WHY DO SOME SIBLINGS ATTACK EACH OTHER? COMPARATIVE ANALYSIS OF AGGRESSION IN AVIAN BROODS

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In many parentally fed species, siblings compete for food not only by begging and scrambling, but also by violently attacking each other. This aggressive competition has mostly been studied in birds, where it is often combined with dominance subordination, aggressive intimidation, and siblicide. Previous experimental and theoretical studies proposed several life-history, morphological, and behavioral variables that may facilitate the evolution of broodmate aggression, and explain its taxonomic distribution. Here we apply phylogenetic comparative analyses for the first time to test the influence of five hypothesized facilitators of the evolution of broodmate aggression, analyzing 69 species in seven avian families using two quantitative measures of aggression: incidence and intensity. We show that incidence and intensity of aggression increase with long nestling periods and indirect feeding, and small brood size is associated with intense aggression. Large food parcels were not correlated with either the incidence or intensity of aggression. Our study suggests that indirect feeding, long nestling periods, and small broods, possibly in combination with other factors, have tended to favor the evolution of aggressive broodmate competition.

KEY WORDS: Brood size, feeding method, feeding rate, length of nestling period, phylogenetic generalized least squares, sibling aggression.

A keystone principle of Darwin's (1859) theory of evolution by natural selection is that individuals compete for limited resources. Such a rivalry is not restricted to unrelated individuals (Hamilton 1964), and in species as diverse as insects, mammals, and birds, siblings compete for limited parental investment, sometimes even killing opponents and reducing the reproductive success of parents (review in Mock and Parker 1997). Sibling competition has been most studied in birds, which present striking variation in the means by which chicks compete for parental investment. In the majority of species, competition is nonviolent, involving begging displays

and scrambling (Wright and Leonard 2002), but in diverse avian species sibling competition also involves violent attacks (aggressive competition) often combined with dominance subordination, aggressive intimidation, and siblicide (Drummond 2006).

In species with altricial young and aggressive competition, hatching asynchrony confers an age and size advantage to elder broodmates, who establish dominance early in the nestling period through pecking and biting (Drummond et al. 1986). Dominance allows senior chicks to distort the pattern of relative begging and gain feeding priority (Drummond 2002). For instance, in great egrets (*Casmerodius albus*, Mock and Parker 1997), blue-footed boobies (*Sula nebouxii*, Drummond et al. 1986), black eagles (*Aquila verreauxi*, Gargett 1980), and laughing kookaburras (*Dacelo novaeguineae*, Legge 2000) junior chicks have a

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higher mortality rate than their siblings, due directly (through lesions) or indirectly (forced starvation or expulsion from the nest) to sibling aggression (Mock and Parker 1997; Drummond 2001b). Compared to begging and scrambling, aggression is an especially effective way for elder chicks to control access to food and ensure their own survival and good condition (Drummond 2002).

Why then, do senior chicks of many species limit themselves to begging and scrambling rather than attacking broodmates? Numerous observational and experimental studies involving a diversity of species have analyzed the proximate causes of aggressive competition (e.g., Gargett 1967; Mock 1984; Evans 1996; Drummond and Canales 1998; Machmer and Ydenberg 1998; Legge 2000), yet surprisingly few studies have attempted to identify the ultimate factors favoring the evolution of this behavior (but see Mock 1985; Mock et al. 1987a; Simmons 1988).

Eight traits have been proposed as having facilitated the evolution of aggressive competition: feeding method (monopolizability of food), effective weaponry (pointed or sharp beaks), limited escape possibilities (nest site topography), and differences in age and size of broodmates (hatching asynchrony; Mock et al. 1990); in addition, Drummond (2002) suggested large food parcel size, small brood size, aggressive potential (maturity and body size), and slow food transfer. Here we test four of these hypotheses chosen for their amenability to quantitative analysis, and we propose and test an additional facilitator of the evolution of aggressive competition. First, according to the feeding method hypothesis (also "prey size hypothesis," Mock 1985), selection favors broodmate aggression in species in which food passes directly from the adult's beak to the chick's beak (direct feeding), allowing dominants to violently exclude competitors. When food is deposited on the nest floor (indirect feeding) and is accessible to all broodmates, aggression is less effective for monopolizing it than seizing mouthfuls and ingesting them quickly (Mock 1985; Mock and Parker 1997). Many species show a transition in feeding method as sensory and motor capabilities of chicks develop, for example, from indirect to direct feeding in herons and pelicans, and from direct to indirect feeding in eagles. The feeding method hypothesis predicts greater use of aggression in species in which direct feeding predominates throughout the nestling period. The feeding method hypothesis is supported by descriptive and experimental field studies (Mock 1984, 1985; Mock et al. 1987a,b; but see Drummond 2001a, 2002).

Second, the size of food parcels fed to chicks could affect the profitability of aggressive competition. According to the food parcel size hypothesis, because aggression is likely to be costlier than mere begging and scrambling, for it to yield a net benefit the food reward for the aggressor has to be high (Drummond 2002). In aggressive species parental food parcels appear to be large and infrequent, and clustered in bouts or meals, resulting in a sizeable payoff for the aggression of dominant chicks (whether they receive food directly or indirectly). Third, brood size probably affects the efficiency of aggression. As brood size increases it may become more difficult and costly to enforce feeding priority by intimidating broodmates and to establish and maintain dominance-subordination relationships (Drummond 2002). Chicks with several broodmates may compete more efficiently by begging and scrambling for parental food deliveries than by trying to intimidate or attack all of them (brood size hypothesis). Fourth, the aggressive potential of altricial nestlings probably emerges during their physical and behavioral development, and may depend less on the particular weaponry of the species than on body size (nestling body size hypothesis, Drummond 2002). According to Vogel (1988), striking opponents is a prerogative of large creatures because only they can confer sufficient momentum to the "projectile" to inflict damage. Small nestlings may be unable to compete aggressively simply because their small head (the projectile) and weak neck muscles (which determine the projectile's speed) make them unable to deliver aversive stimuli or inflict damage.

In addition to these four hypotheses, we suggest long nestling periods should favor aggressive competition because the substantial early investment involved in establishing dominance (e.g., Drummond and Osorno 1992) is more likely to be adequately compensated when broodmates cohabit and compete for parentally provided food for a long period. Long nestling periods give more opportunity for serious food scarcity to arise (nestling period hypothesis).

We use phylogenetic comparative analyses (Martins and Hansen 1997; Freckleton et al. 2002; Blomberg et al. 2003) to test the influence of these five hypothetical facilitators of the evolution of aggressive broodmate competition. Using a maximum-likelihood-based method, we analyze the correlations between two measures of aggressive competition and the five variables: feeding method, food parcel size, brood size, nestling body size at hatching, and length of nestling period.

Methods

DATA AND PHYLOGENY

We included seven avian families for which sibling aggression has been reported in at least one species, and for which a detailed phylogeny is available: Accipitridae (eagles, hawks, and buzzards), Sulidae (boobies), Anhingidae (anhingas), Threskiornithidae (ibises and spoonbills), Ardeidae (egrets and herons), Pelecanidae (pelicans), and Alcedinidae (kingfishers). Only species with brood sizes larger than one were included.

Data on morphometrics (egg size), life history (clutch size, length of nestling period), and behavior (feeding method, feeding rate, incidence of aggression, and intensity of aggression) were collected from primary publications and reference books (see

online Supplementary Appendix S1). Brood size at hatching was available for only 19 of the 69 species, so we used modal clutch size as a proxy variable. Brood size and clutch size were highly correlated in those species for which we had data for both variables ($r_S = 0.832$, $P < 0.001$, $n = 19$ species). We used egg size (egg length × egg breadth) as a proxy for nestling body size at hatching, because data on chick mass were not widely available. Egg size and chick mass at hatching were highly correlated in those species for which we had data for both variables ($r_S = 0.946$, $P < 0.001$, $n = 25$ species). Feeding method was a continuous variable expressed as the proportion of nestling period (from hatching until fledging) during which feeding is direct, ranging from 0 (indirect feeding throughout the nestling period) to 1 (direct feeding throughout the nestling period). For species with a developmental transition in feeding method, we calculated the proportion on the basis of the average age at which chicks switched from one method to the other. Feeding rate was a proxy for food parcel size, based on the assumption that as the number of meals per day decreases the amount of food per meal will increase and so will parcel size. We did not adjust feeding rate for brood size because the important value, for the evolution of aggression, is the potential payoff for the aggressor, not the expected food amount for the average brood member. Feeding rate was also a continuous variable, calculated as the average daily number of feeding bouts per brood (of average size) divided by the average day length (in hours). Feeding rate varies over the nestling period, so we only used data from studies in which observations included the early nestling period, when feeding rates are generally highest (e.g., Fujioka 1985; Drummond et al. 1986) and aggressive competition typically takes place. Average length of the nestling period (days between hatching and fledging) was $\log_{10}$ transformed.

We used two response variables: incidence and intensity of broodmate aggression. Incidence of aggression was the percentage of broods in which aggression was reported: 0 for no broods, 1 for 1–49% of broods, 2 for 50–99% of broods, and 3 for 100% of broods. Intensity of aggression was scored on a 4-point scale by five judges independently, on the basis of qualitative and quantitative descriptions of broodmate aggression in the primary literature: 0 for no aggression observed in any brood, 1 for few fights or few pecks per fight, 2 for an intermediate number of fights or pecks, and 3 for common and/or long fights. The judges were blind in regard to species identity. Scores of the five judges were highly consistent as shown by the pairwise correlations between their scores (r_S range = 0.71–0.88, all P values < 0.0001). We used the median of the five judges' scores for each species. The incidence and intensity of broodmate aggression often vary with offspring age (Drummond 2006), but all descriptions of aggressive competition were from studies that included the early nestling period, when most aggression typically takes place. We carried out an extensive search for behavioral studies of the nestling period of

each species using primary journals, ornithological books, and the reprint collection of the Edward Grey Institute's Library at the University of Oxford, and included only species for which a minimum of three broods were observed during at least 5 h per brood.

Exploratory analyses showed that egg sizes and lengths of nestling period were highly correlated ($r_S = 0.809$, $P < 0.001$, $n = 68$). To avoid colinearity we excluded one of these variables (egg size). Further analyses (not reported) showed that, when length of nestling period was replaced in the model by egg size, egg size was not correlated with either of our dependent variables.

We constructed a composite phylogeny for the seven families using the most recent and detailed molecular phylogenies available (Fig. 1). For the Anhingidae, Ardeidae, Threskiornithidae, Pelecanidae, and Alcedinidae, we used Sibley and Ahlquist (1990); for Accipitridae, Wink and Sauer-Gürth (2000) and Lerner and Mindell (2005); for *Buteo*, Riesing et al. (2003); and for Sulidae, Friesen and Anderson (1997).

COMPARATIVE ANALYSES

To control for the phylogenetic relationships among species we used phylogenetic generalized least squares regression (PGLS; Martins and Hansen 1997; Székely et al. 2004), as implemented by COMPARE 4.6b (Martins 2004). PGLS is a linear regression model in which phylogenetic information is incorporated into the error term, thus controlling for the shared evolutionary history among species (Harvey and Pagel 1991; Martins and Hansen 1997). PGLS introduces a single term (alpha; estimated range: 0–15.5) into the model, which estimates the magnitude of the evolutionary constraint acting on a phenotype (e.g., due to stabilizing selection). Unlike Felsenstein's (1985) phylogenetic independent contrasts (PIC), PGLS does not assume that evolutionary changes follow Brownian motion (Martins and Hansen 1997). For our analyses we set branch lengths to unit values, because we used a composite phylogeny of various sources. Note that the alpha parameter stretches or shrinks branch lengths to fit data at a given phylogeny (Martins and Hansen 1997; Diniz-Filho and Mundim Tôrres 2002; Martins et al. 2002). Zero alpha would indicate unconstrained evolution similar to Brownian motion, thus a PGLS analysis with alpha = 0 is tantamount to an analysis undertaken with PIC. An alpha >> 0 (exact value not provided by COMPARE) indicates that there is no phylogenetic signal in the data (star phylogeny). We refrained from using PICs, because our data did not follow Brownian motion (range of alpha = 2.19–15.5; see Tables 1 and 2); although values of alpha indicated some phylogenetic component in our variables (Blomberg et al. 2003).

We constructed four PGLS models; two models each for incidence and intensity of aggression. Feeding rate was poorly documented in the avian literature (22 species had a missing value), and because COMPARE cannot deal with missing data we
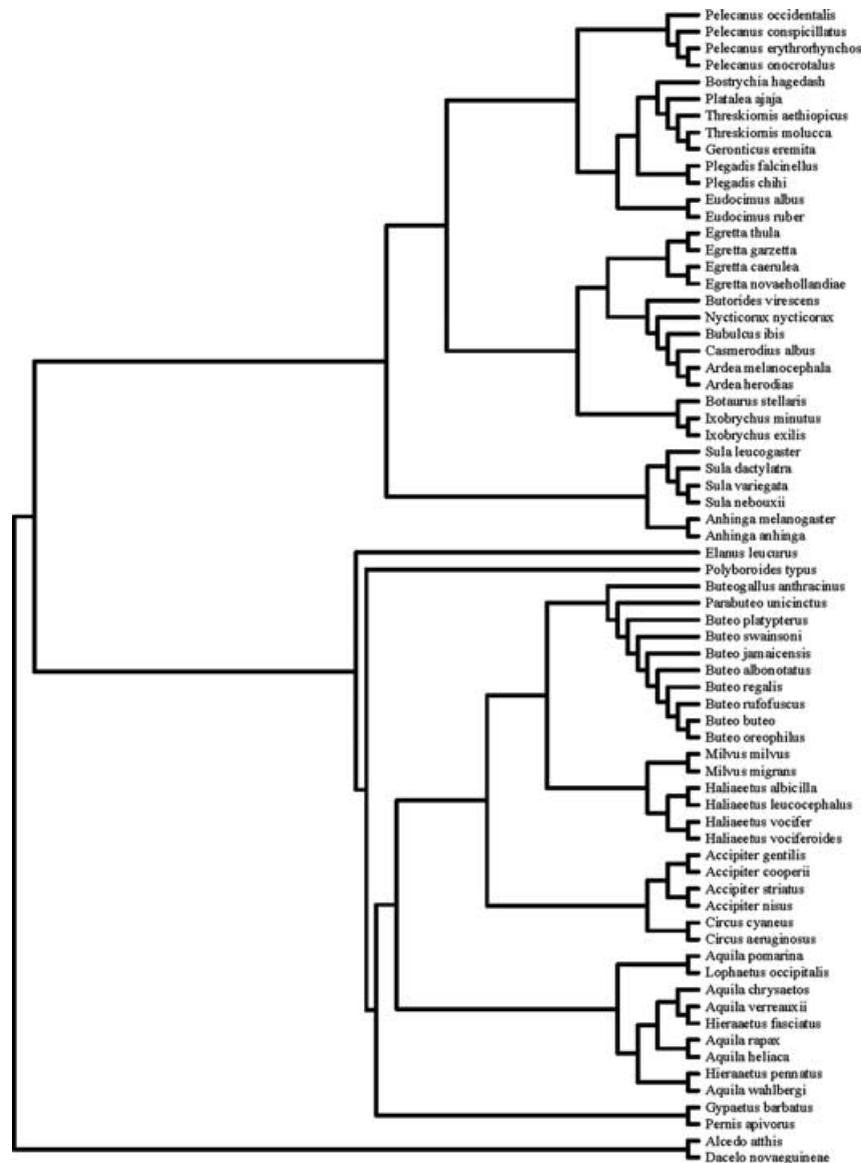
Figure 1. Composite phylogeny of 69 species (seven avian families) used in the comparative analyses.

created two datasets. The first dataset included 47 species for which we had data on feeding rates. This dataset included all independent variables. The second dataset included all 69 species and did not include feeding rate. Models 1 and 3 were constructed using the reduced (47 species) dataset, whereas models 2 and 4 were constructed using the complete dataset.

COMPARE does not calculate the probability of a given partial regression slope (b) so we calculated the corresponding t value by dividing the regression slope by its standard error (E. Martins, pers. com.), and obtained the P value using two tailed t-distribution with appropriate degrees of freedom (df = n – number of parameters in the model). We report the percentage of variance explained by the model, and the P values of partial regression coefficients. Note that for visualization purposes, we plot the species-level data

in figures, and present the bivariate correlation results as calculated by PGLS.

Results
INCIDENCE OF AGGRESSION

Model 1 explained 27.18% of the variance (Table 1) and showed that the incidence of aggression decreased with the proportion of direct feeds ($P = 0.006$), contrary to the feeding method hypothesis, and increased with length of nestling period ($P = 0.022$; Fig. 2A), as predicted by the nestling period hypothesis. Furthermore, the incidence of aggression was unrelated to either feeding rate or brood size (Table 1).

The results of model 2 (19.53% of variance explained) are consistent with those of model 1: the incidence of aggression

Table 1. Multiple regression models of incidence of aggression (response variable) when controlling for phylogeny using PGLS. Partial regression coefficients (β) ± standard errors and their significances are shown. NA indicates variable not included in the model. Statistically significant correlations are underlined. Model 1 included 47 species, alpha (see Methods) = 6.85 and explained 27.18% of variance. Model 2 included 69 species, alpha = 15.50 and explained 19.53% of variance.

	Model 1		Model 2	
	β±SE	P	β±SE	P
Explanatory variables				
Clutch size	−0.15±0.17	0.38	−0.13±0.16	0.42
Feeding method	−1.50±0.52	<u>0.006</u>	−0.88±0.47	0.066
Feeding rate	0.17±0.19	0.38	NA	NA
Length of nestling period	2.35±0.99	<u>0.022</u>	2.49±0.97	<u>0.013</u>

decreased with the proportion of direct feeds (although the partial correlation coefficient was only marginally significant, $P = 0.066$), increased with length of nestling period ($P = 0.013$), and was unrelated to brood size (Table 1).

INTENSITY OF AGGRESSION

Model 3 explained 34.28% of the variance (Table 2) and showed that the intensity of aggression decreased with the proportion of direct feeds ($P = 0.020$), contrary to the feeding method hypothesis, and decreased with brood size ($P = 0.006$, Fig. 3), as predicted by the brood size hypothesis. Intensity of aggression marginally increased with length of nestling period ($P = 0.079$, Fig. 2B, Table 2), and was unrelated to feeding rate.

The results of model 4 (25.86% of variance explained, Table 2) were similar to those of model 3 in that the intensity of aggression decreased with brood size ($P = 0.030$) and increased with length of nestling period ($P = 0.018$). However, the negative relationship between incidence of aggression and feeding method was no longer significant ($P = 0.10$, Table 2).

Discussion

The PGLS models explained a high percentage of the variance (19.5–34.3%), especially considering that in this broad phyloge-

netic study we included seven avian families and the scores for broodmate aggression were based mainly on qualitative descriptions of the behavior because there were only few quantitative studies. Our results confirm that feeding method, length of nestling period, and brood size may have influenced the evolution of sibling aggression in the seven families. Aggression was both more common and more intense among species with indirect feeding and long nestling periods, and more intense in species with small broods. Our main results were consistent regardless of which measure of aggressive competition (incidence or intensity) was used.

Feeding rate (a proxy for food parcel size) was not correlated with incidence or intensity of aggression and in preliminary analyses egg size (proxy for nestling body size and not included in our final analyses because of collinearity with nestling period) was not correlated with either measure of aggression. Thus, neither food parcel size nor body size is likely to have influenced the distribution of aggressive competition in the seven families included in the analysis. However, it is possible that our sample did not include species whose food parcels or nestling body size is small enough to make aggression unprofitable or ineffective, respectively. Certainly other avian families include species with considerably smaller food parcels and nestlings. The mildly aggressive common kingfisher (*Alcedo atthis*) was the species with the highest feeding rate included in our analyses, at 3.8 feeding

Table 2. Multiple regression models of intensity of aggression (response variable) when controlling for phylogeny using PGLS. Partial regression coefficients (β) ± standard errors and their significances are shown. NA indicates variable not included in the model. Statistically significant correlations are underlined. Model 3 included 47 species, alpha (see Methods) = 2.19 and explained 34.28% of variance. Model 4 included 69 species, alpha = 8.06 and explained 25.86% of variance.

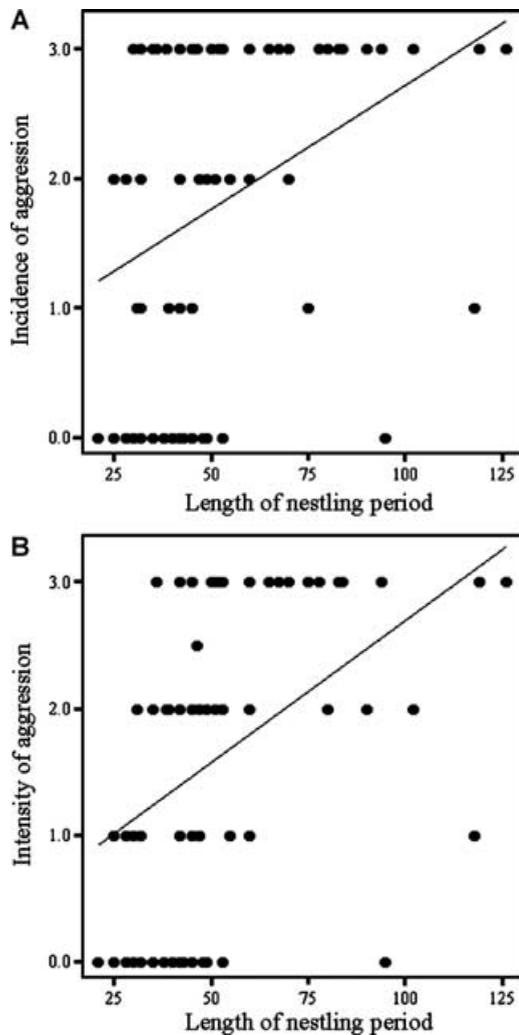|	Model 3		Model 4	
	β±SE	P	β±SE	P
Explanatory variables				
Clutch size	−0.38±0.13	<u>0.006</u>	−0.31±0.14	<u>0.030</u>
Feeding Method	−1.02±0.42	<u>0.020</u>	−0.68±0.41	0.10
Feeding Rate	0.16±0.15	0.29	NA	NA
Length of nestling period	1.44±0.80	0.079	2.07±0.85	<u>0.018</u>

Figure 2. Length of nestling period in relation to (A) incidence of aggression (PGLS: $r^2 = 0.150$, $P = 0.001$, $n = 69$) and (B) intensity of aggression (PGLS: $r^2 = 0.175$, $P = 0.0003$, $n = 69$). Standard least squares regression line fitted, without phylogenetic control, for illustrative purposes.

bouts/h (Rivière 1933; Schultz-Waldmann and Dominiak 1971; Hallet-Libois 1985). In comparison, nonaggressive hooded warbler (*Wilsonia citrine*) broods receive 8 feeding visits/h (Buehler et al. 2002), tree swallow (*Tachycineta bicolor*) broods 15 feeding visits/h (McCarty 2002), and starling (*Sturnus vulgaris*) broods 25 feeding visits/h (Cotton et al. 1996). (Note, however, that house finches, *Carpodacus mexicanus*, which feed chicks with seeds, have particularly low feeding rates among songbirds: 2.68 feeding visits/h [Hill 2002].) Common kingfishers also have the smallest egg size of all species in our dataset (4 g; Schönwetter 1967), compared with 1.6 g for nonaggressive great tits (*Parus major*; Lessells et al. 2002), 1.9 g for barn swallows (*Hirundo rustica*), and 1.9 g for starlings (Cramp 1998). Hence, it remains possible that aggression is absent from some families of birds not included in this study because food parcels are too small for aggression to
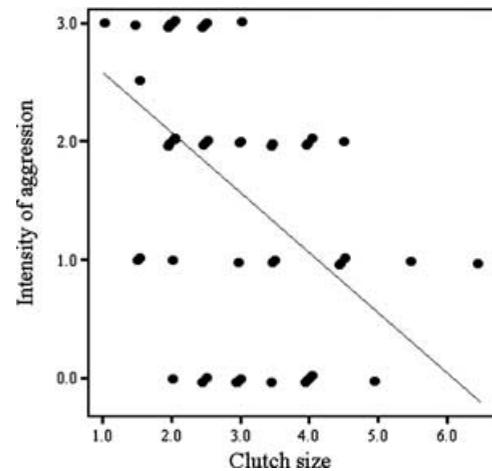

Figure 3. Clutch size (a proxy variable corresponding to brood size at hatching) in relation to the intensity of aggression (PGLS: $r^2 = 0.133$, $P = 0.002$, $n = 69$). Cloud is jittered because of overlap of datapoints. Standard least squares regression line fitted, without phylogenetic control, for illustrative purposes.

be economical or because nestlings are too small for aggression to be effective.

Our results are not consistent with the feeding method hypothesis: both incidence and intensity of aggression were common in species with indirect feeding. Qualitative descriptions of chick behavior from single-species studies also contradict this hypothesis. It is after the switch from direct to indirect feeding that Eurasian sparrowhawk (*Accipiter nisus*) chicks become more aggressive towards their broodmates (Brown and Amadon 1968), and in broad-winged hawk (*Buteo platypterus*) chicks begin fighting (Matray 1974). There are also three independent reports of aggressive competition during indirect feeding in three species of ardeids (Milstein et al. 1970; David and Berril 1987; Ploger and Medeiros 2004) and, indeed, aggression was common in the indirectly fed great blue herons (*Ardea herodias*) that gave rise to the hypothesis (Mock 1985). Thus, rather than being restricted to species with direct feeding, aggressive competition is increasingly common and intense as species engage in more indirect feeding during the nestling period. Finally, the first empirical test of the feeding method hypothesis' assumption that aggression is more efficient for securing a large share of food during direct than indirect feeds (Mock and Parker 1997, p. 106) found no support for it in cattle egrets (*Bubulcus ibis*; Gonzalez-Voyer and Drummond, 2007).

Aggression may be especially effective when chicks compete for food deposited on the nest floor (indirect feeding) because in this location food tends to be simultaneously accessible to all broodmates. Aggression may not enable a single chick to monopolize the deposited prey item, but should be favored if it increases the aggressor's share sufficiently to repay the cost of attacking.

By contrast, during direct feeds dominant chicks' usual advantages in body size and motor maturity could often enable them to outreach siblings and seize prey first, reducing the need to resort to aggression. Precocial chicks feeding from the substrate shift progressively from scramble competition to aggressive resource defense as food becomes experimentally concentrated in a smaller patch (Colon, Hernández, and Drummond unpubl. ms.), and altricial chicks feeding indirectly face a similar situation, competing for a small patch of food on the substrate.

Both incidence and intensity of aggression increased with length of nestling period, supporting the nestling period hypothesis. Nestling periods of aggressive species ranged from 25 days to 126 days, and 80% of them had nestling periods of > 38 days, compared to 50% of nonaggressive species. Aggression is expected to be more common in species with long nestling periods provided aggression is costly to dominant chicks and lengthy cohabitation provides greater opportunity for dominance to yield a benefit. The costs to dominant chicks of establishing dominance include the tissue damage, energy expenditure, and foregone feeding opportunities incurred by both the dominant chick and its subordinate sibling throughout the establishment period. Dominance establishment periods can last anywhere from 10 days in laughing kookaburras (Nathan et al. 2001), two to three weeks in cattle egrets (A. Gonzalez-Voyer, unpubl. data), and three to four weeks in blue-footed boobies (Drummond 2006). However, length of nestling period may not influence the evolution of broodmate aggression in the very small minority of species with obligate siblicide (prompt unconditional elimination of the broodmate), because the period of broodmate cohabitation is very short and the payoff for aggression is guaranteed.

Brood size (our proxy was clutch size) was negatively correlated with both intensity and incidence of aggression, although the latter correlation was not significant. As brood size increases there may be greater risk that while dominant chicks are busy intimidating and excluding broodmates, other broodmates are free to receive the parental feed and thus preempt the dominant chick. Also, hierarchies may be less stable in larger broods if dominant chicks are unable to recognize or gain access to particular individuals and concentrate punishment on them (Drummond 2002). However, our correlations do not allow us to discount the alternative interpretation that causality runs in the other direction and costly sibling conflict selects for parents creating smaller broods (Godfray and Parker 1992).

In our dataset, 80% of aggressive species had a modal clutch of four eggs or fewer, and 81% of the 21 species with intense aggression (code 3) had a modal clutch of two eggs or fewer. The aggressive species with the largest brood size was the common kingfisher, with a modal clutch size of 6.5 eggs and an average brood size of 6.2 chicks (Schultz-Waldmann and Dominiak 1971; Hallet-Libois 1985; Cramp 1998). This may be the species with the largest brood size for which aggressive competition has been reported and its aggression is reportedly atypical: attacks are uncommon and targeted simultaneously by all broodmates on the chick that jumps the feeding queue (Schultz-Waldmann and Dominiak 1971). Aggression may be workable in large broods only in the unlikely circumstance of broodmates coordinating attacks on individuals rather than operating individually.

Reports from field studies indicate that in several species aggression may be more intense in larger broods (e.g., Fujioka 1985; David and Berril 1987; Mock and Parker 1997), and in cattle egrets aggression decreased when three-chick broods were experimentally reduced by removing the eldest or youngest chick (Mock and Lamey 1991). Such observations appear to indicate that at the proximate level, brood size is positively linked with aggression. However, within species, aggression could increase with brood size not as a response to brood size per se but as a result of decreasing per capita food ingestion (Drummond 2001b). In several species of birds food deprivation elicits increased broodmate aggression (Drummond 2001a), so characterizing the proximate effects of brood size on aggression will require controlling for food ingestion.

It is possible that extra-pair paternity could have influenced the evolution of aggressive competition by reducing relatedness between broodmates and thus indirect costs associated with sibling competition (Hamilton 1964; Briskie et al. 1994). Lack of information on extra-pair paternity for a number of the species included in our analysis prevented us from testing this hypothesis.

Although formal reconstruction of ancestral states has not been undertaken, phylogenetic evidence suggests that a parsimonious explanation for the distribution of broodmate aggression involves several independent evolutionary events rather than a single event followed by subsequent loss of aggression in various clades. Sister clades of the eagles, the boobies and anhingas, and the kingfishers are all nonaggressive, therefore it is unlikely that all the ancestors of the clades included in our analyses were aggressive. Thus, our correlations suggest traits that favored the evolution of aggressive competition rather than traits that favored its maintenance.

It is probable that, for aggressive competition to evolve, a species must present a combination of factors that make aggression both effective and profitable. Comparison of two sister clades, the Accipitridae (eagles, hawks, and buzzards; excluding species that have single egg clutches, e.g., old world vultures) and the Falconidae (falcons) is informative. Both clades include predatory species with parentally fed altricial chicks. Eighty-one percent of the 58 accipitrids for which information on sibling competition is available are aggressive compared to none of the 52 falconids (Newton 1979). Accipitrids with nonaggressive competition have clutch sizes and nestling periods similar to those of falcons. Sixty percent of falcons and 60% of nonaggressive

accipitrids have modal clutches of > 2.0 eggs, compared to only 20% of aggressive accipitrids. Only 10% of falcons and 20% of nonaggressive accipitrids have nestling periods of > 44 days compared to 60% of aggressive accipitrids (Thiollay 1994; White et al. 1994). In falconids, as in nonaggressive accipitrids, it may be the combination of short nestling periods, large clutches, and possibly other factors that has closed the door on the evolution of broodmate aggression. When further data on key traits become available, these sophisticated interactions can be statistically tested.

In conclusion, our study, the first phylogenetic comparative analysis of morphometric, life history and behavioral hypotheses of sibling aggression in any vertebrate, showed that indirect feeding, small broods, and long nestling periods are significantly correlated with broodmate aggressive competition. Similar issues have been investigated in parasitoid wasps, although selective forces favoring aggression probably differ between birds and parasitoids (Mayhew 1998; Pexton and Mayhew 2001). We failed to confirm a link between aggression and large food parcels. Because our dataset was limited to families with altricial, parentally fed chicks that include at least one aggressive species, we are reluctant to extrapolate results to avian clades in which there are no aggressive species. However, it is possible that direct feeding, short nestling periods, and large broods in combination with other factors not included in our analyses may have impeded the evolution of aggressive competition in other clades such as the passerines, falconids, and phalacrocoracids (cormorants). Our models explained 19.5–34.3% of variance in use of aggression, even though their explanatory power was probably limited by a coarse scale of the behavioral variables. Additional factors, not considered here, combined with indirect feeding, long nestling periods, and small broods may improve the predictive power of the models. Correlational methods such as PGLS cannot identify cause and effect, therefore further comparative studies based on directional phylogenetic methods are needed to identify the sequences of events that ultimately led to sibling rivalry (Pagel 1994).

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1. Data sources for all variables included in the phylogenetic comparative analyses.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1558-5646.2007.00152.x
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