Sibling competition and the evolution of growth rates in birds

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Variation among bird species in growth rates is traditionally attributed to differences in energy availability and developmental mode. However, the extent and form of competition among siblings for limited food resources may also be an important determinant. Kin-selection-based models of intrabrood competition suggest that nestling growth rates should be highest in those species in which siblings are likely to be less genetically related to one another (half-sibs rather than full-sibs). We test this novel prediction using the frequency of multiple paternity as an index of average sib relatedness within broods. As predicted, we find a significant positive association between the rate of multiple paternity within broods and nestling growth rates. Furthermore, this holds true when we control for the effects of variation in other factors that may be associated with variation in growth rate, such as body size, brood size, mating system and the form of parental care. We suggest, therefore, that variation in growth rate among bird species is not simply dependent on proximate ecological and developmental factors but is also strongly influenced by interactions, over an evolutionary time-scale, among kin.

Keywords: sibling competition; growth rates; parental investment; brood reduction; kin selection; multiple paternity

1. INTRODUCTION

Different species of birds show very different patterns of growth. As originally noted by O'Connor (1977) and Werschkul & Jackson (1979), traditional attempts to explain such variation have been based around ecological and developmental variables such as the effect of diet on energy availability, or whether the species is altricial or precocial (Starck & Ricklefs 1998a), and have not considered the effect of sibling competition. However, recent models (Parker *et al.* 1989; Mock & Parker 1997; Bonabeau *et al.* 1998) indicate that the extent and form of competition among siblings may be an important determinant of growth rates. The role of sibling competition in explaining the huge variation in growth rates among species remains largely untested. The aim of this paper is to provide such a test.

In bird species where parents deliver food to dependent young there is frequent competition for resources (reviewed in Mock & Parker 1997). Where parental investment is distributed unequally within a brood, competition among siblings may lead to rapid growth rates (Werschkul & Jackson 1979; Ricklefs 1982), with the strength of selection dependent on the frequency with which demand exceeds supply and the relationship between offspring solicitation and parental response (Ricklefs *et al.* 1998). Sibling competition can provide a solution to the problem of optimal partitioning of parental investment under condi-

tions of resource limitation (Bonabeau *et al.* 1998), although the ultimate extent of competition is likely to be constrained by an associated reduction in inclusive fitness (Parker *et al.* 1989; Bonabeau *et al.* 1998).

The average relatedness ($\bar{r}$) (Hamilton 1964) between both parents and offspring and among offspring (full siblings) in sexually reproducing, diploid organisms is about half ($\bar{r}=0.5$). In many bird species (Birkhead & Møller 1993; Petrie & Kempemaers 1998), females may copulate with several males during single breeding attempts, with the consequence being that within a brood offspring may have different fathers (half siblings), and share only genes inherited from the maternal side (i.e. $r=0.25$). However, caution is required when predicting how relatedness between offspring will affect sibling competition (Parker 1985; Lessells & Parker 1999). A distinction has been drawn between intrabrood conflict (Parker 1985) and interbrood conflict (Trivers 1974). With intrabrood conflict, the resources available to a given brood can be considered to be fixed, and so extra acquisition of resources by a given chick reduces the amount available to others in the same brood. Then the magnitude of competition within a brood should reduce with increasing average relatedness of sibs (e.g. Briskie *et al.* 1994). With interbrood conflict, however, where the effect of increased competition is felt only by future sibs, average relatedness should not be used as a predictor of the magnitude of competition. What is then important is whether the fitness of one or both parents is constrained by carrying genes for increased sib selfishness (Parker 1985; Lessells & Parker 1999).

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For present purposes, we anticipate that most of the conflict will be of the intrabrood type, so that selection should therefore favour increased competition in broods of mixed paternity. In scrambles or contests between chicks for food, being bigger than siblings can be of high advantage (e.g. Mock & Parker 1997). This may favour a higher growth rate if faster growth can be traded off against some other trait. For example, Charnov (1993) suggests that the negative relationship between asymptotic body size and growth rate found in some taxa (see also Starck & Ricklefs 1998b) represents a trade-off. We test the hypothesis that sibling competition for resources is a major selection pressure on the evolution of maximal growth rates in birds, using a comparative approach.

2. MATERIAL AND METHODS

Data were collected on 40 bird species (Appendix A). The data set was restricted to species that feed dependent young, with a modal clutch size of at least two eggs. Species with a modal clutch size of only one egg were excluded because chicks in these species have no current brood siblings with which to compete. Data on growth rates were obtained, with one exception (*Miliaria calandra*; Hartley *et al.* 1999), from the extensive data set in Starck & Ricklefs (1998a) who assembled data from the literature and fitted measures of body mass W to the logistic function

$$W = A / (1 + e^{(-K^*(t-t_i))}),$$

in which A is the asymptotic body mass, t_i is the inflection point and K is a constant relating to growth rate. Only estimates of K derived from a logistic growth function were used. Where more than one estimate of K was listed for a species, the maximum value was selected. Maximal, rather than average, growth rate provides a truer reflection of the balance between natural selection for rapid growth and the costs (e.g. loss of inclusive fitness, energetic) or constraints (physiological) associated with faster growth. Maximal growth rate therefore provides a clearer indication of the extent of the response to selection for rapid growth through sib competition for a given species than average growth rate, which is likely to reflect the variation in growth rates within a species associated with different populations and/or environments. We therefore chose maximal values of K for the analysis. However, we also present the analysis using average values of K for comparison.

We tested for associations between growth rate (K) and the extent of sibling conflict over parental investment. We used the extent of extra-bond paternity as a measure of sibling conflict. Only species for which there were estimates of the extent of extra-bond paternity based on DNA fingerprinting evidence were included in the final data set. The frequency of extra-bond paternity was measured as the proportion of all young that were extra bond (EBO) and the proportion of broods in which extra-bond young occurred (EBB). Extra-bond paternity was defined as the frequency of fertilizations as a result of copulations outside the traditional mating-system classification (Owens & Hartley 1998). Where there was more than one estimate for one species of the rate of extra-bond paternity (i.e. data from more than one population) we used the mean value.

We also collected data on the potentially confounding variables of mating system, body mass, brood size, fledging success, parental care, breeding density and nest predation rates.

In a previous analysis, Owens & Hartley (1998) found no association between the rate of extra-bond paternity and mating system. Mating system was scored on a four-point scale (Owens & Hartley 1998): 0, polygamy not recorded or extremely rare (<1% of bonds of either sex); 1, occasional, facultative polygamy (1–5% of bonds of one or both sexes); 2, frequent facultative polygamy (>5% of bonds of one or both sexes, but not obligate); and 3, obligate polygamy in one or both sexes. Body mass is negatively correlated with the growth rate constant, K (Starck & Ricklefs 1998b), so we used female body mass (in grams) in our analysis to control for this effect. Brood size was included as it may have an important effect on the extent of sib competition (Godfray & Parker 1992) and hence on the evolution of sibling growth rates. We therefore accounted for the possible effect of brood size by defining extra-bond paternity in terms of both offspring and broods (see above), in addition to collating data on modal (or mean) clutch size. A measure of fledging success, defined as the proportion of chicks fledged of eggs laid, was also used because there is substantial variation across species in pre-fledging mortality, which affects brood size.

Where broods with mixed paternity occur, males may reduce their parental effort when feeding broods (Petrie & Kempenaers 1998), which could result in greater competition among siblings (Briskie *et al.* 1994) and boost the potential for an increase in growth rate. We accounted for this by incorporating an index of the sex bias in parental brood-provisioning behaviour (Owens & Bennett 1994, 1997; Owens & Hartley 1998): 0, both sexes contribute approximately equal amounts of food; 1, both sexes feed young but frequently, or always, one sex feeds more than does the other; 2, one sex usually feeds the young alone but occasionally the other sex provides some care; and 3, only one sex feeds young.

The extent of either polygamy or extra-bond paternity will be dependent upon, to a certain extent, the availability of suitable opportunities for such behaviour, which may, in turn, be a function of breeding density (e.g. Gowaty & Bridges 1991). Although breeding density estimates could not be found for all species in the data set, where possible we used the maximum number of nests per hectare as an indicator of breeding density. Lack (1968) suggested that nest predation or time-dependent mortality rate could also select for rapid growth (see also Halupka 1998). To assess the importance of nest predation on the evolution of growth rates we collated, where possible, data on nest predation rates, defined as the proportion of nests containing eggs or young subject to losses to predators. In addition to the references listed in Appendix A the data were from Cramp & Simmons (1977, 1980, 1983), Cramp (1985, 1988, 1992), Cramp & Perrins (1993, 1994a,b), Bennett (1986), Marchant & Higgins (1991, 1994), Brunning (1993) and the series on the *Birds of North America* edited by Poole *et al.* (1992, 1993) and Poole & Gill (1993, 1994, 1995, 1996, 1997).

All continuous variables, with the exception of K , which was normally distributed, were subjected to an appropriate transformation to normalize the data before analysis (Zar 1996). Female mass, clutch size and breeding density were log₁₀ transformed, whilst EBO, EBB and nest predation rates were arcsin transformed. We analysed the raw data (i.e. taking species as data points) using Pearson's product moment or Spearman's correlation coefficient to look for associations between K and the independent variables. However, because related species cannot be considered to be statistically independent of one another (Harvey & Pagel 1991), we also used the CAIC software package (Purvis & Rambaut 1995) to generate evolutionarily

independent comparisons or 'contrasts' using the CRUNCH algorithm. The CAIC program calculates, for each node in the phylogeny where there is variation in the dependent variable, the amount and direction of evolutionary change in the corresponding independent variable(s). We used the molecular phylogeny of Sibley & Ahlquist (1990), and assumed multiple branching among genera within families, and among species within genera. Branch lengths were set at equal. Relationships between dependent and independent variables were tested using linear regression, forced through the origin (Harvey & Pagel 1991). A significant correlation between the dependent variable (K) and an independent variable suggests that the evolution of maximal growth rate is associated with that of the other variable (Briskie *et al.* 1994). All models were tested for multicollinearity of independent variables, as substantial collinearity can have a marked effect on the validity of the model (Zar 1996). Estimates of statistical power ($1 - \beta$, where β is the probability of not rejecting the null hypothesis when it is actually false; Cohen 1977) for null results are given where $0.05 < p < 0.30$.

In addition to the above analysis, we used a pairwise comparison to assess the effect of sibling competition on the evolution of growth rates. This method has the advantage that it controls for many potentially confounding variables through comparison of closely related species at the tips of the phylogeny and is less reliant upon the accuracy, or otherwise, of the phylogeny (Møller & Birkhead 1992). We found 11 pairs of closely related species where the relative extent of EBO or EBB could be classified for one of the pair as high and the other as low, and compared their respective growth rates (K) using the Wilcoxon signed-ranks test.

3. RESULTS

Analysis of the raw data indicated that growth rate, K (whether maximal (max) or average (ave) values), was positively associated with the extent of both EBO and EBB (table 1). As expected, female mass was also strongly negatively associated with growth rate (following Starck & Ricklefs 1998b). Of the other independent variables, fledging success, clutch size and mating system were also significantly associated with growth rate (table 1). However, there was no relationship between growth rate and sex bias in food provisioning, breeding density or nest predation (table 1).

Analysis of the independent contrasts generated using CAIC showed broad similarities but subtle differences from the raw (species) data analysis. Simple regression of the contrasts of maximal growth rate, $K_{\max}$, with that of EBO ($r^2 = 0.37$, $p = 0.001$; figure 1a) or EBB ($r^2 = 0.31$, $p = 0.003$; figure 1b) indicated that phylogeny did not confound the relationship between growth rate and multiple paternity. Results of simple regression using average growth rate, K_{ave} , were very similar to that obtained using $K_{\max}$ (K_{ave} versus EBO, $r^2 = 0.40$, $p = 0.001$; K_{ave} versus EBB, $r^2 = 0.32$, $p = 0.003$). A multiple regression (backward) with the growth rate (K) as the dependent variable and EBO, female mass, clutch size, mating system and sex bias in food provisioning as the independent variables, showed that only extra-pair paternity, mating system and female mass were significantly (and independently) related to growth rate (40 species, 25 contrasts; EBO, $K_{\max}$ partial $r = 0.59$, $p = 0.002$, K_{ave} partial $r = 0.52$, $p = 0.009$; mating system, $K_{\max}$ partial

Table 1. Raw data analysis of the relationships between both maximal growth rate ($K_{\max}$) and average growth rate (K_{ave}), extra-bond paternity (EBO, EBB) and seven other independent variables

(Data are Pearson's correlation coefficient, except where indicated. Sample sizes are in parentheses.)

independent variables	$K_{\max}$	K_{ave}	EBO	EBB
EBO	0.46** (40)	0.46** (40)	—	0.92** (40)
EBB	0.53** (40)	0.50** (40)	0.92** (40)	—
mating system (Spearman's)	0.31* (40)	0.35* (40)	0.10 (40)	0.11 (40)
female body mass	-0.82** (40)	-0.83** (40)	-0.39* (40)	-0.51** (40)
clutch size	0.36* (40)	0.33* (40)	0.01 (40)	0.23 (40)
sex bias in parental care (Spearman's)	-0.11 (40)	-0.14 (40)	-0.09 (40)	-0.12 (40)
fledging success	0.38* (29)	0.33 (29)	0.48** (29)	0.51** (29)
density	0.05 (29)	0.09 (29)	0.14 (29)	0.20 (29)
nest predation	0.03 (24)	0.12 (24)	-0.23 (24)	-0.22 (24)

* $p < 0.05$; ** $p < 0.01$.

$r = 0.61$, $p = 0.002$, K_{ave} partial $r = 0.54$, $p = 0.006$; female mass, $K_{\max}$ partial $r = 0.50$, $p = 0.014$, K_{ave} partial $r = -0.51$, $p = 0.012$). Neither sex-bias in food provisioning ($K_{\max}$ partial $r = -0.13$, $p = 0.56$, K_{ave} partial $r = -0.19$, $p = 0.39$), or clutch size ($K_{\max}$ partial $r = -0.03$, $p = 0.88$, K_{ave} partial $r = -0.14$, $p = 0.53$) were related to growth rate. Results using EBB, instead of EBO, in otherwise identical analyses were quantitatively similar.

Incorporation of the term fledging success into a multiple regression of $K_{\max}$ with EBO or EBB, female mass, mating system and fledging success as independent variables resulted in the term fledging success being dropped from the model at the first step (29 species, 19 contrasts; EBO partial $r = 0.12$, $p = 0.64$; EBB partial $r = 0.22$, $p = 0.40$). Despite the reduced sample size, all three remaining variables remained significantly and independently related to growth rate. Conversely, use of average values of K (K_{ave}) instead of $K_{\max}$ resulted in EBO (partial $r = 0.28$, $p = 0.29$, power = 0.16) or EBB (partial $r = 0.39$, $p = 0.12$, power = 0.35) being dropped from the regression. However, the standard errors of the partial regression coefficients of K_{ave} with either EBO or EBB were large due to high covariance between the terms fledging success and EBO or EBB. Removal of the term fledging success from the multiple regression restored EBO or EBB to the model. In contrast, when EBO or EBB was removed from the multiple regression of $K_{\max}$ with female mass, mating system and fledging success, fledging success remained non-significantly related to growth rate. In separate multiple regressions controlling for female mass, mating system and extra-bond paternity, neither density (EBO: 29 species, 21 contrasts; partial

Figure 1. Relationships between contrasts generated using CAIC of $K_{\max}$ and the frequency of (a) extra-bond offspring (EBO) and (b) extra-bond broods (EBB). Data are presented for the simple linear regression of maximal growth rate and extra-bond paternity ($n = 25$ contrasts and 40 species in both cases).

$r = -0.21$, $p = 0.38$; EBB: 29 species, 21 contrasts; partial $r = -0.19$, $p = 0.41$), nor nest predation (female mass removed due to substantial covariation with nest predation rate; 24 species, 18 contrasts; EBO partial $r = -0.05$, $p = 0.84$; 24 species, 18 contrasts; EBB partial $r = 0.02$, $p = 0.93$) were associated with maximal growth rate, whilst the rate of extra-bond paternity remained the most important variable associated with growth rate. Results of similar regressions using K_{ave} rather than $K_{\max}$ did not affect the outcome substantially (all $p > 0.6$).

The pairwise comparisons of closely related species at the tips of the phylogeny indicated that species with higher rates of extra-bond paternity also had higher maximal growth rates (EBO: Wilcoxon $Z = 2.49$, $n = 11$ pairs, $p = 0.013$; EBB: Wilcoxon $Z = 2.76$, $n = 11$, $p = 0.006$; table 2). Species with higher rates of extra-bond paternity also had higher average growth rates, when expressed in terms of broods (EBB: Wilcoxon $Z = 2.22$, $n = 11$, $p = 0.026$), but not when extra-bond paternity was expressed in terms of offspring (EBO: Wilcoxon $Z = 1.51$, $n = 11$, $p = 0.13$). However, the power to detect such a difference was low (0.63) with only 11 pairs.

4. DISCUSSION

The analyses show that there is a positive association between growth rate, K , and the frequency of extra-bond paternity in birds that feed dependent young. Furthermore, the analysis using evolutionarily independent contrasts indicates that this relationship remains highly significant both with and without controlling for the effects of other independent variables that are also associated with K (female mass and mating system).

Our finding that breeding density was not associated with the evolution of maximal (or average) growth rate shows that the relationship between extra-pair paternity and growth rate is not confounded by covariation with this trait. This result is in agreement with the analyses of Westneat & Sherman (1997), who found no across-species correlation between extra-bond paternity and density. Nor was K inversely related to survival rate during the period of development (fledging success), as suggested by Williams (1966). Conversely, there is some empirical support for a positive association between nest predation risk and growth rate (Bosque & Bosque 1995). Our sample sizes were rather low, so it could be argued that nest predation was not associated with maximal growth rate in our analysis as a consequence of low statistical power. However, from our data at least two reasons suggest nest predation is unlikely to be an important selective factor in the evolution of growth rates. Despite the small sample sizes the multiple regression revealed that, while nest predation rate was not significantly associated with K , the frequency of extra-pair paternity (EBO and EBB) remained the most strongly associated of the variables left in the model. In addition, the partial coefficient of nest predation rate was extremely low. We thus concur with the view of Ricklefs *et al.* (1998) that nest predation rate appears not to be a significant factor in the evolutionary diversification of growth rates.

The positive, independent association between growth rate and both extra-bond paternity and mating system was not confounded by a sex bias in food provisioning care, as would be expected if a reduction in male parental care of developing nestlings contributed to this association. However, it is possible that overall parental investment may be reduced as a consequence of sexual conflict (Maynard Smith 1977; Parker 1985). This would intensify competition further, as the amount of food available for growth and development would be reduced.

Although intrabrood competition over divisible parental resources is potentially wasteful of parental investment (e.g. the energy cost of scrambling), sibling competition may maximize parental fitness in unpredictable conditions, as it provides a solution to the problem of which chick to feed if resources are limited (Bonabeau *et al.* 1998). Indeed, in many species of bird, parents preferentially feed the largest, most competitive chicks in a brood (review in Mock & Parker 1997); a characteristic that is exploited by brood parasites. Parasitic brown-headed cowbirds (*Molothrus ater*), for example, use their superior size and competitive ability to sequester the majority of resources when their host species is the considerably smaller yellow warbler (*Dendroica petechia*). However, when the host species is of similar size to that of the parasite (e.g. red-winged blackbirds *Agelaius phoeniceus*),

Table 2. Paired between-species comparisons of the frequency of extra-bond paternity, in terms of offspring (EBO) and broods (EBB), with maximal growth rate ($K_{\max}$) and average growth rate (K_{ave})

(Pairs represent one species with relatively low rates of extra-bond paternity compared with a closely related species with relatively high rates of extra-bond paternity.)

family group	species pair ^a	EBO (%)	EBB (%)	$K_{\max}$	K_{ave}
Falconidae	<i>Falco tinnunculus</i>	1.9	2.7	0.309	0.295
	<i>Falco sparverius</i>	11.2	10.0	0.350	0.292
Muscicapidae	<i>Sialia sialis</i> ^b	8.4	24.0	0.484	0.484
	<i>Turdus grayi</i> ^c	38.0	53.0	0.475	0.441
	<i>Erethacus rubecula</i>	4.0	12.5	0.450	0.429
	<i>Oenanthe oenanthe</i>	11.0	29.0	0.502	0.481
Paridae	<i>Parus montanus</i>	0.9	4.2	0.406	0.406
	<i>Parus atricapillus</i>	17.0	37.5	0.480	0.480
	<i>Parus caeruleus</i>	8.5	29.8	0.430	0.402
	<i>Parus major</i>	15.0	50.0	0.480	0.392
Hirundinidae	<i>Delichon urbica</i>	16.8	33.5	0.377	0.335
	<i>Progne subis</i>	21.4	37.2	0.384	0.384
	<i>Hirundo pyrrhonota</i> ^d	2.0	—	0.573	0.558
	<i>Hirundo rustica</i>	26.1	50.8	0.550	0.485
	<i>Tachycineta albilinea</i> ^c	—	26.0	0.406	0.406
	<i>Tachycineta bicolor</i>	60.0	77.7	0.492	0.460
Sylviidae	<i>Phylloscopus sibilatrix</i>	0.0	0.0	0.532	0.532
	<i>Phylloscopus trochilus</i>	14.0	29.0	0.574	0.574
Corvidae	<i>Corvus monedula</i>	0.0	0.0	0.284	0.261
	<i>Pica pica</i>	5.0	13.8	0.332	0.284
Emberizidae	<i>Cardinalis cardinalis</i>	14.0	16.0	0.516	0.516
	<i>Spizella pusilla</i>	18.0	29.0	0.656	0.621
	<i>Miliaria calandra</i>	0.0	0.0	0.504	0.490
	<i>Zonotrichia leucophrys</i>	14.0	26.0	0.639	0.576

^a References for extra-bond paternity data not found in Appendix A.

^b Meek *et al.* (1994).

^c Stutchbury 1998.

^d Brown & Brown 1988.

cowbird chicks are unable to regularly outcompete host chicks (Lichtenstein & Sealy 1998). We note that, while both yellow warblers and red-winged blackbirds have high rates of extra-bond paternity, yellow warblers have relatively low growth rates (fast growth would not enhance survival prospects in competition with the larger cowbird parasite) while red-winged blackbirds have relatively high growth rates. Thus, under unequal parental resource allocation, the largest, most competitive chick (whether parasite or not) is likely to sequester the majority of available resources and is more likely to survive if resources are limited.

Parker *et al.* (1989) modelled the effects of relatedness in moderating intrabrood sib selfishness over acquisition of unequally distributed parental resources as either a strict hierarchy (contest), where stronger siblings have priority of access to resources, or a begging scramble for resources, where stronger siblings are more effective at gaining food (see also Mock & Parker 1997; Mock *et al.* 1998). With two chicks the hierarchical model predicts that, with full siblings (i.e. $r=0.5$), the stronger sibling should increase its resource share until its marginal gain in fitness reduces to equal half that of the weaker sibling. For broods of greater than two the difference in resource share between two consecutive chicks in the hierarchy will increase down the hierarchy so that the greatest difference in fitness exists between the bottom two chicks. In the begging scramble model, stronger siblings will always have greater net

fitness, even though, counter-intuitively, the asymmetry in begging effort between chicks increases as the amount of available resources increases. Both types of model predict that fitness differences among chicks will be most exaggerated when food is scarce (Parker *et al.* 1989). Competition for food will lead to weight differentiation within the brood if there is a positive feedback such that increasing size asymmetry results in larger individuals taking a greater share of available food (Bonabeau *et al.* 1998). In fact, if the asymmetry in competitive ability is sufficiently great the predictions from the scramble model converge towards that of the hierarchy model so that stronger siblings have almost complete control over food shares (Parker *et al.* 1989; Mock *et al.* 1998).

The effect of a reduction in average intrabrood relatedness as a consequence of increased extra-bond paternity is to lower the inclusive fitness costs of increased competition. Brood reduction is a common outcome when resources are limited (Magrath 1990; Stoleson & Beissinger 1995), and a reduction in inclusive fitness costs as above will also increase the threshold at which brood reduction is expected to occur (O'Connor 1978). Even though in many species competitive asymmetries within broods are primarily determined by hatching asynchrony rather than growth rate *per se*, growth rate differences maintain the resulting competitive asymmetries. In addition, as EBO rate increases, the probability that the strongest chick is also an extra-bond chick increases. In this situation, in

contrast to the situation with full siblings, the strongest chick should increase its resource share until its marginal gain in fitness reduces to a quarter of that of its (half) sibling(s). This represents an indirect effect of reduced intrabrood relatedness on growth rates. It is also possible that the direct presence of just one extra-bond chick within a brood may be enough to stimulate extra competition as a consequence of a reduction in inclusive fitness benefits. So, given the apparent benefits to survival of rapid growth why do chicks of all species not grow at the maximum possible rate?

Ultimately, the upper limit on growth rates will be set by internal, physiological constraints (Stearns 1992; Ricklefs *et al.* 1998). The fact that growth rates are apparently maintained well below their physiological capacity (Sibly & Calow 1986) suggests that there may be trade-offs operating between growth rates and other life-history traits (Charnov 1993), and that very high growth rates carry a cost (Gotthard *et al.* 1994). For example, there may be adaptive variation in growth rates if there is a negative physiological trade-off between high growth rate and survivorship under certain environmental conditions (Sibly & Calow 1986). That such a trade-off may exist has been most convincingly demonstrated in insects (e.g. Gotthard *et al.* 1994; Blanckenhorn 1998) and reptiles (e.g. Forsman & Lindell 1991; Sorci *et al.* 1996), but some evidence also exists for birds (Griffiths 1992). The potential costs associated with an increase in growth rate in birds are likely to vary between species depending on their life-history characteristics. Furthermore, as Clarke (1998) points out, there is little evidence to support the contention that individuals that develop faster also survive longer or produce more viable offspring than slower growing individuals.

Slow growth would be beneficial to the survival prospects of both parents and offspring if food availability is limited and time-dependent mortality rates are not

prohibitively high (Schew & Ricklefs 1998). However, sibling competition for limited parental resources may preclude this option. For example, chicks in species with a clutch size of one, such as the Atlantic puffin *Fratercula arctica*, redirect resources away from all characters except those essential for maintenance and survival during periods of food shortage (Øyan & Anker-Nilssen 1996). In contrast, chicks of species with a brood size of two or more preferentially divert resources to components of growth most useful in competing with their siblings if resources are limiting (e.g. marsh tits, *Parus palustris*; Nilsson & Svensson 1996; see also O'Connor 1977).

The data presented here suggest that increased skew in the distribution of parental resources to chicks, arising as a consequence of increased sibling competition through reduced intrabrood relatedness, has a positive effect on chick growth rates. The effects on life-history characteristics of species may be substantial. However, if there is no intrabrood sibling competition, then growth rates should not be affected by the degree of extra-bond paternity. In birds, intrabrood competition is absent if: (i) offspring are produced singly; (ii) parental allocation of resources is always equitable among chicks within a brood; or (iii) as in precocial species, parents do not feed divisible resources to offspring. There is a lack of empirical data on parental feeding 'decisions' but (ii) is, nevertheless, biologically rather unlikely. Failure to demonstrate the negative growth rate–extra-bond progeny relationship in (i) and (iii) would represent an appropriately contrasting support for the hypothesis. At present there is insufficient information available to make this comparison.

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APPENDIX A. SPECIES-SPECIFIC DATA USED IN THE MAIN COMPARATIVE ANALYSIS

species	$K_{\max}$	K_{ave}	EBO	EBB	MS ^a	FM ^b	CS ^c	NP ^d	FS ^e	Den ^f	PB ^g	rel ^h
<i>Accipiter gentilis</i>	0.232	0.232	1.3	2.6	0	1137.0	3.5	—	—	0.03	2	1
<i>Acrocephalus arundinaceus</i>	0.529	0.529	3.1	5.4	2	28.4	5	—	42	75	0	2
<i>Agelaius phoeniceus</i>	0.598	0.556	23.7	41.0	3	41.5	4	—	—	—	3	3
			28.0	47.0								4
			35.0	55.0								5
			25.1	38.5								6
<i>Anthus spinoletta</i>	0.528	0.518	5.2	12.4	1	19.2	5.5	39	67	5	0	7
<i>Cardinalis cardinalis</i>	0.516	0.516	14.0	16.0	0	43.9	3.5	—	—	—	2	8
<i>Catharacta lonnbergi</i>	0.185	0.158	0.0	0.0	2	1735.0	2	—	54	4	1	9
<i>Columba livia</i>	0.220	0.220	0.0	0.0	0	305.0	2	19	47	200	0	10
<i>Coragyps atratus</i>	0.109	0.102	0.0	0.0	0	1828.7	2	—	—	—	0	11, 12, 13
<i>Corvus monedula</i>	0.284	0.261	0.0	0.0	1	243.0	5	24	26	50	1	14
<i>Delichon urbica</i>	0.377	0.335	14.5	32.0	0	19.7	3.5	10	55	6.4	0	15
			19.0	35.0								16
<i>Dendroica petechia</i>	0.408	0.408	37.0	59.0	0	9.2	4.5	—	—	—	1	17
<i>Erithacus rubecula</i>	0.450	0.429	4.0	12.5	0	19.9	5	22	55	170	1	18
<i>Falco columbarius</i>	0.319	0.260	0.0	0.0	0	212.0	4	13	57	0.001	2	19
<i>Falco sparverius</i>	0.350	0.292	11.2	10.0	0	137.4	5	—	67	—	2	20, 13

(Cont.)

Appendix A (Cont.)

species	$K_{\max}$	K_{ave}	EBO	EBB	MS ^a	FM ^b	CS ^c	NP ^d	FS ^e	Den ^f	PB ^g	ref ^h
<i>Falco tinnunculus</i>	0.309	0.295	1.9	2.7	1	193.0	4.7	23	52	10	2	21
<i>Ficedula hypoleuca</i>	0.536	0.508	4.0	15.0	2	13.0	7.5	12	44	30	0	22
			24.0	43.0								23
<i>Hirundo rustica</i>	0.550	0.485	22.2	45.5	0	18.6	4.5	9	72	8	1	24
			30.0	56.0								25
<i>Lanius collurio</i>	0.459	0.453	5.2	16.6	1	31.7	5	34	83	—	2	26
<i>Larus occidentalis</i>	0.154	0.154	0.0	0.0	0	800.0	3	20	45	600	0	27
<i>Miliaria calandra</i>	0.504	0.490	0.0	0.0	2	39.6	4	10	50	35	2	28, 29
<i>Oenanthe oenanthe</i>	0.502	0.481	11.0	29.0	0	22.4	6.1	28	72	42	1	30
<i>Otus asio</i>	0.264	0.264	0.0	0.0	1	120.0	4	50	32	—	1	31
<i>Parus atricapillus</i>	0.480	0.480	17.0	37.5	1	11.4	7	—	—	17	0	32
<i>Parus caeruleus</i>	0.430	0.402	11.0	31.0	2	11.4	9.5	35	61	140	0	33
			6.0	28.6								34
<i>Parus major</i>	0.480	0.392	15.0	50.0	0	17.9	11	23	54	30	1	34
<i>Parus montanus</i>	0.406	0.406	0.9	4.2	0	11.7	7.7	41	71	1	0	35
<i>Passer domesticus</i>	0.443	0.420	14.0	26.1	2	28.5	4.5	6	53	500	0	36
<i>Phalacrocorax aristolelis</i>	0.190	0.171	18.0	20.0	1	1598.0	3	28	62	500	0	37
<i>Phylloscopus sibilatrix</i>	0.532	0.532	0.0	0.0	2	8.9	6	47	50	24	0	38
<i>Phylloscopus trochilus</i>	0.574	0.574	0.0	0.0	1	9.1	6.5	38	56	200	0	38
			28.0	58.0								39
<i>Pica pica</i>	0.332	0.284	5.0	13.8	0	181.5	6.5	20	—	3	1	40
<i>Progne subis</i>	0.384	0.384	23.9	50.0	1	54.5	4.5	—	39	—	1	41, 42
			18.8	24.4								42, 43
<i>Setophaga ruticilla</i>	0.680	0.680	40.0	59.0	2	8.1	4	—	—	14	0	44
<i>Spizella pusilla</i>	0.656	0.621	18.0	29.0	0	11.0	4	51	—	3	0	45
<i>Sturnus vulgaris</i>	0.446	0.409	9.7	28.6	2	76.0	5.5	—	71	200	1	46
			8.7	31.8								47
<i>Tachycineta bicolor</i>	0.492	0.460	51.5	71.4	2	20.7	5	—	83	—	1	48
			68.5	84.0								49, 50
<i>Taeniopygia guttata</i>	0.255	0.255	2.4	8.0	0	11.7	5	66	42	36	1	51, 52
<i>Troglodytes aedon</i>	0.464	0.464	7.4	26.0	2	11.2	7	—	67	—	0	53
			10.2	28.0								53
<i>Vireo olivaceus</i>	0.536	0.536	58.0	57.0	0	15.0	4	—	—	—	0	54
<i>Zonotrichia leucophrys</i>	0.639	0.576	14.0	26.0	1	20.7	4	—	—	10	1	55

^a Mating system; ^b female mass; ^c clutch size; ^d nest predation; ^e fledging success; ^f breeding density; ^g sex-bias in parental feeding of young; ^h references for data on extra-bond paternity and on the other variables when data source not as per list in methods: 1 Gavin *et al.* 1998; 2 Hasselquist *et al.* 1995; 3 Westneat 1993; 4 Gibbs *et al.* 1990; 5 Grey 1996; 6 Westneat 1995; 7 Reyer *et al.* 1997; 8 Richison *et al.* 1994; 9 Millar *et al.* 1994; 10 Lovell-Mansbridge 1995; 11 Decker *et al.* 1993; 12 Wilbur & Jackson 1983; 13 Newton 1979; 14 I. Henderson, personal communication; 15 Riley *et al.* 1995; 16 Whittingham & Lifjeld 1995; 17 Yezerinac *et al.* 1996; 18 J. Tobias and I. Hartley, personal communication; 19 Warkentin *et al.* 1994; 20 Villaroel *et al.* 1998; 21 Korpimäki *et al.* 1996; 22 Lifjeld *et al.* 1991; 23 Gelter & Tegelstrom 1992; 24 Smith *et al.* 1991; 25 Primmer *et al.* 1995; 26 Fornasari *et al.* 1994; 27 Gilbert *et al.* 1998; 28 Hartley *et al.* 1993; 29 Hartley *et al.* 1999; 30 Currie *et al.* 1998; 31 Lawless *et al.* 1997; 32 Otter *et al.* 1994; 33 Kempnaers *et al.* 1992; 34 Gullberg *et al.* 1992; 35 Orell *et al.* 1997; 36 Wetton & Parkin 1991; 37 Graves *et al.* 1992; 38 Gyllenstein *et al.* 1990; 39 Fridolfsson *et al.* 1997; 40 Parrott 1995; 41 Morton *et al.* 1990; 42 Allen & Nice 1952; 43 Wagner *et al.* 1996; 44 Perreault *et al.* 1997; 45 Petter *et al.* 1990; 46 Pinxten *et al.* 1993; 47 Smith & von Schantz 1993; 48 Lifjeld *et al.* 1993; 49 Dunn & Robertson 1993; 50 Dunn *et al.* 1994; 51 Birkhead *et al.* 1990; 52 Zann 1996; 53 Soukup & Thompson 1997; 54 Morton *et al.* 1998; 55 Sherman & Morton 1988.

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