Sexual differences in energy allocation of Capercaillie *Tetrao urogallus* chicks

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The energy allocation was studied in captive male and female Capercaillie chicks up to the age of one month. The higher energy requirement of the males was at first mostly due to their greater activity and thermoregulation costs. As the chicks grew older, the proportion of energy devoted to growth and resting metabolism increased. To study the allocation of growth energy in detail, chick bodies were divided into five body component groups (integument, digestive organs, flying muscles, legs and "other body components"). Females allocated proportionately more of their growth energy to flying muscles and males to legs and "other body components".

The higher activity and thermoregulation costs are supposed to be an indirect consequence of the faster growth of male chicks. To obtain the additional growth energy, males must be more active and are exposed for longer to harsh weather conditions. The legs and "other body components" of adult males are relatively larger than those of adult females. Growing male chicks must invest more in these body components and hence less energy is available for the growth of breast muscles. Male chicks with small breast muscles are probably inferior flyers and more vulnerable to predators.

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Introduction

In a growing chick the allocation of food resources should ensure the highest possible expected lifetime reproduction. The functions and body components affecting the survival of the chicks are of essential importance, but resources must also be channelled to the body components important for the fitness of adult birds (Sibly and Calow 1986). The allocation pattern in chicks is the outcome of the prevailing, possibly conflicting, selective pressures.

Most of the energy allocation studies deal with altricial birds (for reviews see Dunn 1980, Williams & Nagy 1985). In these species the adults provide brooding and food for the nestlings. In contrast, the chicks of precocial species can at least partly take care of their own thermoregulation and in many species the chicks can feed themselves. Consequently, the amount of energy obtained is strongly dependent on the activity and efficiency of the chicks. Differences can also be seen between the energy budgets of altricial and precocial species (Dunn 1980).

The Capercaillie *Tetrao urogallus* is a large precocial grouse. The chicks feed themselves and there is pronounced sexual size dimorphism (Wittenberger 1978). The growth rate is faster and the growth period much longer in male than in female chicks (Lindén 1981). In an earlier study, we have observed sex-related differences in the development of body components (Milonoff & Lindén 1989). In this paper we construct energy budgets for both sexes of Capercaillie chicks up to the age of one month, concentrating on the allocation of growth energy and comparing the allocation patterns of male and female chicks. The consequences of sexual differences are evaluated and selective pressures behind the differences are discussed.

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[1] Offprint requests.

Material and methods

The study was conducted at Meltaus Game Research Station, Finnish Lapland (66°55′N, 25°20′E). Energy consumption experiments were carried out in the laboratory in 1978–79 (42 experiments, Lindén 1981) and experiments in "outdoor" conditions in 1981 (18 experiments, Lindén et al. 1984). The body component data come from the years 1982–83 (13 males and 14 females, Milonoff & Lindén 1989). All the birds belonged to the northern subspecies T. u. urogallus (e.g. Johansen 1957). Eggs were collected from the wild or were laid by captive hens. They were artificially incubated and the chicks were raised in semi-natural conditions (details in Lindén 1981).

In the energy consumption experiments, a gravimetric technique was used (see Kendeigh 1975, Lindén 1981). During the experiments the birds were kept in cages (in laboratory 55×115 cm and in outdoor 55×195 cm, the outdoor cage being larger to allow also colder temperatures inside the cage). The cages had food (ad libitum) at one end and a thermo lamp (instead of a hen) at the other (Lindén 1981, Lindén et al. 1984). The situation in the laboratory is regarded as "optimum", because the thermoregulation costs were minimal. On the other hand, in the "outdoor" experiments the feeding chicks were exposed to varying weather conditions (temperature +9°C to +25°C, wind 0–9 m/s and occasionally rain). The chicks were weighed before and after each experiment.

Assimilation (A) was calculated by substracting the energy of the feces (F) from the energy of the food consumed (FC). Although resting metabolism estimates are available for the Capercaillie (Hissa et al. 1983), the resting metabolism (RE) was calculated according to Stivens (1961, for blue grouse), to achieve agreement with earlier studies (Lindén 1981, Lindén et al. 1984):

RE for males = $0.22W^{0.98}$ and
RE for females = $0.21W^{1.00}$,

where W = the average body weight of experimental birds in different age groups (see Results). The total growth requirements (G) were calculated by multiplying the growth during an experiment by the average energy content of the tissues (see Results) and by the value 1.43 (costs of biosynthesis according to Brody 1945; cf. Ricklefs 1974). The total growth requirements and resting metabolism in "optimal" conditions were subtracted from the assimilation in "optimal" conditions (AOC). The remainder is treated as activity in "optimal" conditions. the difference between the energy consumed by activity and thermoregulation in "outdoor" conditions and the activity in "optimal" conditions is called the additional costs of "outdoor" conditions (ACOC = A – G – RE – AOC).

The energy contents of the body components were measured by dissecting birds into 10 parts (integument, head, wings, pectoral muscles, legs, heart, liver, stomach, intestine and the remainder of the body, see Milonoff & Lindén 1989). The water, fat and ash contents were determined by the methods of Ricklefs (1975). The protein content was calculated by substracting water, fat and ash from the wet weight. The energy content of the body components was estimated by multiplying the fat content by 39.50 kJ/g and the protein content by 23.62 kJ/g (Brody 1945, cf. Johnston 1970).

The body components were divided into five groups: integument, flying muscles (wing and pectoral muscles and wing bones), legs, digestive organs (liver, stomach and intestine) and "other body components" (head, heart and the remainder of the body, OB). The total growth energy (data from 1981) was divided between the different body component groups in accordance with the increase in their energy content (increase in the energy content of a body component group/increase in the total energy content of the bird × 100%, data from 1982–83).

Eight functions were fitted to the different data and the function giving the highest coefficient of determination was chosen. Covariance analysis was used to test differences in energy consumption between male and female chicks. To examine sexual differences in the proportions of energy in the body component groups, pairs of male and female chicks of the same age (±1.5 days) were separated (10 pairs) and the Mann-Whitney U-test was applied.

Results

Weight and energy contents

The weight of male and female chicks followed the equations $W = e^{0.088x + 3.30}$ ($R^2 = 96.8$ %, n = 13) and $W = e^{0.077x + 3.40}$ ($R^2 = 94.1$ %, n = 14), where x = age. The average energy content of the tissues followed the equations $E = 6.1 \ln x - 0.2$ ($R^2 = 45.7$ %, n = 13) in males and $E = 6.6 \ln x - 0.3$ ($R^2 = 66.4$ %, n = 14) in females.

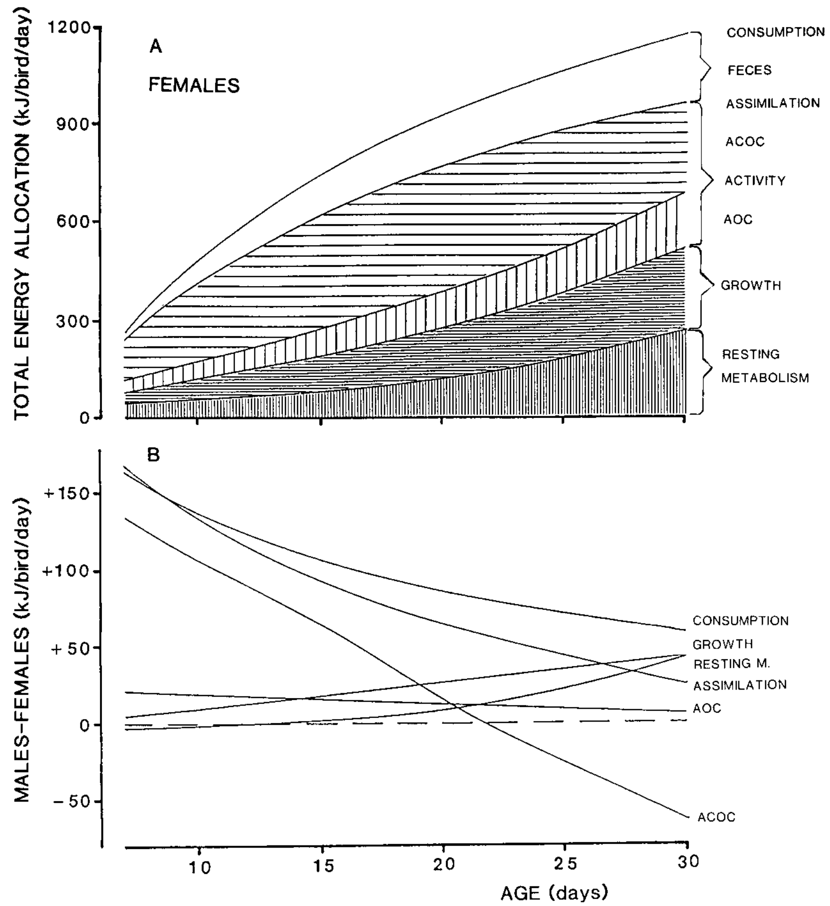

Fig. 1. (A) The energy allocation of female Capercaillie chicks and (B) differences between male and female chicks. The cumulative curves are drawn on the basis of the equations in Table 1. ACOC = additional costs of "outdoor" conditions and AOC = activity in "optimal" conditions.

Energy allocation

Figs. 1 and 2 show the energy allocation patterns of the chicks. The regression equations are presented in Tables 1 and 2. The rather low coefficients of determination permit only cautious conclusions. Two thirds of the assimilated energy was consumed by thermoregulation and activity, although their proportion began to diminish after the age of two weeks (Fig. 1A). At the same time the proportions of growth and resting metabolism increased and at the age of one month they together accounted for over 50 % of the assimilated energy. The most distinct sexual differences were the higher food consumption and assimilation of male chicks (Fig. 1B and Tab. 1). These differences diminished as the chicks became older, whereas the differences in growth requirements and resting metabolism increased. ACOC was at first higher in males, but after the age of three weeks it seemed to be higher in females.

A higher proportion of growth energy is allocated to integument, digestive organs and legs in young than in old chicks (Fig. 2). In the two other body component groups the trend is the opposite. Females allocate a higher proportion than males to flying muscles. After the age of two weeks, females also seemed to allocate proportionately more growth energy to integument. Males allocated more to legs and OB. Male chicks less than one week old seemed to invest relatively more energy in integument. In this small sample, the sexual difference in the proportions of energy in different body component groups was statistically significant only for the flying muscles ($U=20$, $P<0.05$, $n=10$) and legs ($U=21$, $P<0.05$, $n=10$).

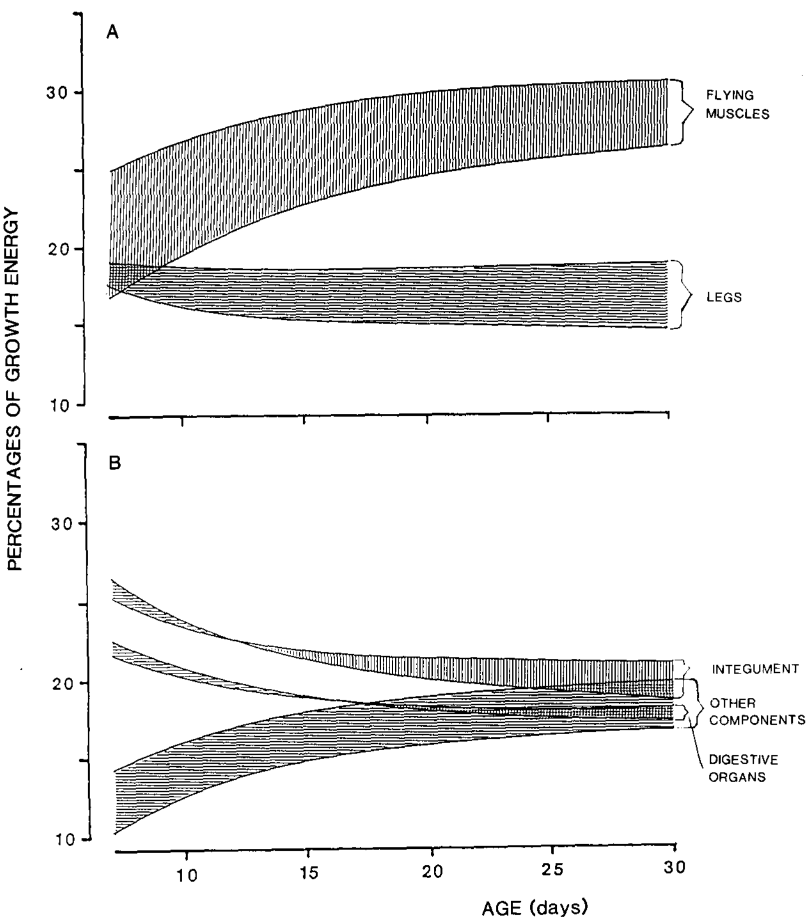

Fig. 2. The growth energy allocation of Capercaillie chicks. The curves are drawn on the basis of the equations in Table 2. Horizontal hatching = proportion larger in males than in females and vertical hatching = proportion larger in females than in males.

Discussion

The energy allocation pattern of Capercaillie chicks is typical of precocial self-feeding chicks (see Dunn 1980). A large part of the energy is consumed by activity and thermoregulation. Only a small proportion of the assimilated energy remains for growth. In the wild, the proportion allocated to growth is probably even lower than in our experiments. Furthermore, the growth rate of Capercaillie chicks has been shown to be highly dependent on the weather conditions (Lindén et al. 1984). The allocation of the growth energy is also typical of a precocial species in at least two features: young chicks allocate much energy to integument and limbs, the wings, in particular, developing earlier than in altricial species (see Lilja 1983). The information about the developmental pattern of precocial species is, however, sparse.

The faster growth of male Capercaillie chicks is believed to be one of the most important reasons for their higher energy requirements (Lindén 1981, Lindén et al. 1984). However, the effect is partly indirect; ACOC seemed to be the main cause of the high requirements of young male chicks. This holds true till the age of about three weeks, when the chicks are capable of effective thermoregulation (see Hissa et al. 1983). The temperature-sensitiveness of the energy requirements of male chicks has been noted in an earlier study as well (Lindén et al. 1984). Only in older chicks will the higher growth energy and resting metabolism mostly account for the difference in energy requirements.

Milonoff & Lindén (1989) suggested that the small breast muscles of male Capercaillie chicks are an energetic consequence of their fast growing legs. There were no distinct sexual differences in the rela-

Table 1. The regression equations of total energy allocation of Capercaillie chicks up to the age of one month. Y=energy (kJ $bird^{-1}$ day^{-1}), x=age in days and W=average weight in grams (see Methods). Differences between sexes were tested using covariance analysis. * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$. [a] After Stivens (1961).

	Equation	R2 (%)	F	N
Food consumed				
Females	$y=638.2\ln x-987.4$	63.0***		23
			26.2***	36
Males	$y=569.1\ln x-692.4$	52.4**		13
Assimilation				
Females	$y=509.1\ln x-755.3$	55.8***		23
			20.0***	36
Males	$y=411.2\ln x-396.1$	44.5**		13
Activity in "optimal" conditions				
Females	$y=5.6x-5.6$	51.1***		32
			1.5	68
Males	$y=4.9x+21.4$	42.3***		36
Growth energy				
Females	$y=9.5x-30.0$	53.0***		23
			6.3*	36
Males	$y=11.2x-35.8$	46.1**		13
Resting metabolism[a]				
Females	$y=0.21W^{1.00}$			
Males	$y=0.22W^{0.98}$			

Table 2. The regression equations of growth energy allocation of Capercaillie chicks up to the age of one month. For explanations see Table 1.

Body component group	Equation	R^2 (%)	N
Integument			
Females	$y=0.4x^2+3.3x+47.6$	94.5***	14
Males	$y=0.3x^2+10.1x+25.7$	90.7***	13
Digestive organs			
Females	$y=0.3x^2+3.6x+15.9$	99.4***	14
Males	$y=0.3x^2+8.8x+0.1$	95.3***	13
Flying muscles			
Females	$y=0.7x^2-0.7x+10.9$	96.3***	14
Males	$y=0.7x^2-0.8x+10.9$	87.1***	13
Legs			
Females	$y=0.3x^2+2.5x+27.3$	94.4***	14
Males	$y=0.4x^2+5.0x+18.7$	92.1***	13
"Other body components"			
Females	$y=0.4x^2-1.9x+93.2$	96.1***	14
Males	$y=0.5x^2+0.8x+88.8$	92.5***	13

tive weight of OB (Milonoff & Lindén 1989), but male chicks seemed to allocate more energy to these components as well as to the legs. The head and the remainder of the body (see Material and methods) are proportionately larger in adult males than in adult females (Milonoff & Lindén 1989) and this can lead to delicate allocation differences in chicks. At the time when the females were allocating more to integument (after the age of two weeks), their ACOC also grew beyond the costs of male chicks. These results seemed to be contradictory. However, the first moult of the chicks begins at the age of about two weeks and the allocation differences can be caused by sexual differences in the moult (see Kalske & Lindén 1988).

In the Capercaillie sexual selection has led to dimorphism in size and body composition (Milonoff & Lindén 1989). The large size of adult cocks forces male chicks to grow faster than female chicks. When obtaining the additional growth energy, male chicks must be more active and exposed for longer to harsh weather conditions; the effect of fast growth is multiplied. Adult males have relatively large legs and "other body components", so that male chicks must allocate proportinately more energy to these body components than females. Consequently, less energy is available for the growth of flying muscles and the flying ability of males develops more slowly than that of females (Kalske & Lindén 1988). Large and clumsy male chicks are presumably more vulnerable to predators and they must therefore compromise their survival for the sake of subsequent fitness.

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Selostus: **Metson koiras- ja naaraspoikasten erot energian käytössä**

Alle kuukauden ikäisten metson poikasten energian käyttöä tutkittiin Meltauksen riistantutkimusasemalla vuosina 1978–79 ja 1981–83. Hautomakoneessa kuoriutuneille poikasille tehtiin energiankultuskokeita sekä sisä- että ulkotiloissa. Poikasten ruumiinrakenteen kehitystä seurattiin paloittelemalla eri-ikäisiä poikasia ja analysoimalla ruumiinosien (nahka, ruoansulatuselimet, lentolihakset luineen, jalat ja loppuruho) rasva- ja proteiinipitoisuudet. Energiankulutuksen mittauksessa käytettiin menetelmää, jossa syödyn ravinnon sisältämästä energiasta vähennettiin ulosteiden energia. Tulokseksi saatu assimiloitu energia jaettiin eri käyttömuotojen kesken. Lepoaineenvaihdunta arvioitiin poikasten painon perusteella. Kasvuun kulunut energia laskettiin kertomalla painonlisäys kudosten energiapitoisuudella. Jäljelle jääneestä assimiloidun energian osasta vähennettiin vielä energiamäärä, joka samanikäisillä poikasilla oli kulunut aktiivisuuteen sisätiloissa. Loppuosaa kutsuttiin ulko-olosuhteiden lisäkustannukseksi ja se kuluu lähinnä poikasten suurempaan aktiivisuuteen sekä lämmönsäätelyyn. Energian käytön kuvaamiseen käytettiin regressioyhtälöitä (Taulukot 1 ja 2).

Pesäpakoisille lintulajeille tyypillisesti metson poikaset käyttivät suurimman osan assimiloidusta energiasta aktiivisuuteen ja lämmönsäätelyyn (Kuva 1). Pesäviipyjiin verrattuna nuoret poikaset käyttivät suuremman osan kasvuun jäävästä energiasta nahan ja raajojen kasvattamiseen (Kuva 2). Koiraiden naaraita suurempi energiankulutus johtui alle kaksi viikkoisilla poikasilla pääasiassa korkeammasta ulko-olosuhteiden lisäkustannuksesta, mutta vanhemmilla poikasilla eron aiheutti koiraiden nopeampi kasvu ja vilkkaampi lepoaineenvaihdunta (Kuva 1A). Naaraat sijoittivat suhteellisesti suuremman osan kasvuun jääneestä energiasta lentolihaksiin ja koiraat vastaavasti jalkoihin ja loppuruhoon (Kuva 2A).

Koiraiden suuremman ulko-olosuhteiden lisäkustannuksen uskottiin olevan epäsuora seuraus nopeammasta kasvusta. Hankkiakseen enemmän energiaa kasvuun koiraspoikasten täytyy ruokailla aktiivisemmin ja ne joutuvat altistamaan itsensä pitempään kylmälle. Aikuisten metsokukkojen jalat ja loppuruho ovat suhteellisesti suuremmat kuin aikuisten naaraiden. Koiraspoikasten täytyy sijoittaa suurempi osa kasvuun jäävästä energiasta näihin ruumiinosiin ja rintalihasten kasvattamiseen jää vähemmän energiaa. Poikasen painoon nähden pienempien lentolihasten seurauksena koiraspoikaset ovat luultavasti kömpelömpiä lentäjiä ja jäävät helpommin petojen saaliiksi.

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