The growth dynamics of sexually dimorphic birds and Fisher's sex ratio theory: does sex-specific growth contribute to balanced sex ratios?

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Abstract. From Fisher's (1958) theory which states that the sex ratio at the termination of parental care should reflect total cost of producing each sex, a biased secondary sex ratio towards the smaller sex has often been expected for sexually dimorphic birds. The absence of such a sex ratio bias in sexually dimorphic birds has motivated studies which attempted to show, under the so-called sex-specific growth hypothesis, that the differential growth dynamics of males and females counters the difference in energetic costs expected from the size disparity and equalizes the energetic expenditure on males and females. These studies show that the smaller sex (1) shows faster feather growth, (2) attains adult measurements relatively faster, (3) fledges earlier and (4) shows lower variability of growth parameters than the larger sex, and argue that these developmental differences between males and females render the smaller sex as costly as the larger sex. It is shown here that the arguments used in support of the hypothesis that sex-specific growth equalizes the costs of males and females are invalid, and that some of the proposed mechanisms actually increase the cost difference between the sexes. In addition a review of male and female chick growth with respect to weight, tarsus and feathers showed no evidence in support of the sex-specific growth hypothesis in any of the dimorphic species. The energy investment in males and females may be a poor representation of parental cost. The available sex ratio data from stressed and unstressed populations suggest that the reproductive value *sensu* Williams (1966) is a more precise correlate of parental cost and hence is a better predictor for the sex ratio.

Key-words: Fisher, sex ratio, sex-specific growth, sexual dimorphism

Introduction

In bird species where male and female chicks grow towards different asymptotes, the parental expenditure seems *a priori* higher for the chicks of the bigger sex and, according to Fisher's (1958) theory, which states that the sex ratio at the termination of parental care should reflect equal total expenditures on the two sexes, a bias in the secondary sex ratio towards the smaller sex can be expected. With a few exceptions, no such bias has been found in sexually dimorphic birds (Clutton-Brock, 1986). The discrepancy between the predictions from Fisher's theory and the empirical evidence from sexually dimorphic birds led Richter (1983) to propose the sex-specific growth hypothesis which states that despite the sexual dimorphism in body weights at fledging, for a sex ratio of unity, the energy expended on the two sexes is equalized by the difference in the growth pattern of male and female nestlings. The hypothesis is based on the observations that the smaller sex grows costly structures at a faster rate, attains fledging weight and size closer to adult values, completes growth earlier, fledges earlier and shows lower variability in growth than the larger sex.

Richter's interpretation of sex-specific growth serving to equalize the costs of males and females led me to review the studies which investigate the growth patterns of sexually dimorphic birds, and to examine more closely the arguments in favour of the sex-specific growth hypothesis. To further evaluate the hypothesis of equal investment in males and females, I perform an interspecific comparison of the growth patterns of males and females of sexually dimorphic species. If the sexual weight dimorphism at the end of the period of parental care is compensated by an inverse dimorphism in other morphological characters such as feathers or bones, which are costly to produce, then this gives evidence in support of the hypothesis that sex-specific growth equalizes the investment in males and females. As an example, the heavier weight of males at fledging would be energetically compensated if females had longer bones, feathers or other costly features at fledging

than males. Thus, in an interspecific comparison a negative correlation between increasing body weight dimorphism and increasing tarsus or wing dimorphism is evidence in favour of the sex-specific growth hypothesis, while a positive correlation gives evidence against the hypothesis.

A critique of the evidence for the sex-specific growth hypothesis

Richter (1983, 1984) demonstrates that female yellow-headed blackbird chicks (the smaller sex):

1 Show initially faster and then equally fast feather growth than male chicks over the first 10 days after hatching.
2 Attain adult measurements relatively faster.
3 Fledge earlier than males.
4 Show lower variability of growth parameters than males.

He takes these observations as evidence of heavier investment in females, which equalizes the energetic expenditure on males and females. This is the wrong conclusion to be drawn from the four observations:

1 The argument that females are equally costly because they have relatively longer wings at fledging, compared to their body size than males does not hold, since absolute, not relative, investment is the currency to be equalized according to Fisher's theory. Absolute investment is smaller in females, as seen from the shorter wings at fledging and the high disparity for the two sexes in all other body measurements. This observation therefore provides no evidence that the smaller sex is as costly as the bigger sex, unless it could be shown that the smaller sex not only completes growth faster but also starts costly thermoregulation earlier than the bigger sex. So far there is no evidence that thermoregulation starts at different ages for the two sexes.
2 Richter takes the fact that females, at fledging, are closer to the adult measurements than males as a proof of heavier investment in females. Fisher's theory is concerned only with the period of parental investment, and for that reason it does not matter at all what the fledging size is with respect to adult size.
3 The observations that females fledge earlier than males is interpreted by Richter as a cost increase, reducing the cost disparity between males and females. Correctly interpreted, earlier fledging of the females reduces their costs to the parents, and this therefore rather increases the disparity between male and female costs.
4 Higher variance in body weights during the

nestling period is associated with the larger sex, the males, in yellow-headed blackbirds (Richter, 1983), common grackles (Howe, 1979), hooded crow (Rofstad, 1986), and with the larger sex, the females, in the sparrowhawk (Moss, 1979). Sex ratio studies on birds have shown no significant deviation from unity at hatching (Clutton-Brock, 1986), and most studies have shown no deviation at fledging (e.g. Selander, 1960; Willson, 1966; Newton & Marquiss, 1979; Richter, 1983; Clutton-Brock, 1986, for a review). Even if the larger sex, say males, show higher variability of the growth parameters, these studies demonstrate that their higher variability in growth does not increase their pre-fledging mortality. These findings are in agreement with Richter's argument of a fledging sex ratio of unity. However, using the energetic requirements of nestlings as the currency for parental expenditure (Richter, 1983), it follows from these studies that, despite the higher variability in growth parameters of males, the cost disparity of producing males and females is still reflected by the ratio given by the energy invested in fledged males divided by the energy invested in fledged females. The cost difference between the sexes will thus increase with increasing sexual dimorphism and it is obvious that variability in growth cannot reduce the disparity in energy requirement of males and females below that expected on the basis of the differential metabolic needs for producing males and females of a given body weight.

Materials and methods

For a comparison of weight gain and tarsus growth of male and female chicks I used either the growth parameters of the logistic model given in the source, or if the parameters were not given, I fitted logistic equations of the form:

$$y = a/(1 + b \times \exp [-kT])$$

to the graphed growth curves of the chicks, using an iterative least squares fitting method. Here, y refers to a body measurement at age T, a represents the asymptote, k the rate constant of the logistic equation and b the constant of integration which translates individuals on a common time scale. The parameter b is not relevant in the context of the present study and is disregarded in the interspecific comparison. Logistic equations of the above form produce curves which are symmetric with respect to the point of inflection (I), $y = a/2$. The instantaneous growth rate at age T is given by differentiation of the original equation:
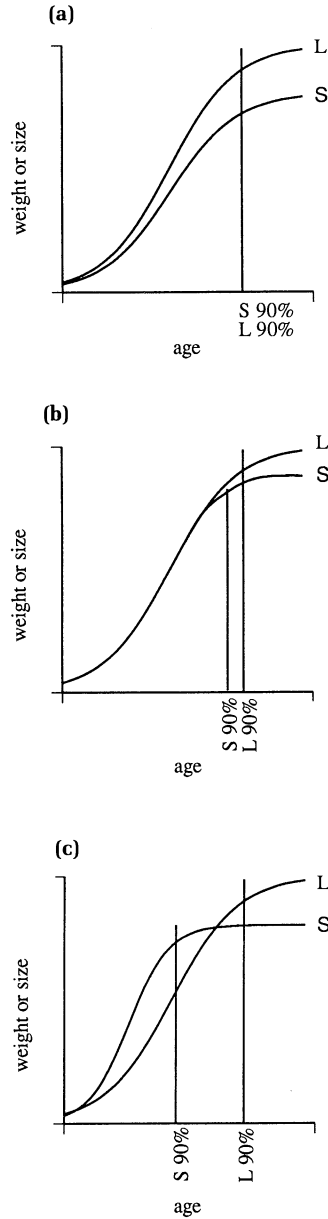
Fig. 1. Hypothetical growth forms of the larger sex (L) *vs* the smaller (S) in sexually dimorphic bird species. g_{max} is the maximum growth rate occurring at the inflection point, and k is the rate constant of the logistic equation. The smaller sex in Fig. 1a shows a lower g_{max} than the larger but k-values are equal in both sexes; in Fig. 1b, g_{max} values are equal but the smaller sex will show a slightly higher k-value; in Fig. 1c, both g_{max} and k are higher in the smaller sex. The vertical lines indicate the age at which 90% of asymptotic size is reached by the smaller (S 90%) and by the larger sex (L 90%).

$$dy/dT = ky(1 - y/a)$$

The maximum growth rate (g_{max}) which occurs at the point of inflection is thus given by:

$$dy/dT = (ka/2)(1 - a/2a)$$

which reduces to:

$$g_{max} = Ka/4$$

A clear distinction should be made between the growth rate and the growth constant k. The growth rate, also referred to as instantaneous growth rate, represents weight increase per unit time, given by differentiation of the logistic equation. It is close to zero at the beginning of chick growth, increases to a maximum (g_{max}) at the inflection point, and approaches zero again at the end of chick growth. The growth constant k is the rate constant of the logistic equation whose units are 1/time. It is proportional to the time span required to grow from hatching size to asymptotic fledging size.

In Fig. 1a the larger sex (L) grows at higher instantaneous growth rates towards a higher asymptote than the smaller sex (S), but the two sexes reach their respective asymptotes at the same time, i.e. g_{max} is lower in the smaller sex but k-values are equal. In Fig. 1b the sexes grow at similar instantaneous rates over a large part of the growth period, then the smaller sex levels off earlier growing towards a lower asymptote. The values of g_{max} are equal but the smaller sex will show a slightly higher k-value. In Fig. 1c the smaller sex shows much higher instantaneous growth rates over a large part of the growth period and reaches its lower final size much earlier than the larger sex. Both g_{max} and k will be higher in the smaller sex.

For a comparison of wing or feather growth of male and female chicks, I have either used the growth parameters of a linear regression model given in the source or, if the parameters were not given, calculated the linear regression coefficient of wing or feather lengths on age during the linear part ($r^2 > 0.95$) of the curve from the given graphs. The logistic model cannot be used since feather growth is incomplete at fledging.

The following species, for which growth data were available separately for males and females, are compared: hooded crow (*Corvus corone cornix*), carrion crow (*Corvus corone corone*), jackdaw (*Corvus monedula*), yellow-headed blackbird (*Xanthocephalus xanthocephalus*), red-winged blackbird (*Agelaius phoeniceus*), boat-tailed grackle (*Quiscalus major*), great-tailed grackle (*Cassidix mexicanus*), house sparrow (*Passer domesticus*), merlin (*Falco columbarius*), american kestrel (*Falco sparverious*), hen harrier (*Circus cyaneus*), sparrowhawk (*Accipiter nisus*), bald eagle (*Haliaeetus leucocephalus*), and golden eagle (*Aquila chrysaetos*).

Results

The dynamics of weight gain of male and female chicks in sexually dimorphic bird species

Sex-specific weight gain of passerines. An interspecific comparison shows that in all passerine species, except the hooded crow, the smaller sex gains weight at a lower rate than the larger sex over the entire growth period, and the two sexes reach the fledging weight at roughly the same time, as indicated by the similar k-values for males and females (Table 1). Only in the hooded crow does the smaller sex reach fledging weight much earlier than the larger sex. For nestling weight gain the curves of all species correspond to Fig. 1a, excluding the hooded crow which follows Fig. 1c. In the hooded crow the instantaneous growth rates of females are higher for more than the first half of the growth period than those of males, then slowing down and crossing the growth curves of males, and females reaching their lower fledging weight much earlier than males.

Sex-specific weight gain of species with reversed sex dimorphism. To investigate further the phenomenon of faster instantaneous growth rates of the smaller sex, I analysed published growth data for birds which exhibit reversed sex dimorphism. These are principally birds of prey of the order Falconiformes (Table 1), ranging in body mass from 250 g in the case of the merlin, to over 4000 g in the bald eagle.

In all five of the investigated species, the males, which are the smaller sex, reach their asymptotic body weight at the same time or faster than the bigger females, as indicated by the growth constant k of males and females. However, in none of these species does the smaller sex grow at a faster instantaneous rate than the bigger sex, as demonstrated by the lower maximum growth rates of the smaller sex. Thus, including the Falconiformes in the comparison, the hooded crow stands out as a unique example showing higher growth rates of the smaller sex over a large part of the growth curve.

Sex-specific tarsus and feather growth

In all species the tarsus of the smaller sex grows at a lower or equal rate than that in the larger sex, except in hooded crows, where the females show higher growth rates of tarsus than males after hatching to the age of 18 days (Table 2). The smaller sex reaches the fledgling tarsus length at roughly the same time as the larger sex, except in hooded crows and sparrowhawks, where fledgling tarsus length is reached considerably earlier by the smaller sex. The growth forms of the tarsus of male and female hooded crows therefore correspond to Fig. 1c, while most other species follow Fig. 1a and the sparrowhawk Fig. 1b (see Table 4).

In all five dimorphic species where feather growth was reported, the feathers of males and females grow at similar rates corresponding to Fig. 1b (Tables 2 and 3), except in the hooded crow, where the feathers of females grow at a faster rate than in males, corresponding to Fig. 1c (Table 4).

A comparison of the growth forms of all species which show sexual weight dimorphism at fledging demonstrates a sexual dimorphism in tarsus and feather length at fledging which is again in favour of the heavier sex. Thus, the strongly positive correlation (Fig. 2) between increasing body weight dimorphism and tarsus length dimorphism ($r = 0.91$), or body weight dimorphism and wing length dimorphism ($r = 0.83$) presents clear evidence against the interpretation that sex-specific growth will equalize the costs of producing males and females. It shows that if species are compared with respect to sexual dimorphism, the sex which is more costly to the parents in terms of production of body mass, is also more costly in terms of bone or feather production.

Maximum growth rates and growth constants with respect to sex dimorphism

A comparison of the sex-specific maximum growth rates among the passerines shows increasing male–female g_{max} ratios with increasing ratios of body size dimorphism (Fig. 3). At the same time the male–female ratios of the growth constant k remain similar over a wide range of body size dimorphisms (Fig. 4). This indicates that despite a strong increase in sexual dimorphism from the house sparrow to the boat-tailed grackle, through increasing growth rate differences with increasing dimorphism, the males reach their higher asymptote in all species at roughly the same time as the females. Only in the hooded crow do the females grow at a much higher instantaneous rate than the males, and hence reach their asymptote much faster than the males. In all other species the smaller sex reaches the asymptote at same time or only marginally earlier than the larger sex.

Nestling periods

The nestling period is considered as the time span from hatching to fledging. In passerines, the

Table 1. Fledging weight (fw) and sex-specific parameters for mass gain of passerines and of birds with reversed sex dimorphism from the order Falconiformes. The logistic model was used to compute the asymptote (a), the growth constant (k) and the maximum growth rate (g_{max}).

		fw	a	k	g_{max}	Source
Hooded crow[1,3]	Male		410	0·217	22·3	Rofstad (1986)
	Female		361	0·268	24·2	
Carrion crow[2]						Richner (1989)
Rural habitat	Male	453	455	0·268	30·5	
	Female	381	397	0·279	27·8	
Urban habitat	Male	397	393	0·230	22·5	
	Female	320	319	0·247	19·7	
Jackdaw	Male	213	208	0·24	12·5	P. Heeb (personal communication)
	Female	196	189	0·26	12·3	
Yellow-headed blackbird[4]	Male	54·0	57·0	0·54	7·7	Willson (1966)
	Female	36·0	40·0	0·54	5·4	
Yellow-headed blackbird[1]	Male	46·6	51·3	0·542	7·0	Richter (1983)
	Female	33·6	35·4	0·535	4·7	
Red-winged blackbird[4]	Male		42·0	0·536	5·6	Williams (1940)
	Female		32·0	0·496	4·0	
Red-winged blackbird[2,5]	Male	42·6	40·8	0·548	5·6	Cronmiller & Thompson (1980)
	Female	33·0	32·0	0·516	4·1	
Red-winged blackbird[2,5]	Male	40	41·4	0·564	5·8	Fiala (1981)
	Female	29	30·5	0·577	4·4	
Boat-tailed grackle[1]	Male	96·2	101·5	0·385	9·8	Bancroft (1984)
	Female	58·6	65·7	0·403	6·6	
Great-tailed grackle[6]	Male	105			7·9	Gotie & Kroll (1973)
	Female	71			4·0	
House sparrow[1]	Male	23·8	24·8	0·443	2·7	Schifferli (1980)
	Female	23·0	23·8	0·425	2·5	
Species with reversed sex dimorphism						
Merlin[1]	Female	250	258	0·312	20·1	Picozzi (1983)
	Male	197	201	0·320	16·1	
American kestrel	Female		138	0·239	8·3	Bird & Clark (1983)
	Male		133	0·250	8·3	
Hen harrier[1]	Female	500	520	0·227	29·5	Picozzi (1980)
	Male	375	379	0·262	24·8	
Sparrowhawk[1]	Female	253	261	0·257	16·8	Newton (1978, 1979)
	Male	163	168	0·253	10·6	Moss (1979)
Golden eagle[2]	Female		3834	0·119	114·1	Collopy (1986)
	Male		3198	0·139	111·1	
Bald eagle[2,7]	Female	5172		0·068	130·0	Bortolotti (1984a)
	Male	4066		0·068	102·0	

[1]Growth parameters calculated from graph.
[2]Growth parameters given in source.
[3]Fledgling weight not known (birds killed at age of 24 days).
[4]Parameters given in Ricklefs (1968).
[5]Fledging weight calculated from graph.
[6]g_{max} equals slope of linear regression model given in source.
[7]Growth parameters calculated by Gompertz equation.

smaller sex fledges 5% earlier (9·7 *vs* 9·2 days) in red-winged blackbirds (Holcomb & Twiest, 1970), and 5% earlier (12·6 *vs* 12·0 days) in yellow-headed blackbirds (Richter, 1983). In raptors, the smaller sex fledges between 7 and 13% earlier than the larger sex in five species reviewed by Newton (1979). Thus, parents continue to invest for a longer time in the already larger sex in all dimor-

Table 2. Fledging size (fs) and sex-specific parameters for tarsus and wing growth of passerines and of birds with reversed sex dimorphism from the order Falconiformes. The logistic model was used to compute the asymptote (a), the growth constant (k) and the maximum growth rate (g_{max}) for tarsus growth. Since feather growth is incomplete at fledging, g_{max} was calculated as the slope from the linear regression of feather length on age.

		fs	a	k	g_{max}	Source
Tarsus length						
Hooded crow[1]	Male	54·5	58·4	0·181	2·6	Rofstad (1986)
	Female	54·5	56·4	0·211	3·0	
Carrion crow						
Rural[23]	Male	70·5	71·5	0·214	3·8	Richner (1989)
	Female	65·5	66·9	0·220	3·7	
Urban	Male	66·0	66·9	0·200	3·3	
	Female	60·2	60·5	0·214	3·2	
Jackdaw	Male	43·2	43·9	0·235	2·6	P. Heeb (personal communication)
	Female	41·6	42·2	0·234	2·5	
Yellow-headed blackbird[1]	Male	36·0	39·3	0·379	3·7	Willson (1966)
	Female	32·0	34·0	0·395	3·5	
Yellow-headed blackbird[1]	Male	33·3				Richter (1983)
	Female	29·1				
Boat-tailed grackle[1]	Male	44·7	49·5	0·302	3·7	Bancroft (1984)
	Female	38·2	41·1	0·325	3·3	
American kestrel	Female		43·6	0·182	2·0	Bird & Clark (1983)
	Male		42·9	0·207	2·2	
Sparrowhawk[1]	Female	69	73	0·171	3·1	Newton (1978, 1979)
	Male	60	61	0·205	3·1	Moss (1979)
Bald eagle	Female	74·0				Bortolotti (1984b)
	Male	71·4				
Wing or feather length						
Hooded crow[1,4,7]	Male	166			7·6	Rofstad (1986)
	Female	159			8·1	
Carrion crow						
Rural[1,5,8]	Male	171			8·8	Richner (1989)
	Female	168			8·8	
Urban	Male	154			7·6	
	Female	152			7·6	
Jackdaw[10]	Male	171			6·3	P. Heeb (personal con
	Female	168			6·3	
Yellow-headed blackbird[1,6]	Male	28·6			3·7	Richter (1983)
	Female	27·7			3·4	
Sparrowhawk[1,9]	Female	62			3·7	Newton (1978, 1979)
	Male	56			3·2	Moss (1979)

[1] Growth parameters calculated from graph.
[2] Growth parameters given in source.
[3] Tarsus length measured as distance between joints bent to a right angle.
[4] Fledgling weight and size not known (birds killed at age of 24 days).
[5] Wing length for carrion crow at age of 24 days to allow comparison with hooded crow.
[6] g_{max} is calculated as the regression coefficient of feather lengths on age (5–10 days).
[7] g_{max} is calculated as the regression coefficient of wing lengths on age (6–24 days).
[8] g_{max} is calculated as the regression coefficient of wing lengths on age (7–23 days).
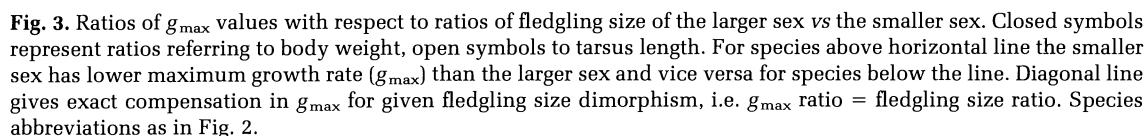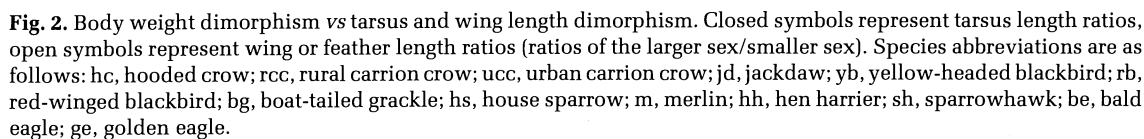[9] g_{max} is calculated as the regression coefficient of feather lengths on age (8–24 days).
[10] Wing length at age of 31 days.

Table 3. Ratios of fledging weights and sizes (fws), k-values and g_{max} values of males/females in passerines and females/males in Falconiformes.

	fws ratio	k-ratio	g_{max} ratio	Source
Body weights				
Hooded crow	1·14	0·81	0·92	Rofstad (1986)
Carrion crow rural	1·19	0·96	1·10	Richner (1989)
Carrion crow urban	1·24	0·93	1·14	Richner (1989)
Jackdaw	1·09	0·93	1·02	P. Heeb (personal communication)
Yellow-headed blackbird	1·50	1·00	1·43	Willson (1966)
Yellow-headed blackbird	1·39	1·01	1·49	Richter (1983)
Red-winged blackbird	1·31	1·08	1·40	Williams (1940)
Red-winged blackbird	1·29	1·06	1·37	Cronmiller & Thompson (1980)
Red-winged blackbird	1·38	0·98	1·34	Fiala (1981)
Boat-tailed grackle	1·64	0·96	1·48	Bancroft (1984)
House sparrow	1·03	1·04	1·08	Schifferli (1980)
Merlin	1·27	0·98	1·25	Picozzi (1983)
American kestrel		0·96	0·99	Bird & Clark (1983)
Hen harrier	1·33	0·87	1·19	Picozzi (1980)
Sparrowhawk	1·55	1·02	1·58	Newton (1978, 1979); Moss (1979)
Golden eagle	1·20	0·86	1·03	Collopy (1986)
Bald eagle	1·27	1·00	1·27	Bortolotti (1984a)
Tarsus lengths				
Hooded crow	1·04	0·86	0·87	Rofstad (1986)
Carrion crow rural	1·08	0·97	1·03	Richner (1989)
Carrion crow urban	1·10	0·94	1·03	Richner (1989)
Jackdaw	1·04	1·00	1·05	P. Heeb (personal communication)
Yellow-headed blackbird	1·13	0·96	1·06	Willson (1966)
Yellow-headed blackbird	1·14			Richter (1983)
Boat-tailed grackle	1·17	0·93	1·12	Bancroft (1984)
American kestrel		0·88	0·89	Bird & Clark (1983)
Sparrowhawk	1·15	0·83	1·00	Newton (1978, 1979); Moss (1979)
Bald eagle	1·04			Bortolotti (1984b)
Feather lengths				
Hooded crow[1]	0·96		0·94	Rofstad (1986)
Carrion crow rural	1·02		1·01	Richner (1989)
Carrion crow urban	1·01		1·00	Richner (1989)
Jackdaw	1·02		1·01	P. Heeb (personal communication)
Yellow-headed blackbird	1·03		1·09	Richter (1983)
Sparrowhawk	1·11		1·16	Newton (1978, 1979); Moss (1979)

[1]Feather length ratio at age of 24 days (birds killed before fledging).

Table 4. Growth of sexually dimorphic birds. Fit with models a, b or c from Fig. 1.

	Body weight	Tarsus length	Wing length	Source
Hooded crow	c	c	c	Rofstad (1986)
Carrion crow	a	a	b	Richner (1989)
Jackdaw	a	a	b	P. Heeb (personal communication)
Yellow-headed blackbird	a	a	b	Willson (1986)
Yellow-headed blackbird	a		b	Richter (1983)
Red-winged blackbird	a			Williams (1940)
Red-winged blackbird	a			Cronmiller & Thompson (1980)
Boat-tailed grackle	a	a	a	Bancroft (1984)
Great-tailed grackle	a			Gotie & Kroll (1973)
Merlin	a			Picozzi (1983)
American kestrel	b	b		Bird & Clark (1983)
Hen harrier	a	a/b	a/b	Picozzi (1980)
Sparrowhawk	a	b	b	Newton (1978)
Golden eagle	a			Collopy (1986)
Bald eagle	a			Bortolotti (1984a)

Fig. 2. Body weight dimorphism *vs* tarsus and wing length dimorphism. Closed symbols represent tarsus length ratios, open symbols represent wing or feather length ratios (ratios of the larger sex/smaller sex). Species abbreviations are as follows: hc, hooded crow; rcc, rural carrion crow; ucc, urban carrion crow; jd, jackdaw; yb, yellow-headed blackbird; rb, red-winged blackbird; bg, boat-tailed grackle; hs, house sparrow; m, merlin; hh, hen harrier; sh, sparrowhawk; be, bald eagle; ge, golden eagle.

Fig. 3. Ratios of g_{max} values with respect to ratios of fledgling size of the larger sex *vs* the smaller sex. Closed symbols represent ratios referring to body weight, open symbols to tarsus length. For species above horizontal line the smaller sex has lower maximum growth rate (g_{max}) than the larger sex and vice versa for species below the line. Diagonal line gives exact compensation in g_{max} for given fledgling size dimorphism, i.e. g_{max} ratio = fledgling size ratio. Species abbreviations as in Fig. 2.

phic species for which nestling periods have been studied in detail. It is clear that continued investment in the larger sex increases its cost and hence the cost disparity between the sexes.

Discussion

Studies on the sex-specific growth of animals have been strongly motivated by Fisher's (1958) sex ratio theory which states that the proportion of the total parental expenditure invested in male and female offspring should be at unity. The theory was later made explicit in mathematical terms (e.g. MacArthur, 1965; Charnov, 1975; Charlesworth,

1977). In sexually dimorphic birds the sex ratio at the end of parental investment is therefore expected to vary inversely to the degree of dimorphism. The absence of a significant deviation from a sex ratio of unity in dimorphic birds prompted Richter (1983) to investigate possible means by which parents distribute expenditures to offspring of the two sexes more equally than that suggested by the differences in their fledging weight. Richter thus challenges the assumption that energetic expenditure on the two sexes is positively correlated with the differential body mass of males and females at fledging. However, all four arguments outlined by Richter fail to show that the sexual differences in
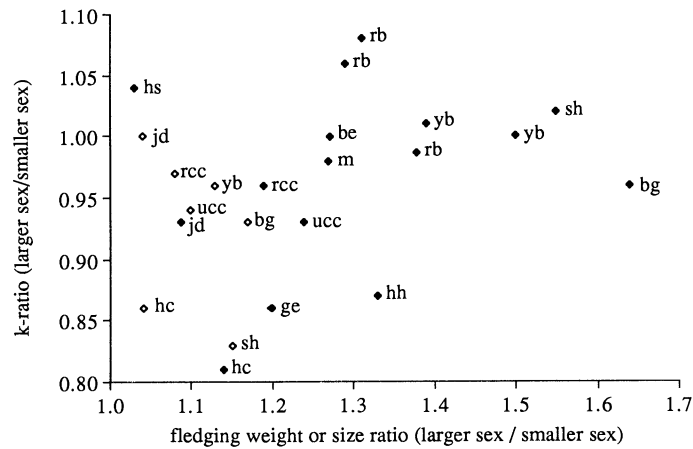
Fig. 4. Ratios of k-values with respect to ratios of fledgling size of the larger sex *vs* the smaller sex. Closed symbols represent ratios referring to body weight, open symbols to tarsus length. Species abbreviations as in Fig. 2.

growth dynamics *per se* could counter the cost difference expected from the disparity in body weight, and hence that they could serve to equalize energetic expenditure on males and females. Richter's (1983) observation of earlier feather development in females led Rofstad (1986) to interpret his observations of faster growth of female hooded crows in the light of the sex-specific growth hypothesis. Rofstad's observation of faster attainment of both fledging weight and size, and higher growth rates in the smaller sex is interesting, but as shown here, it is an exception among all other dimorphic bird species and cannot be used as evidence in support of Fisher's theory, or of Richter's sex-specific growth hypothesis, or for other generalizations concerning sexually dimorphic birds.

Richter (1983) proposes further that females, as a consequence of relatively faster feather growth, may start the energetically costly thermoregulation earlier than males, which would decrease the difference in investment in males and females, but he does not find direct evidence for earlier thermoregulation in females. Feathers are an essential prerequisite for economic thermoregulation and the fact that the smaller sex grows the feathers at the same absolute rate as the larger sex, may in fact indicate that thermoregulation starts at the same time in both sexes. Data of the great-tailed grackle (Gotie & Kroll, 1973) suggest no difference in age of males and females at the onset of endothermy.

The strongest evidence against Richter's sex specific growth hypothesis so far stems from two studies which both show, by using the doubly labelled water technique, that the difference in body size of male and female nestlings corresponds closely to a sexual difference in parental

energy investment (Fiala & Congdon, 1983; Teather & Weatherhead, 1988).

The question of why sexually dimorphic birds show sex ratios of unity remains open. The results of the studies on dimorphic birds invite however an explanation. Under normal rearing conditions the fledging sex ratio is at unity (e.g. Selander, 1960; Willson, 1966; Newton & Marquiss, 1979; Richter, 1983; Clutton-Brock, 1986), whereas under stressed conditions it becomes female biased through higher male mortality (e.g. Holcomb & Twiest, 1970; Howe, 1977; Myers, 1978; Wegge, 1980; Cronmiller & Thompson, 1981; Fiala, 1981; Bancroft, 1984; Roskaft & Slagsvold, 1985; but see Dhondt, 1970). Thus, a sex ratio change can occur under stressful conditions and the energetic investment in males and females can then be equalized by raising a lower number of chicks of the more expensive sex. This may indicate that there is little extra cost in raising both females and the bigger males at equal numbers under plentiful conditions, but there is a cost increase under stressed circumstances. As noted by Fiala (1981), energy investment in the chicks of the current brood may be a poor measure of parental expenditure. In fact, Fisher himself pointed out in his chapter on 'Natural selection and the sex ratio', that 'the influence of selection on the sex ratio may be most exactly examined by the aid of the concept of reproductive value'. He defines reproductive value of an individual of a given age and sex as the present value of their future offspring. However, later in the same chapter he refers to parental expenditure as an expenditure of time, activity and nutriments, and it was not before Williams (1966) that parental expenditure was equated to reproductive value. According to Williams, it can be expected that the

sex ratio would correspond to the male and female cost in terms of their residual reproductive value, defined as the total reproductive value of an individual minus the expenditure on the current brood. The explanation for a sex ratio of unity of fledglings in sexually dimorphic birds is thus that male and female chicks are equally costly in terms of future reproductive success of the parents, and not, as Richter and Rofstad postulate, because of equalized energetic requirements as a consequence of a difference in growth dynamics.

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