant	A,B	B	C,D	Loughrey & Stinson (1955), Janda (1965), Hill (1985)
Gallus gallus	Domestic fowl (free-ranging)	B	B	C	Brownlee (1939), Savory et al. (1978)
Terraogallus caucasicus†	Caucasian snowcock	D	D	D	Baziev (1965)

* A, >90%; B, 50–90%; C, 10–50%; D, <10%. In most cases categories are assigned on the basis of mean percentages by volume or dry weight, mainly from crop contents but a few from faecal analyses.

† In these cases categories are assigned either wholly or partly on the basis of explicit quantitative descriptions in Cramp & Simmons (1980) or Johnsgard (1983).

grouse with the tipulid *Molophilus ater* and grey (*Perdix perdix*) and red-legged (*Alectoris rufa*) partridges with aphids, then peak numbers of insects in June/July tend to occur soon after chicks hatch, when their consumption of IF is highest, and decline in insect availability coincides with decline in percentage IF (Potts, 1970; Savory, 1977; Table 2). This might suggest that variation in consumption of IF with age is mainly a consequence of variation in availability, and it is quite possible that cases where substantial proportions of IF are still eaten in the second month of life (Table 1) may indeed reflect continued high availability. However, there are examples where proportions of IF in chick crops do decline at a time when there is no concomitant decline (from June to July) in insect availability (Kastdalen & Wegge, 1986), or when younger chicks are still eating much higher proportions (Loughrey & Stinson, 1955). Also, 'selection' for IF (y) by broods of red grouse chicks, as indicated by dividing the mean percentage IF (of the total number of food items) in their crops by the number of insects caught per 100 sweeps of a sweep net at the time and place where the brood was captured, was related to age (x_1, eight categories ranging from 0–5 to 21–35 d, based on weights and wing lengths of chicks) and insect abundance (x_2, number per 100 sweeps) by the following formula: $y = 2 \cdot 06 - 0 \cdot 25x_1 - 0 \cdot 01x_2$; R^2 $0 \cdot 29$; regression coefficients x_1, $P < 0 \cdot 001$, x_2, not significant (by t test); with 46 df. In other words, selection for IF declined with age (mainly between 10 and 20 d, Fig. 1) regardless of variation in insect availability (Savory, 1974). Furthermore, the frequency of occurrence of IF in crops of red grouse chicks fell from >90% in the first 2 weeks to about 50% in the third week of life (Savory, 1977). Presumably, therefore, the decline in selection for, and consumption of, IF with age can be accounted for by a change in nutritional requirements of the chicks.

In Table 3, the chemical composition of some representative invertebrates is compared with that of typical plant foods (PF) and with nutrient requirements of young poultry chicks. On average, IF provides about four times as much protein as PF, and this difference is even greater in terms of the amount of protein digested because the digestibility of protein in IF and other animal food is about 70–90% (Stiven, 1961; Bolton & Blair, 1974; Sugimara *et al.* 1984), whereas that of protein in PF may range from as low

Table 2. *Abundance of all invertebrates and of the tipulid* Molophilus ater, *and percentages of invertebrate food (IF) in crops of red grouse (*Lagopus *lagopus scoticus) chicks at different dates (from Savory, 1977 and unpublished results)**

(Mean values with their standard errors)

Sample size† . . .	May last week 12		June first week 11		June second week 14		June third week 8(12)		June fourth week 3(12)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
No. of insects/ 100 sweeps	14·1	2·8	22·3	4·3	26·9	7·2	13·3	3·5	10·0	4·4
Molophilus ater	6·7	2·3	17·5	4·0	19·1	6·7	8·3	3·0	0·3	0·3
Percentage IF:										
By dry weight	8·9	2·9	6·3	1·9	6·4	3·4	1·1	0·3	3·0	2·0
By number of items	25·5	6·8	21·0	5·4	19·8	4·5	4·2	1·4	3·5	1·6

*The mean hatching date of red grouse chicks on the study area is normally in the last week in May or first week in June.

†Sample sizes represent nos. of broods sampled which had insect abundance measured at the site of capture, except those in parentheses which refer to percentage IF and which include additional broods.
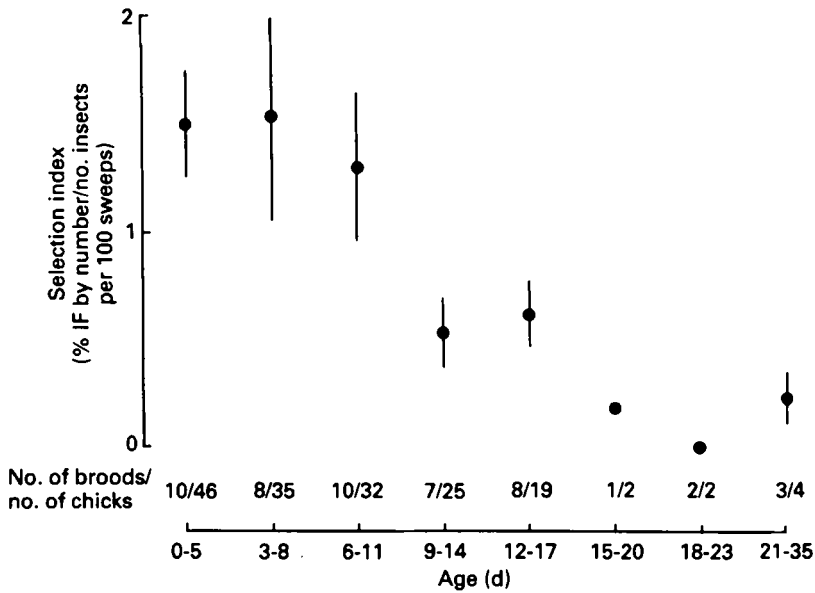
Fig. 1. Mean indices of selection for invertebrate food (IF) by broods of red grouse (*Lagopus lagopus scoticus*) chicks at eight age-categories based on wing lengths and body-weights. Points are means with standard errors represented by vertical bars (J. Savory, unpublished results).

as 24–48% in heather (*Calluna vulgaris*; Moss & Parkinson, 1972) to >80% in some poultry foods (Bolton & Blair, 1974). Some of the crude protein (nitrogen × 6·25) in IF is present in the form of indigestible chitin, but since chitin accounts for only about 4 and 6% dry weight of larval and adult insects, and contains 6·6% N (Tsao & Richards, 1952), this proportion is probably no more than 5%. Protein in IF also contains higher concentrations of methionine and cystine, the two (sulphur) amino acids that are essential for feather synthesis (Bolton & Blair, 1974), and which are not present in sufficient concentrations in most plant protein to meet the needs of growing chicks. Energy can be obtained from carbohydrate, fat and protein components of the diet, but it is from soluble carbohydrates (N-free extract) that it is most readily available, and these are more abundant in PF than in IF. The mineral composition of IF and PF are fairly similar, although concentrations of calcium in PF and of phosphorous in IF are closest to the levels required by growing chicks. IF is also a richer source of most vitamins, particularly vitamin B_{12}, which is practically non-existent in PF, and which is essential for the growth of chicks (Bolton & Blair, 1974). Vitamin C, however, is more abundant in PF, and although it is synthesized in the kidney, there is evidence that some chicks may require substantial amounts of this vitamin from external sources in order to avoid developing typical deficiency symptoms (Hanssen *et al.* 1979). Vitamins are also synthesized by bacteria in the hind-gut, particularly in the caeca, but it may take a few days after hatching for the microbial population to form, and there is evidence that caecal droppings are not produced at that time (R. Moss, personal communication). There is also doubt about whether vitamins synthesized by bacteria are available to the host unless coprophagy occurs (McNab, 1973). IF thus provides more digestible protein, S-amino acids, P and vitamin B_{12} than PF, but less soluble carbohydrates, Ca and vitamin C.

Table 3. *Chemical composition (g/kg dry matter) and metabolizable energy (ME; kJ/g) of invertebrate and plant foods, compared with requirements of poultry in the first 4 weeks of life*

	Invertebrate food*	Plant food†	Requirements of young poultry‡
Crude protein (nitrogen × 6·25)	520–700	60–300	190–280
Methionine	10–16	1–4	5–9
Cystine	5–10	1–3	3–5
ME	10–14	6–13	11–13
Soluble carbohydrates	< 10–240	60–640	
Crude fat	30–110	10–160	
Crude fibre	< 10–100	50–270	
Calcium	1–6	1–12	5–12
Phosphorous	8–9	1–8	4–8
Potassium	2–12	4–42	2–4
Sodium	1	0·1–2	1·5–2

*From Stiven (1961), Savory (1977 and unpublished results), Street (1978), Sugimura *et al.* (1984).

†From Stiven (1961), Gardarsson & Moss (1970), Moss *et al.* (1974), Bolton & Blair (1974), Savory (1977), Spidso (1980), Moss & Hanssen (1980).

‡From Bolton & Blair (1974).

Gallinaceous birds have been shown to develop specific appetites for various nutrients when these are in short supply relative to their requirements (Hughes, 1979), and are also known to feed selectively in the wild (e.g., Moss, 1972; Savory, 1983). Laying hens can regulate their protein intake when offered a choice of diets containing different levels of protein (Holcombe *et al.* 1976). When young broiler chicks were allowed to self-select from 11 d of age between a high-protein fraction consisting of soya-bean meal with added minerals, vitamins and methionine (456 g protein/kg), and a high-carbohydrate fraction consisting of maize meal with added minerals and vitamins (86 g protein/kg), the proportion of protein they selected in their total daily intake declined from 230–250 g/kg at 2 weeks of age to about 150–170 g/kg in the second month (Fig. 2, from Kaufman *et al.* 1978). Over this period they gained weight as fast as a control group fed on a commercial starter diet (minimum 210 g protein/kg), and the proportions of protein they selected agree well with recommended dietary levels for starting and finishing broilers commercially (Bolton & Blair, 1974). The observed decline in their relative protein intake resulted from increasing consumption of the maize fraction, while daily intake of the soya-bean fraction remained much the same (Fig. 3). Likewise, many of the declines in percentage IF in the diets of wild chicks may simply be due to increasing consumption of PF at a time when absolute intake of IF is not declining (cf. Kastdalen & Wegge, 1986). Gallinaceous chicks thus appear to be capable of regulating their protein intake like adults, and, judging from the results of Kaufman *et al.* (1978), the proportion they select declines between about 2 and 4 weeks of age. In just the same way, the percentage IF eaten by wild mallard (*Anas platyrhynchos*) ducklings declines from >50 to <10 over the same period (Street, 1977), and relative consumption of crop 'milk' (composed mainly of proteins and lipids) by young pigeons (*Columba livia*) also declines at about the same time (Vandeputte-Poma, 1980).

Apart from food items presented by jungle fowl (*Gallus gallus*) hens to their young, and their 'tidbitting' which stimulates the young to feed (Stokes, 1971), gallinaceous chicks are not normally fed by their parents and have to forage for themselves from soon after hatching. There is evidence that it may not be until about the third day of life that
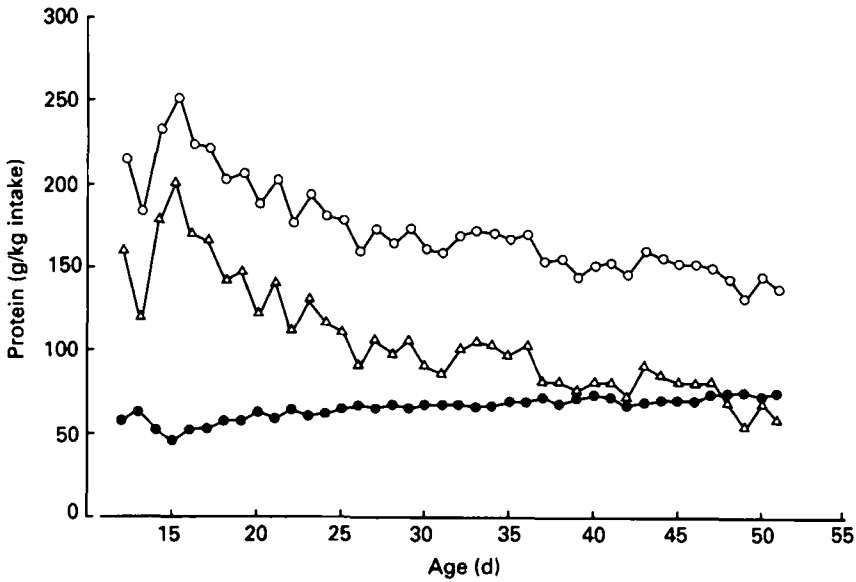
Fig. 2. Mean daily intake of protein (g/kg total intake) selected by domestic chicks (*Gallus gallus*) (*n* 7) with *ad lib*. access to a high-protein (soya-bean) fraction (460 g protein/kg) and a high-carbohydrate (maize) fraction (90 g protein/kg), and mean proportions from each fraction (from Kaufman *et al.* 1978). (O), Total protein; (△), protein from soya-bean fraction; (●), protein from maize fraction.
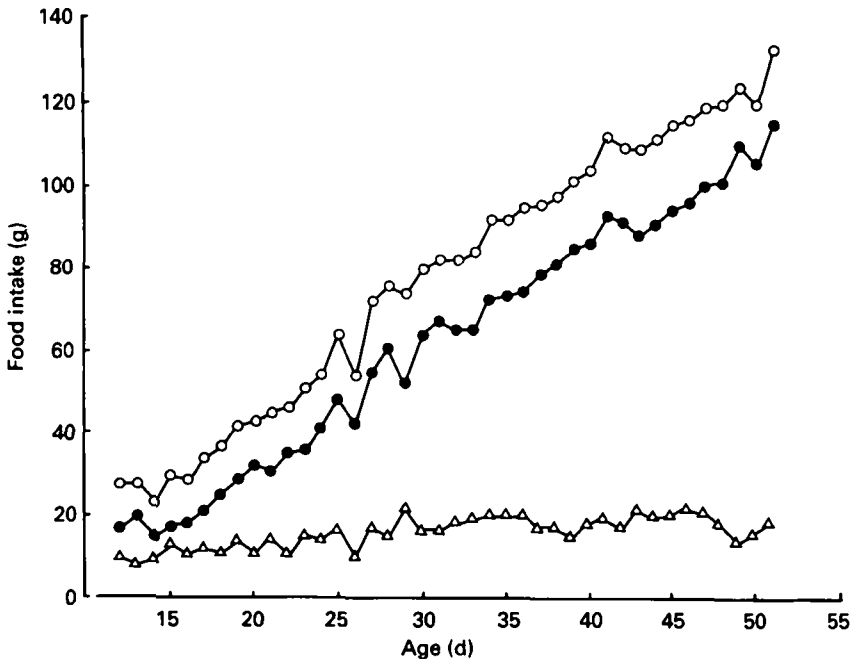

Fig. 3. Mean total daily intake and intake of each diet fraction selected by domestic chicks (*Gallus gallus*) (*n* 7) with *ad lib*. access to a high-protein (soya-bean) and a high-carbohydrate (maize) fraction (from Kaufman *et al.* 1978). (O), Total intake; (△), intake from soya-bean fraction; (●), intake from maize fraction.

chicks learn to discriminate food from non-food items (Hogan, 1971, 1973), and it may also take 1 or 2 d before they select protein appropriately (Yokota & Segawa, 1979). Quartz grit was found in the gizzards of the youngest, 1- or 2-d-old, red grouse chicks caught by Savory (1977), so presumably they can grind PF then, but they may not be able to digest it well until the microbial population in the hind-gut and caecal function have developed fully. These points may not matter, however, because chicks continue to derive nutrients from yolk in their yolk sacs for at least the first 3 or 4 d of life (Romanoff, 1960). What does matter is that they should minimize the period when they are most vulnerable to predation, and so need to be able to escape, either by running or flying, as soon as possible. Movement depends on synthesis of muscle protein and flight on synthesis of feathers for which the S-amino acids that are present in higher concentrations in IF (Table 3) are essential. Relative growth rate (weight gain per unit body-weight) of domestic chicks is highest in the first 2–3 weeks (Kaminska, 1979) and red grouse chicks start to fly in their third week of life (Savory, 1977). If this critical period is also typical of other species, then a reduction thereafter in the relative needs for protein and especially the S-amino acids could account for the observed declines from about 2 weeks onwards in selection for IF (Fig. 1), selection for protein with added methionine (Fig. 2), and percentage IF in the diet (Table 1). With pheasant (*Phasianus colchicus*) chicks, growth rate is higher with a high-protein (280 g/kg) diet than a low-protein (180 g/kg) one, but only during the first 3 weeks of life (Warner *et al.* 1982).

Reasons for variation in consumption of IF within species at the same age

The mean percentage IF by number of items (y) in crops of separate broods of red grouse chicks was related to insect abundance (x_1, number per 100 sweeps) at the time and place of capture and to age (x_2, eight categories ranging from 0–5 to 21–35 d) by the following formula: $y = 21 \cdot 05 + 0 \cdot 36x_1 - 2 \cdot 91x_2$; R^2 $0 \cdot 21$; regression coefficients x_1, $P < 0 \cdot 05$, x_2, $P < 0 \cdot 05$ (by t test); with 46 df. In other words, chicks tended to eat more insects when more were available, regardless of their age. This relationship was not significant, however, when percentage IF was expressed on a dry weight basis (Savory, 1974, 1977). Thus consumption of IF by red grouse chicks was high in early June when insects were most abundant in their habitat (Table 2), and on average they ate four times as much IF on boggy ground as on dry ground, coinciding with the fact that insects were five times as abundant on the boggy ground. Of forty-eight broods found by a dog on the study area, 77% were in boggy areas and only 23% on dry heather, which was the dominant vegetation, suggesting that during early development red grouse broods prefer to spend most time in places where insects are most abundant (Savory, 1977; see also Lance, 1978). Similar variation in IF availability between vegetation types, and in corresponding habitat selection, has been found with partridge (Southwood & Cross, 1969; Green, 1984), pheasant (Hill, 1985), capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*) (Kastdalen & Wegge, 1986) chicks. In the red grouse work, only about half as many insects were caught in the sweep-net samples in the morning as at other times, but consumption of IF was not significantly lower in the morning, and it was in the evening that selection for, and intake of, IF were lower (differences all $P < 0 \cdot 05$) than in the morning and afternoon combined (Table 4). This reduction in selection for IF may have been a consequence of increased feeding rates in the evening, as indicated by weights of crop contents (Table 4), when birds store food in their crops to be digested overnight (cf. King, 1968; Savory, 1980, 1983). Moreover, in the first 2 weeks of life, there was a weak negative correlation ($P < 0 \cdot 1$) between selection for IF and weights of crop contents (J. Savory, unpublished results). If chicks are less selective in the evening, this suggests that analyses of droppings collected from overnight roost piles (Green,

Table 4. *Mean abundance of invertebrates, consumption of and selection for invertebrate food (IF), and dry weights of crop contents of red grouse* (Lagopus lagopus scoticus) *chicks at different times of day (from Savory, 1974)*

(Mean values with their standard errors)

Sample size* . . .	Morning (before 12.00 hours) 8		Afternoon (12.00–1800 hours) 18		Evening (after 18.00 hours) 22	
	Mean	SE	Mean	SE	Mean	SE
No. insects/100 sweeps	9·1	1·6	18·0	2·6	23·5	4·9
Percentage IF:						
By dry weight	6·1	3·9	7·4	1·8	2·9	0·8
By number of items	12·8	7·7	27·7	5·3	12·1	2·5
Selection index (% IF by number/insects per 100 sweeps)	1·0	0·5	1·4	0·2	0·7	0·2
Dry weight of crop contents per chick (g)	0·15	0·08	0·12	0·02	0·51	0·14

*Sample sizes represent nos. of broods sampled which had insect abundance measured at the site of capture.

1984; Hill, 1985; Hudson, 1986) may tend to underestimate overall consumption of IF. Availability of IF is also affected by air temperature, significantly ($P<0.05$) more insects being caught in the sweep-net samples at 10–15° than above or below this range, and this may account for the reduced number caught in the morning (Table 4), but numbers in the sweeps did not differ between calm and windy weather or between dry and damp (overcast with occasional rain, no samples were taken in heavy rain; Savory, 1974).

Just as variation in consumption of IF among broods of the same age may reflect variation in availability of IF, so also do frequencies of different arthropod groups in chick crop contents tend to reflect their frequencies in samples of insect abundance in surrounding habitat, in blue (*Dendragapus obscurus*) (Stiven, 1961; King, 1968), willow (*Lagopus lagopus lagopus*) (Spidso, 1980) and red (Savory, 1977) grouse, grey and red-legged partridges (Southwood & Cross, 1969; Green, 1984) and pheasants (Hill, 1985). With red grouse, frequencies of different orders in the crop contents were much more like those in sweep-net samples than those from pitfall traps, suggesting that chicks took more arthropods from aerial parts of the vegetation than from ground-dwelling fauna (Savory, 1977). Some types of arthropod may appear more frequently in crop contents than would be expected from their occurrence in the samples, either because they are caught more easily than others (such as inactive and flightless ones), or because they are selected for their greater nutritional value (such as some of the larger types of larvae).

Reasons for variation in consumption of IF between species at the same age

Variation in availability of IF may also account for much of the observed variation in its consumption between species at the same age (Table 1). Thus, using the same sampling method, Savory (1977) showed that insect abundance in June was five times as high in rough grassland occupied by grey partridges (mean 107 per 100 sweeps, n 6) as it was at the same time on the nearby red grouse study area (mean 19 per 100 sweeps, n 48). Using a (43%) larger sampling net, Picozzi & Hepburn (1986) obtained much higher densities of insects (means ranging from 201 to 545 per twenty-five sweeps) in habitats

occupied by black grouse chicks, also not far from Savory's (1977) study area. These differences in abundance reflect the fact that both grey partridge and black grouse consume much more IF than red grouse (Table 1). Only a few of the publications referred to in Table 1 provide information on insect abundance, but presumably, for consumption of IF to be sustained at >50%, there would have to be plenty of it available.

Not all variation in consumption of IF can be accounted for by variation in availability, however. Grey and red-legged partridges, for example, sharing the same habitat at the same time, differ significantly ($P<0.01$) in their intake of IF in the first 2 weeks of life, red-legged chicks eating less than half the proportion taken by grey partridges at that
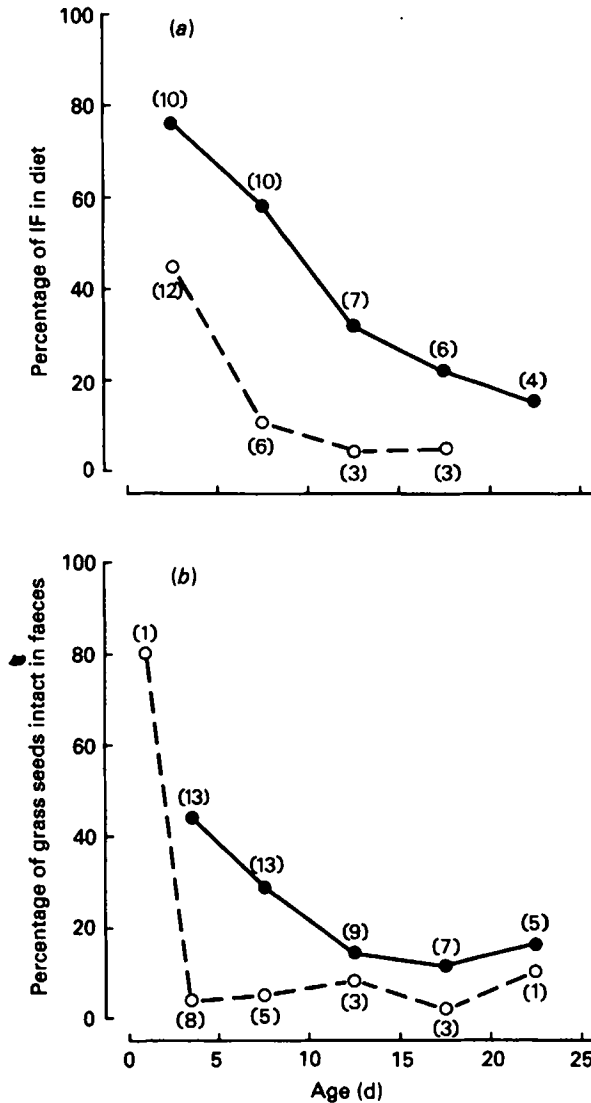

Fig. 4. Mean percentages of invertebrate food (IF), from corrected (Green, 1984) faecal analysis (*a*), and of unbroken grass seeds in faecal droppings (*b*), of grey (*Perdix perdix*) (●), and red-legged (*Alectoris rufa*) (○) partridges at different ages. Values shown in parentheses are the nos. of broods contributing to each point (from Green *et al.* 1987).

time, judging from faecal analyses (Fig. 4(a); Green, 1984; Green et al. 1987). A similar difference was also indicated from analyses of crop contents (Vickerman & O'Bryan, 1979). The reason for this may be that grey partridges appear to be less efficient at breaking up grass (and cereal) seeds in the milky stage (the main PF of both species; Green, 1984) in the first week or so, judging from the greater proportions which remain intact in their faecal droppings at that age (Fig. 4(b)). Red-legged partridge chicks, which are 40% heavier than grey partridges at hatching (Green et al. 1987), had a high proportion of intact seeds in their droppings at 1 d old, but nearly all were broken thereafter, possibly reflecting greater grinding ability of their gizzards than those of grey partridges at the same age. Some variation in consumption of IF may, therefore, reflect differences in digestibility of PF.

Another possible reason for variation in consumption of IF between species is that it may reflect differences in energy requirements for thermoregulation at different ambient temperatures. In two experiments, domestic chicks were kept from 7 to 28 d of age in either warm (35°) conditions day (12 h) and night (12 h), warm by day and cool (15°) by night, cool by day and warm by night, or cool by day and night, and were allowed to self-select in daytime only between a high-protein fraction (soya-bean meal, 450 g protein/kg) and a high-carbohydrate fraction (maize meal, 80 g protein/kg), both with added vitamins and minerals (Hayne et al. 1986). The proportion of protein that was selected increased throughout the day with all four treatments, was greater during warm days than cool days, and was greatest when nights were warm as well (Fig. 5). Selection of carbohydrate was thus related positively to 24 h energy requirements, and so was daily food intake and growth rate (Hayne et al. 1986). In another experiment (J. Savory, unpublished results), ten groups of three medium-hybrid chicks were kept at 32° and were allowed to self-select from hatch until 5 weeks of age between a 1:1 (w/w) mixture of earthworms and herring meal (670 g protein/kg) and barley meal (110 g protein/kg), both with added vitamins and minerals. Their daily intake of the barley increased until about 16 d, while the animal fraction was first increasing and then decreasing, but then barley consumption declined, while the animal fraction increased again to about 60% of total intake (Fig. 6). This effect of age on selection of protein and carbohydrate is quite different from that found by Kaufman et al. (1978) with chicks kept at about 25° (Fig. 2), and presumably reflects the facts that 32° is within or above the zone of thermoneutrality of chicks after the first week or so of life, whereas 25° is below, and that it takes at least 2 weeks for chicks to achieve complete homeothermy (Freeman, 1963). Thus, chicks kept at 32° do not require carbohydrate as a source of thermoregulatory energy after becoming completely homeothermic, whereas those at 25° do. Considerable heat is also produced during metabolism of protein (Tasaki & Kushima, 1980), so chicks kept at higher ambient temperatures must limit protein consumption in order to avoid heat stress, and daily food intake and growth rate decline rapidly with increasing temperature above about 26° (Warner et al. 1982; Howlider & Rose, 1987). In the wild, therefore, percentage IF in chick diets may be related positively to ambient temperature for thermoregulatory reasons, irrespective of variation in availability. Thus, the species that eat least IF in the first 2 weeks, red grouse, (some) rock ptarmigan (Lagopus mutus) and snowcock (Table 1), all live in cool environments, and in their first week of life red grouse do eat many moss capsules (15% dry weight of diet) and rock ptarmigan eat berries (19% dry weight), both of which are rich sources of soluble carbohydrates (Theberge & West, 1973; Moss et al. 1974; Savory, 1977). It may still be true, however, that chicks living in cool environments would eat more IF if more was available.

Recommended dietary crude protein levels (g/kg) for starting gallinaceous chicks commercially range from 190–210 in chicken layer stock, 190–230 in broiler stock,
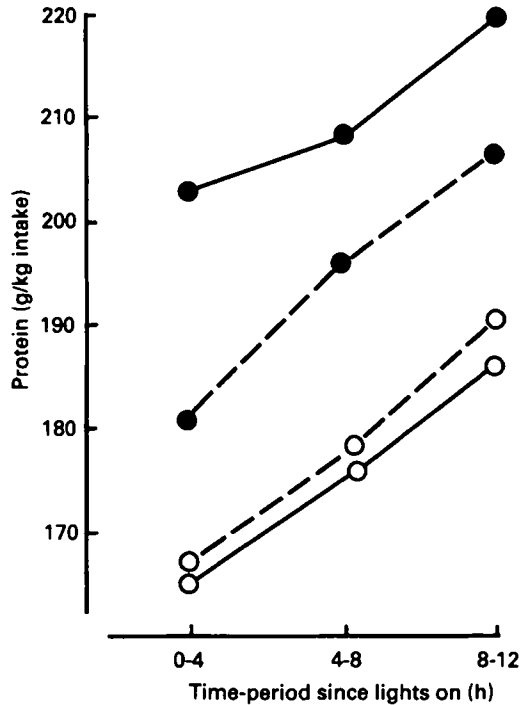
Fig. 5. Mean intake of protein (g/kg total intake) selected during three equal parts of a 12 h photoperiod by domestic chicks (*Gallus gallus*) with *ad lib.* access to a high-protein (soya-bean) fraction (450 g protein/kg) and a high-carbohydrate (maize) fraction (80 g protein/kg), and exposed to four different ambient temperature treatments (*n* 10 for each treatment) (from Hayne *et al.* 1986). (●——●) Warm day, warm night; (●- - -●) warm day, cool night; (○- - -○) cool day, warm night; (○——○) cool day, cool night.

230–250 in guinea fowl (*Numida meleagris*), 240–280 in pheasants and Japanese quail (*Coturnix coturnix japonica*), and 280 in turkeys (*Meleagris gallopavo*) and Bobwhite quail (*Colinus virginianus*) (Andrews *et al.* 1973; Bolton & Blair, 1974; Woodward *et al.* 1977; Hastings Belshaw, 1985). These are minimum levels required to achieve maximum growth rates, and they do indicate that there may be inherent differences in protein requirements between species that might contribute to some of the observed variation in consumption of IF in Table 1. Other factors that probably also cause consumption of IF to vary are: parental influence on feeding behaviour and habitat selection; time available for foraging, depending mainly on day length, weather and time spent brooding (cf. Theberge & West, 1973; Boggs *et al.* 1977; Green, 1984); 'cost' of obtaining IF in terms of time and energy spent per item; availability of alternative high-protein PF.

How do species manage which eat <10% IF?

The three species that were recorded as eating <10% IF in early life were red grouse, rock ptarmigan and snowcock (Table 1). The snowcock reference is from Cramp & Simmons (1980), based on work described by Baziev (1965), and states that animal food is insignificant for both adults and young, food of the young differs quantitatively, legumes being most important (51% of PF) and the proportion of grasses and allies reduced (17%). 'As legumes are most protein-rich of alpine plants, presumably (their consumption) constitutes an adaptation to compensate for lack of insect food normally required by growing young'. Only one of the three recorded values for rock ptarmigan is
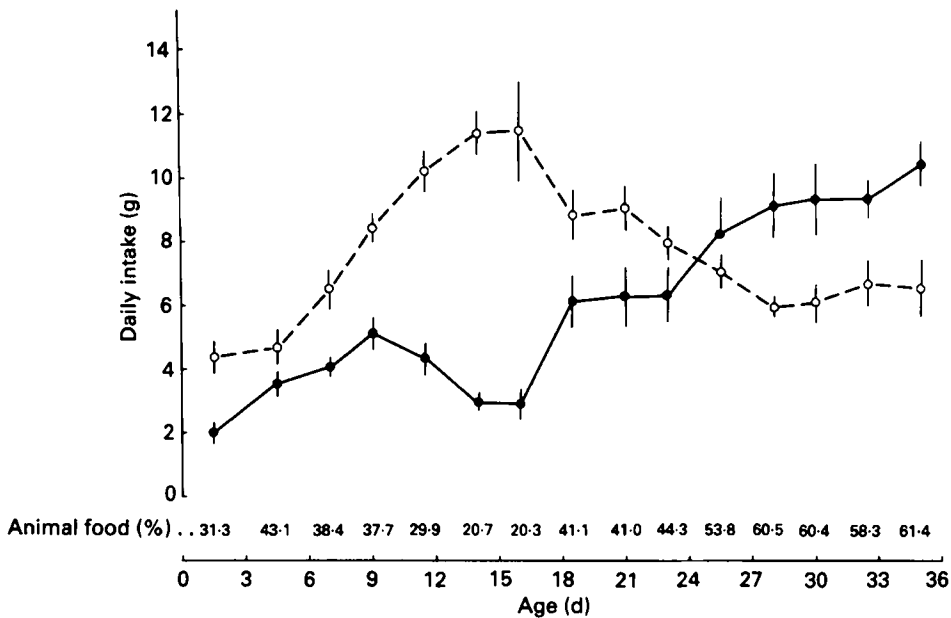
Fig. 6.   Mean daily intake of each diet fraction selected by domestic chicks (*Gallus gallus*) (*n* 10) kept at 32°
with *ad lib*. access to a high-protein (herring/earthworm (1:1, w/w)) fraction (670 g protein/kg) (●) and a
high-carbohydrate (barley) fraction (110 g protein/kg) (○). Points are means with their standard errors
represented by vertical bars (J. Savory, unpublished results).

<10% (8% dry weight) IF (Weeden, 1969), and this does not actually specify the precise
age of the chicks examined. Nevertheless, it is significant that the main PF items in the
diet of ptarmigan chicks, in the studies of both Weeden (1969) and Gardarsson & Moss
(1970), were spikes and bulbils of *Polygonum viviparum* (47 and 63% respectively),
which, like the legumes eaten by snowcock chicks, are rich in protein (200 g/kg,
Gardarsson & Moss, 1970). In fact, growth trials with chicks of different species show
that they can thrive on diets consisting of 100% PF when protein contents are high
enough (Woodward *et al*. 1977; Kaufman *et al*. 1978), and do not grow faster when 50 g
fishmeal/kg is added (Hermes *et al*. 1984).

Unlike snowcock and rock ptarmigan, the main PF items of red grouse chicks, heather
shoot tips, which account for about 80% dry weight of the diet in the first week, and
more thereafter, are not rich in protein (145 g/kg, Savory, 1977). The red grouse studied
by Savory (1977) ate only about 5% IF (by dry weight, from combined contents of all
crops) in the first 2 weeks of life, and doubt has been raised about how such chicks could
be sustained by a diet containing so much heather and so little IF (Wise, 1982). Wise
(1982) estimated amounts of dry matter that would have to be consumed daily in the first
2 weeks of life, relative to body-weight, in order to meet the growing chicks'
requirements for methionine, cystine and energy. These were based on proportions of
heather in the diet ranging from 80–100%, and of IF from 0–20%, and on assumed
compositions of heather and IF (Table 5). With standard starter-mash diets, daily food
intake may range from about 16–27% of body-weight in the first 2 weeks with domestic
chicks of broiler and layer stocks (Savory, 1975; Kaminska, 1979). Even with higher-fibre
diets eaten by wild chicks, it is difficult to see how daily dry matter intake could exceed

Table 5. *Daily dry matter intake of red grouse (*Lagopus* lagopus scoticus) chicks during the first 2 weeks (% of body-weight) estimated to satisfy requirements for methionine + cystine and for energy on four hypothetical diets (from Wise, 1982)*

Diet	Heather (*Calluna vulgaris*) only*	Heather 95%, insects 5%†	Heather 90%, insects 10%	Heather 80%, insects 20%
Methionine + cystine	132	111	37	21
Energy	25	24	23	21

*Assumed composition of heather (g/kg): digestible crude protein 30, methionine + cystine 0·9, metabolizable energy 6 kJ/g.

†Assumed composition of insects (g/kg): digestible crude protein 610, methionine + cystine 24, metabolizable energy 11 kJ/g.

about 40% of body-weight, so clearly Wise's (1982) estimate of 111% needed to satisfy requirements for methionine plus cystine, with the 5% IF recorded by Savory (1977), must be impossible (Table 5). How then can we reconcile this apparent anomaly?

Wise's (1982) value of 30 g/kg for digestible crude protein in heather (Table 5) was taken from Moss & Parkinson (1972), who found 70 g protein/kg in heather shoot tips in spring and about 45% digestibility of that protein by adult grouse then. In fact, the mean N content of heather in crops of chicks collected by Savory (1977) was higher (2·32%, or 145 g crude protein/kg) than that in crops of adult grouse shot at the same time of year (1·87%, or 117 g protein/kg), and both are higher than the 70 g protein/kg of Moss & Parkinson (1972). Thus, since digestibility of protein increases with protein content (Moss & Parkinson, 1972; Bolton & Blair, 1974), digestible crude protein in heather for chicks should be more like 70 g/kg instead of 30 g/kg. The reason why grouse chicks 'select' more N (and P) in heather than adults (Savory, 1977) is that nutrients concentrate in the tips of shoots, selection for N and P is correlated negatively with mean weights of heather particles eaten in spring (Savory, 1983), young chicks eat smaller shoot tips (<2 mg, J. Savory, unpublished results) than adults at that time (mean 4 mg, most 5–15 mm long, Savory, 1974, 1978), and so chicks consume more nutrients per mg eaten. Wise's (1982) value of 0·9 g/kg for methionine plus cystine was obtained by multiplying the 30 g/kg digestible crude protein by the 29 g/kg methionine plus cystine found by Moran & Pace (1962) in heather protein (Table 6), assuming that all methionine and cystine in digested protein is available. Moran & Pace (1962) determined amino acid composition of the protein 'in the green shoots' taken from heather samples in early summer; this probably represents all current year's growth and hence shoot tips considerably longer than those eaten by grouse chicks. To see what effect particle size has on protein and amino acid levels, J. Savory and R. Moss (unpublished results) collected three bunches of heather (two mature and one about 2–4 years old) from two Scottish moors in early June 1984, and a 10 g (wet weight) sample of each was prepared by cutting off the top 5 mm of green shoots, which is more like the size of particle eaten by chicks. The crude protein content of these 5 mm particles was 130–150 g/kg (Table 6), which agrees well with the 145 g/kg in heather actually eaten by chicks (Savory, 1977), and which is higher than the 90–100 g/kg in the larger shoots of Moran & Pace (1962). Methionine levels were also higher in protein from the smaller particles, while cystine was about the same as that found by Moran & Pace (1962) (Table 6). Applying the same calculation as Wise (1982), therefore, available methionine plus cystine in heather shoot tips eaten by

Table 6.   *Contents of crude protein (nitrogen × 6·25; g/kg), methionine and cystine (g/kg crude protein) in 5-mm shoot tips of three heather* (Calluna vulgaris) *samples collected by J. Savory and R. Moss, compared with those in 'green shoots' of heather collected on two moors by Moran & Pace (1962)*

| | J. Savory and R. Moss (unpublished results) (top 5 mm of green shoots) | | | Moran & Pace (1962) (100% of green shoots) | |
	Auchencorth moss (mature)	Banchory (mature)	Banchory (young)	Moor A	Moor B
Crude protein	136	132	151	96	89
Methionine	20	23	21	17	17
Cystine	10	11	11	12	13

chicks should be 32 g/kg (mean from Table 6) multiplied by the 70 g digestible crude protein/kg (see above), or 2·24 g/kg, which is 2·5 times the 0·9 g/kg of Wise (1982) (Table 5). The rest of Wise's (1982) calculations (Table 5), which were not specified in his paper, are based on an assumed weight gain of 40 g by red grouse chicks in their first 14 d (which is within the range in Savory, 1977) and the assumption that red grouse require levels of amino acids and energy equivalent to fowls and turkeys for a given gain in weight. It is, therefore, not possible to repeat all Wise's (1982) calculations here, but the 2·5-fold difference in the methionine plus cystine content of the heather eaten would reduce his dry matter intake of 111% body-weight with a 95% heather diet (Table 5) to more like 40–50%, albeit still dubiously high.

Assuming about 600 g crude protein/kg in IF and 145 g/kg in PF eaten by red grouse chicks (Savory, 1977), then the overall protein content of their recorded diet of 5% IF and 95% PF in the first 2 weeks would be about 170 g/kg, with about 28% digestible crude protein coming from the IF and 72% from the PF. In fact, pheasant chicks can be grown satisfactorily on a diet containing 180 g protein/kg, although not as fast as with 280 g/kg (Warner *et al.* 1982). Likewise, Marquiss (1977) grew captive red grouse chicks from hatch on either *ad lib.* turkey starter diet plus heather (about 240 g protein/kg) or a low-protein ration consisting of 50% of the controls' intake of turkey starter plus *ad lib.* maize and heather (about 170 g protein/kg). The captives on the low-protein diet gained weight at the same rate as wild chicks and significantly (*P*<0·001) slower than the controls on the high-protein diet (Fig. 7), thus indicating that the protein in the wild chicks' diet is about 170 g/kg as calculated above, and is limiting with respect to growth. Low protein intake by wild chicks was also indicated by the percentage of their faecal droppings with white urate 'caps', which was similar (63 and 78% on two areas) to that of the captives fed on the low-protein ration (79%), but lower than that of the controls (99%; Marquiss, 1977). Energy does not appear to be limiting in the wild chicks' diet (Tables 2, 3) and they do not 'select' soluble carbohydrates from heather (Savory, 1977).

The relationship between IF and growth rate in red grouse was also studied by Hudson (1986), who measured numbers of insect fragments per 100 units of heather in chick droppings from roost piles of ten broods followed by radiotelemetry in 1982. He found that the mean weight of chicks in each brood at 10 d of age was correlated (*P*<0·001) positively with the brood's index of IF consumption from faecal analysis (Fig. 8). He also showed that captive chicks cannot survive on a diet of heather alone, and that they grow faster when fed on heather with *ad lib.* insects than on heather with a limited insect supply (Hudson, 1986), just as Cross (1966) showed that captive grey partridge chicks
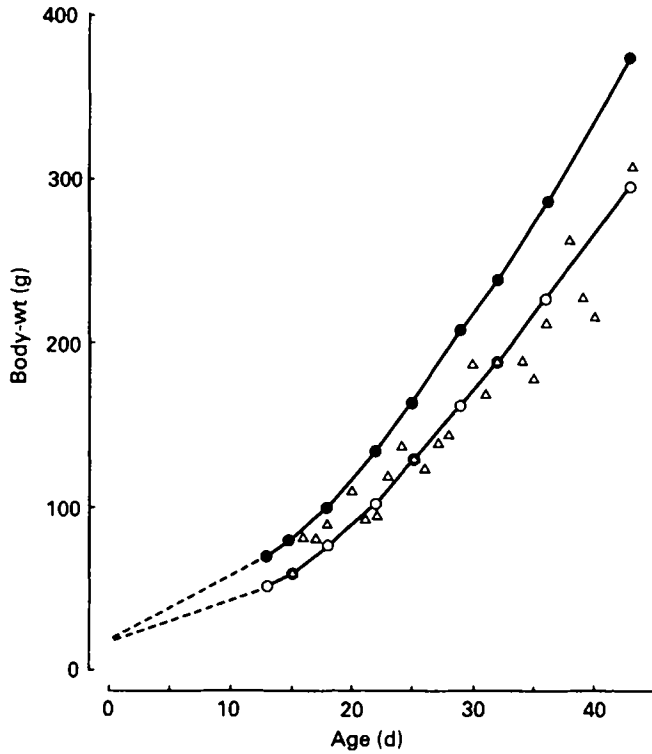
Fig. 7. Mean growth rates of captive red grouse (*Lagopus lagopus scoticus*) chicks fed *ad lib.* on either a control diet (about 240 g protein/kg, *n* 39) (●) or a low-protein diet (about 170 g protein/kg, *n* 30) (○), compared with mean body-weights of wild chicks of known age (*n* 2–14) (△) (from Marquiss, 1977).

grow and feather faster when insects are added to a diet of weed seeds and grasses. These differences in growth and development can presumably all be explained by variation in the protein and S-amino acid contents of the diets.
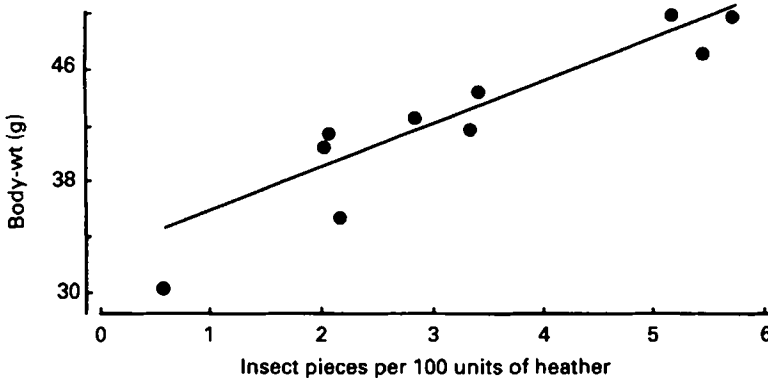

Fig. 8. Mean body-weights at 10 d of age of ten wild broods of red grouse (*Lagopus lagopus scoticus*) chicks in relation to indices of their consumption of invertebrate food from faecal analysis (from Hudson, 1986).
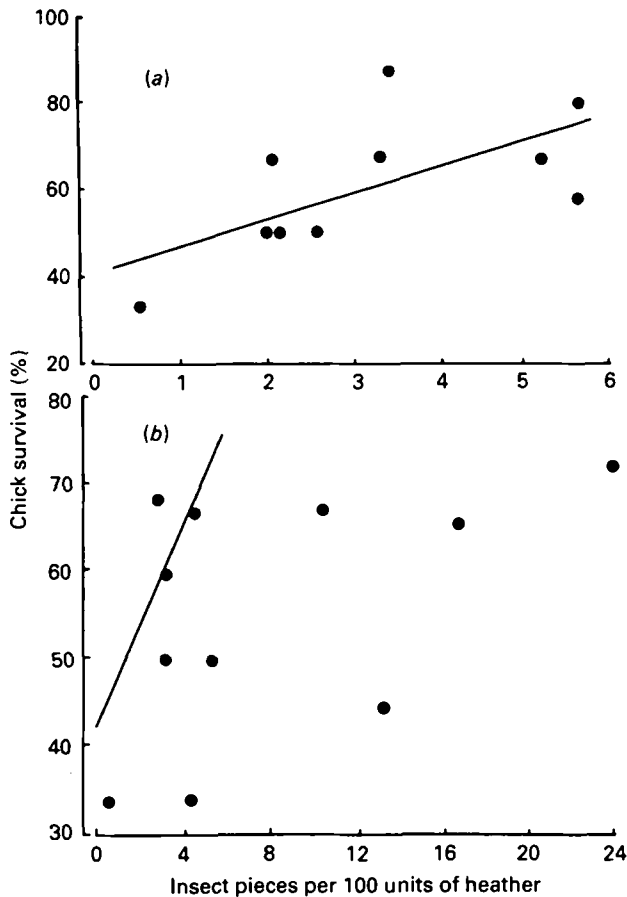
Fig. 9. Proportions of chicks surviving at 10 d of age in wild broods of red grouse (*Lagopus lagopus scoticus*) in relation to indices of their consumption of invertebrate food from faecal analysis. (*a*), 1982; (*b*), 1983 (from Hudson, 1986).

Hudson (1986) found that his indices of IF consumption by radio-tracked broods of red grouse were correlated significantly ($P<0.05$) with the proportions of chicks in each brood which survived to 10 d in 1982 (Fig. 9(*a*)), but not in 1983 (Fig. 9(*b*)), when some broods did not survive well in spite of eating many insects, possibly because hen grouse then carried high parasite burdens which may have affected parental care. Other evidence also indicates that the relationship between consumption of IF and red grouse chick survival is not well defined. Thus, variation in breeding success (number of young in July per adult) between (4) years was not related to variation in mean % IF by dry weight during early growth (Savory, 1977), and Lance (1978) found that growth rates (of seven radio-tracked broods) were not higher in broods which spent most time in insect-rich boggy vegetation, while survival was better in those which preferred drier heathery ground (see also Savory, 1977). In fact, much of the observed variation in chick survival may be predetermined before hatching, possibly because the nutrition of laying hens affects egg quality (Jenkins *et al.* 1965; Moss, 1969; Moss *et al.* 1981), and Lance (1978) found that growth and survival tended to be better in broods hatched on

territories with N-rich heather, even though the broods did not use that heather after hatching. Significant correlations between breeding success/chick survival and insect abundance have also been shown with grey partridges and pheasants, however, both between (Southwood & Cross, 1969) and within (Green, 1984; Hill, 1985) years. While it is debatable whether all these correlations are necessarily direct, causal ones, nevertheless it is possible that insufficient protein during early life could increase mortality by reducing the ability to withstand periods of bad weather, and by extending the period of maximum vulnerability to predation (Ryser & Morrison, 1954; Scott *et al.* 1955). In experimental conditions, mortality of pheasants during the first 2 months of life was greater with 160 g than 200 g protein/kg in their (all-PF) diet, and greater with 200 than 240 or 280 g/kg (Woodard *et al.* 1977).

Do species which eat >90% IF really need so much?

In order to assess the importance of IF for young mallards, Street (1978) compared the growth rates of four groups of ten ducklings fed *ad lib.* from hatch to 14 d on either blowfly (*Calliphora vulgaris*) larvae (520 g protein/kg), barley meal (130 g protein/kg), turkey starter crumbs (260 g protein/kg) or chick starter crumbs (210 g protein/kg). The group fed on 100% IF grew no faster than the one fed on turkey starter, and only slightly faster than the one fed on chick starter, while the group fed on barley meal gained weight only very slowly (Fig. 10). Street (1978) also measured food conversion efficiencies of the four groups, and found that the dry weight of food eaten/g (estimated) dry weight gain in
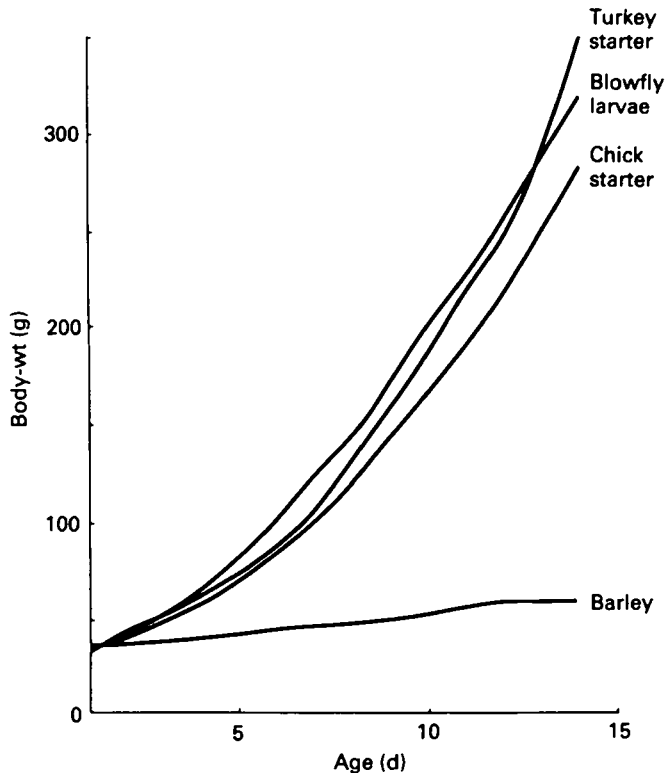
Fig. 10. Mean growth rates of four groups (*n* 10) of captive mallard (*Anas platyrhynchos*) ducklings fed *ad lib.* on blowfly (*Calliphora vulgaris*) larvae (520 g protein/kg), barley (130 g protein/kg), turkey starter (260 g protein/kg) or chick starter (210 g protein/kg) (from Street, 1978).
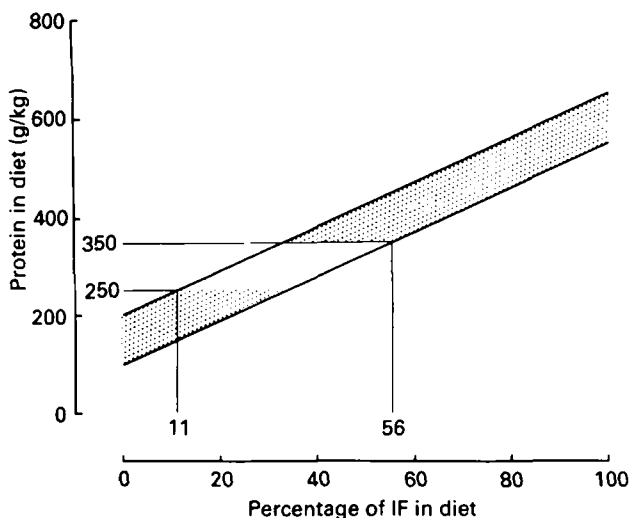
Fig. 11.   The relationship between the proportion of invertebrate food (IF) in the diet and total protein (g/kg), assuming 550–650 g protein/kg for most IF and 100–200 g/kg for most plant food. The values shown represent estimated minimum and maximum proportions of IF required to achieve maximum growth rates.

body-weight was 3·1 g with blowfly larvae, 17·2 g with barley, 5·3 g with turkey starter and 5·8 g with chick starter. Thus, although the ducklings did not require more than 260 g protein/kg in their diet to achieve maximum growth rate, their food conversion efficiency was related closely to the protein content of the diet. Presumably, therefore, young birds can achieve maximum growth rates with lower (total) food consumption when they eat high percentage IF than with lower percentage IF, assuming that energy is not limiting (cf. Stiven, 1961). Dietary levels of crude protein required to produce maximum growth rates in gallinaceous chicks range from <250 g/kg to nearer 300 g/kg. Even allowing for some species with greater intrinsic protein requirements, and for variation in digestibility of crude protein (in IF and PF), it should still be true that maximum growth rates could be achieved by all species within the range 250–350 g/kg. Assuming 550–650 g crude protein/kg in most IF and 100–200 g/kg in most PF, then 250–350 g dietary protein/kg can be reached with 11–56% IF (Fig. 11). Thus, chicks which eat >50% IF can probably achieve maximum growth rate with reduced food intake.

The question remains whether chicks which eat very high proportions of IF really need to eat so much. Presumably the circumstances which could be associated with high percentage IF intake are: high protein requirements, high ambient temperature, high availability of IF relative to high-protein PF, reduced digestibility of PF, and low total food intake. Little or no information is available on these factors for the ten species which were recorded with >90% IF in the first 2 weeks of life (Table 1). However, it may be that the environments occupied by the only two species to continue eating >90% IF after the first 2 weeks, prairie chicken and sharp-tailed grouse, are warmer than most others, in which case their apparent rejection of PF might be analogous to that in Fig. 6 (sharp-tailed grouse did not eat <10% IF until they were 12 weeks old; Kobriger, 1965; Pepper, 1972). Some of the species with >90% IF probably live in cooler environments where the reduced food intake associated with high percentage IF may allow more time for brooding. Free-ranging domestic chicks, which were brooded by their mothers for about 40% of the day in the first few weeks, ate about 65% IF and grew as fast then as a

control group kept indoors and fed on a 250 g protein/kg starter diet (Savory *et al.* 1978). Increased abundance of all food may increase time available for brooding because of less time spent foraging, and this could result in reduced energy expenditure and better food conversion efficiency, better protection against weather and predators, and hence better survival. This might explain why survival of grey partridges, which eat mainly IF, is correlated with IF availability, while that of red-legged partridges in the same environment, which eat more seeds and <50% IF, is correlated with both IF and grass spikelet densities (Potts, 1970; Green, 1984; Rands, 1985). Nevertheless, in favourable climatic conditions and with low risk of predation, it might be true that some species which eat >90% IF could actually grow as fast and survive as well by eating less IF and more PF.

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Printed in Great Britain