

Barn swallow chicks beg more loudly when broodmates are unrelated

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Abstract

Parents of a variety of animal species distribute critical resources among their offspring according to the intensity of begging displays. Kin selection theory predicts that offspring behave more selfishly in monopolizing parental care as relatedness with competitors declines. We cross-fostered two eggs between barn swallow (*Hirundo rustica*) clutches and compared the loudness of begging between mixed and control broods under normal feeding conditions and after a period of food deprivation. Begging loudness was higher in mixed broods under normal but not poor feeding conditions. Survival was reduced in mixed than control broods. Call features varied according to parentage, possibly serving as a cue for self-referent phenotype matching in mixed broods. This is the first evidence within a vertebrate species that competitive behaviour among broodmates depends on their relatedness. Thus, kin recognition and relatedness may be important determinants of communication among family members, care allocation and offspring viability in barn swallows.

Introduction

Kin selection theory predicts that individuals should be more willing to subtract limiting resources to conspecifics as genetic relatedness to the competitors decreases (Hamilton, 1964). This is expected because the indirect fitness cost of a selfish act will decrease with decreasing relatedness to the recipient.

Offspring in a family often compete among themselves for depreciable parental care (Clutton-Brock, 1991). Because of the extensive occurrence of extra-bond fertilizations and brood parasitism in diverse animal taxa (Birkhead & Møller, 1998), however, the level of scramble competition among family members can be expected to vary according to their actual genetic relatedness, decreasing as average relatedness increases. In fact, Briskie *et al.* (1994) showed that the loudness of vocalizations that nestling birds use to solicit care increases across species with the frequency of extra-pair paternity.

Begging displays are common among birds (Kilner, 2002) and include visual and vocal signals (e.g. gaping,

loudness of calls) which increase in intensity according to hunger (Johnstone & Godfray, 2002). As the marginal benefit of obtaining additional food is expected to decrease with increasing satiation (Parker & Macnair, 1979), each offspring should strike the optimal balance between the direct fitness benefits of obtaining more food by increasing begging intensity, and the indirect fitness costs of subtracting food to nestmates, which in turn depends on relatedness to the competitor.

In the barn swallow population we studied, extra-pair paternity is frequent, and approximately half of the broods contain extra-pair offspring (Saino *et al.*, 1997a). Brood parasitism is relatively rare (this study; Møller, 1994). Food is limiting, as shown by correlational and manipulative studies where feedings received by individual nestlings, body mass and feather growth, and immune response have been shown to decline with brood size, and high-quality food supplementation enhances offspring phenotypic quality (e.g. Saino *et al.*, 1997b, 2000). In another study on a different sample from the same population, we found that nestlings increase the loudness of their begging calls after a short period of food deprivation and that loudness of begging calls of individual nestlings positively predicts their subsequent short-term body mass gain as a result of increased parental food provisioning (Boncoraglio *et al.*,

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2007). Based on kin selection theory, these findings led us to predict that scramble competition for food within barn swallow broods, as reflected by the overall level of collective begging loudness during feeding events, should increase as the average level of relatedness among the offspring declines.

In the present study we produced clutches with experimentally lowered average relatedness by reciprocally cross-fostering eggs between synchronous nests to test whether broods of mixed origin compete more harshly than natural broods. This approach was adopted because decreasing the average relatedness of broodmates by manipulating the frequency of extra-pair paternities in a free-living breeding population of birds would be technically very difficult. Loudness of begging calls of whole broods was used as an index of the overall level of scramble competition among broodmates during feeding events, and was recorded both before and after a period of food deprivation to investigate whether the predicted increase in loudness after food deprivation differed between the two groups of broods. Finally, we recorded individual nestlings in mixed broods to test whether sonographic features of begging calls varied according to the origin of the nestlings, thus possibly serving as a self-referent phenotypic cue to non-kin discrimination (see Hauber & Sherman, 2001).

Methods

We studied barn swallows at eight colonies east of Milano (Northern Italy) during spring 2005. The adults were captured, marked and subjected to blood sampling. The colonies were visited daily to record breeding events and identify social pairs by observation.

We identified pairs of synchronous clutches (Appendix S1 for supplementary methods) with four to six eggs and located in different colonies. Two randomly chosen, marked eggs were reciprocally cross-fostered between paired nests by day 8 of incubation (Appendix S1 for details). Each 'mixed' clutch was matched to a control clutch (thus forming a 'dyad' including a control and a mixed clutch) with four to six eggs from the same colony and therefore exposed to the same ecological conditions.

Control clutches were subjected to the same manipulations as mixed clutches, except that the eggs were returned to their original nest. We created 44 mixed clutches. We decided to record begging calls only in dyads where at age 12 each brood contained at least four nestlings, and final sample was therefore reduced to 24 dyads ($n = 24$ control and 24 mixed broods with 115 and 110 nestlings respectively). Mean extra-pair paternity (= proportion of nestlings in a brood that were not sired by the social partner of their mother) did not differ between 23 mixed broods and a sample of 10 control broods (t -test on arcsine square-root transformed data, $t_{31} = 0.82$, $P = 0.42$; mean frequency of EPP within

brood: mixed = 0.258 ± 0.05 SE; control = 0.270 ± 0.13 SE; Appendix S1 for paternity analyses and sample sizes). As reciprocally cross-fostered clutches were in different colonies, average relatedness among nestlings was assumed to be smaller in mixed than in control broods, where relatedness depended on the normal level of extra-pair paternity and brood parasitism for this species. For example, in a control (and unparasitized) brood of four nestlings including one (= 25%) extra-pair offspring, average relatedness among broodmates was 0.375, whereas in a mixed brood of two resident and two transferred nestlings again including one extra-pair offspring out of four chicks, average relatedness was 0.125. Our treatment simulated a situation where brood parasitism and not extra-pair paternity was more frequent in mixed than in control broods. Although the latter condition would be certainly more natural for barn swallows, experimental manipulation in the wild of extra-pair paternity seems at present extremely difficult for this species. Nonetheless, this protocol allowed us to test for the effects of the reduction of average relatedness among broodmates on nestling behaviour.

Importantly, we chose to alter clutch rather than brood composition, i.e. we created mixed broods by swapping eggs rather than hatchlings, to prevent any possible influence of early imprinting of nestmates or attending adults on nestling behaviour.

At hatching, mixed clutches were visited every third hour during daytime (from 06:00 to 18:00 hours) to assign hatchlings to their original clutch (Appendix S1 for parentage analysis of the nestlings that could not be matched to their original egg) and to measure the total duration of hatching ('hatching spread', hereafter defined as the number of hours between the first visit when at least one egg was found to have hatched and the first visit when all the eggs had hatched), and so were control broods. Visiting the nests more frequently during daytime or during the night to record the exact moment of the hatch of each individual in mixed and control broods would have caused excessive disturbance to the incubating females and the nestlings. Thus, a more accurate estimate of hatching time of individual nestlings was not possible. However, the accuracy of the estimate of hatching time is similar to the highest standards adopted in field studies of hatching asynchrony in birds. Hatchlings were marked and a blood sample was taken at age 7. At age 11 we measured body mass, tarsus and wing feather length, and did an *in vivo* test of nestling immunocompetence (Saino *et al.*, 1997b).

At age 12 we recorded the begging calls produced by control and mixed broods during three feeding events. Mixed and control broods did not differ in brood size (paired t -test, $t_{23} = 0.96$, $P = 0.35$; mean brood size: mixed = 4.58 ± 0.15 SE; control = 4.71 ± 0.13 SE) nor in hatching spread (paired t -test, $t_{23} = 0.69$, $P = 0.50$; mean hatching spread \pm SE: mixed = 27.40 ± 1.73 h;

control = 26.25 ± 1.07 h). Vocalizations were recorded on entire broods so that the nestlings were perceiving the normal number of competitors for that brood. We then measured air temperature, and food-deprived all broods for 1.5 h by removing from the nest all nestlings, except a randomly chosen one to prevent parents from deserting the brood. After the nestlings had been returned, three begging events were recorded starting 15 min later. This protocol allowed us to test the independent and combined (interaction) effects of the manipulation of brood composition and food deprivation on the loudness of begging calls produced by all nestlings collectively. Barn swallow nestlings start to beg very quickly when perceiving an adult approaching the nest and high overlapping of begging calls among nestmates thus occurs before feeding assignation. Therefore, calls uttered by each individual could not be measured just before feeding assignation, when the level of scramble competition for food is expected to be maximum. High values of begging loudness of the whole brood could be due to three different, nonmutually exclusive phenomena, i.e. louder begging calls of individual nestlings, higher individual begging rates resulting in more extensive overlap among individual calls, or higher number of calling nestlings at any given time. All these conditions are expected to occur for escalating levels of competitive behaviour among broodmates. Therefore, we considered the loudness of begging calls of the entire brood as a reliable index of the intensity of overall scramble competition among broodmates during feeding events, independently of which specific mechanism(s) determined the observed loudness of the calls.

To test for parentage effects (Appendix S1 for parentage analyses) on acoustical features of begging, at age 14 we recorded the begging calls of individual nestlings from mixed broods during feeding visits while temporarily removing their nestmates. Sequence of recording of nestlings was randomized.

Nestling survival was measured at day 14 on a larger sample of broods than that used to measure the effect of brood composition on begging calls to increase the power of statistical tests. This sample included 32 control and 41 mixed broods with 150 and 186 hatched nestlings respectively.

Recording and analysis of begging calls

Barn swallow nests are small (*c.* 7 cm internal radius) and half-cup-shaped. Begging vocalizations were recorded using a Sony TCD-D7 DAT recorder (Sony Corporation, Tokyo, Japan) connected to a Sony ECM C-115 microphone always positioned on the nest rim, half way between the extremities of the rim and oriented towards the centre of the nest. Recordings were made blindly with respect to brood treatment (Appendix S1). All recording sessions were carried out in the absence of disturbing sources of background

noise. After starting, the first three feeding events were recorded for each session. DAT recording settings (i.e. intake volume level) were calibrated manually with a Lutron SL-4022 sound level meter (Luton Electronics Co., Inc., Coopersburg, PA, USA) at the beginning of the field season and kept constant across all sessions. Such calibration was checked onto the recorder before starting each session.

Brood recordings were analysed using PRAAT v.4.4.04 (<http://www.praat.org>). As the amplitude of nestling begging calls increases with food deprivation (Saino *et al.*, 2000; G. Boncoraglio, R. Martinelli and N. Saino, unpublished data), we focused on this feature (Briskie *et al.*, 1994). Begging relative amplitude (dB, corrected for background amplitude) was sampled every 0.01 s and averaged across whole begging bouts. The maximum value of begging call amplitude across each bout was also recorded.

Vocalizations at age 14 of nestlings from mixed broods were recorded with the same equipment and settings we used at age 12, and were analysed using Avisoft SAS Labpro (Avisoft SASLab, Berlin, Germany). For up to eight individual begging calls we measured: mean syllable duration (ms); peak amplitude frequency (Hz) and relative amplitude (dB). Call values for each nestling were averaged across calls.

All sonographic analyses were conducted blindly with respect to brood manipulation (age 12: mixed or control broods) or nestling origin (age 14: resident or transferred nestlings). Variation in brood size between mixed and control broods composing the dyads at age 12 was accounted for by initially including brood size as a covariate in all the statistical analyses (see Results).

Statistical analyses

We used generalized linear mixed model analyses of variance to investigate the effects of brood composition (mixed or control) and foster status of the nestlings (resident or transferred) (fixed effects) on brood begging calls, nestling morphological and immunity variables, and nestling survival. Food deprivation (before or after) was included as a fixed factor in the analyses of brood begging calls. Separate analyses on the data collected either before or after food deprivation were also performed. In the models, depending on the variable under scrutiny, we included dyad of broods, and nest of origin and nest of rearing nested within dyad (random factors). Nestling survival at day 14 was treated as a two state response variable (1 = surviving; 0 = not surviving), assuming a binomial error distribution and a logit-link function. Parameter estimates were obtained by restricted maximum likelihood method. Degrees of freedom were estimated by Satterthwaite's approximation. Residuals of the models were tested for prerequisite conditions of normality and homogeneity of variances for the application of analyses of variance. Normality

(Kolmogorov–Smirnov test; $P > 0.05$) and homoscedasticity (Levene test; $P > 0.05$) were met in all cases.

Results

The effect of brood composition on begging loudness of whole broods ($n = 24$ control and 24 mixed broods with 115 and 110 nestlings respectively) was first analysed while including in the same model the calls recorded before and after food deprivation. Loudness of begging did not vary according to brood composition, whereas it significantly increased after food deprivation (Table 1; Fig. 1). In addition, air temperature negatively predicted the loudness of calls (Table 1; Appendix S1). However, the interaction term between brood composition and food deprivation showed a significant effect on begging loudness (Table 1). We therefore carried out separate analyses of variance on the data obtained either before or after food deprivation and found that begging loudness was larger in mixed than in control broods before ($F_{1,23.1} = 6.96$, $P = 0.015$) but not after ($F_{1,45} = 0.79$,

$P = 0.380$) food deprivation. Air temperature negatively predicted the loudness of calls both before [$F_{1,44.7} = 6.22$, $P = 0.016$; coefficient (SE) = -0.621 (0.249)] and after [$F_{1,45} = 10.66$, $P = 0.002$; coefficient (SE) = -0.861 (0.264)] food deprivation (Appendix S1). In addition, following food deprivation, begging loudness increased in control ($F_{1,119} = 14.80$, $P = 0.001$) but not in mixed ($F_{1,119} = 0.21$, $P = 0.648$) broods. Exclusion of temperature from the models or inclusion of a factor ‘tetrad’ accounting for pairs of mixed clutches where egg swapping was performed and their associated control broods did not alter qualitatively the results (details not shown; Appendix S1). In addition, when included in the models, brood size did not significantly predict begging loudness whereas the significant effect of the other factors (see Table 1) was confirmed. Qualitatively similar results were obtained when the same analyses were performed on maximum rather than on average amplitude of brood begging calls recorded across each bout (details not shown).

Mixed model analyses of variance with dyad and brood nested within dyad showed no significant effect of brood composition on nestling body mass, tarsus or wing feather length, and an index of immunocompetence ($P > 0.10$ in all cases; see above for sample sizes). In these analyses, the effect of the nest of rearing on nestling phenotype was significant for body mass ($z = 3.92$, $P < 0.001$), tarsus ($z = 2.21$, $P = 0.014$) and wing feather length ($z = 3.09$, $P = 0.001$), but not for the immunocompetence index ($z = 1.17$, $P = 0.120$). The variance in nestling phenotypic traits was homogeneous after controlling for among-nests variability (Levene tests; P always > 0.05). In the 24 mixed broods no significant difference between resident ($n = 60$) and transferred ($n = 44$) nestlings existed for any phenotypic trait (P always > 0.18 ; the origin of six nestlings could not be identified). However, a mixed model analysis of variance with dyad and brood nested within dyad as random factors and brood composition as fixed factor showed that survival was lower in mixed than in control broods ($F_{1,132} = 5.09$, $P = 0.026$; percentage of hatched nestlings surviving at day 14: mixed broods = 85.8%; control broods = 97.9%; see Methods for sample sizes). Nestling survival was also significantly affected by the nest of rearing ($z = 4.27$, $P < 0.001$), whereas no significant effect was found for the dyad factor ($z = 0.00$, $P = 1.00$). Survival of nestlings was not influenced by the nestling being resident or transferred in mixed broods ($F_{1,140} = 3.19$, $P = 0.076$).

Sonographic features of begging calls of individual nestlings in mixed broods ($n = 130$ nestlings; 36 broods) were subjected to analyses of variance with dyad, and nest of origin and nest of rearing nested within dyad as random effects. Syllable duration was found to vary among nests of origin ($z = 2.35$, $P = 0.009$). Conversely, no significant effects on syllable length were found for dyad ($z = 1.34$, $P = 0.090$) or nest of rearing ($z = 0.56$,

Table 1 Effects of brood composition (mixed vs. control) and food deprivation (before vs. after) on loudness of brood begging calls.

	<i>z</i>	<i>F</i>	d.f.	<i>P</i>	Coefficient (SE)
Dyad	0.45			0.330	
Brood (dyad)	2.94			0.002	
Brood composition		3.14	1, 22.8	0.090	
Food deprivation		8.59	1, 238	0.004	
Brood composition × food deprivation		5.09	1, 238	0.025	
Air temperature		9.23	1, 42.5	0.004	-0.727 (0.239)

Amplitude data recorded at three feeding events were used as repeated measures. We included dyad of broods and brood nested within dyad as random factors and air temperature (°C) as a covariate.

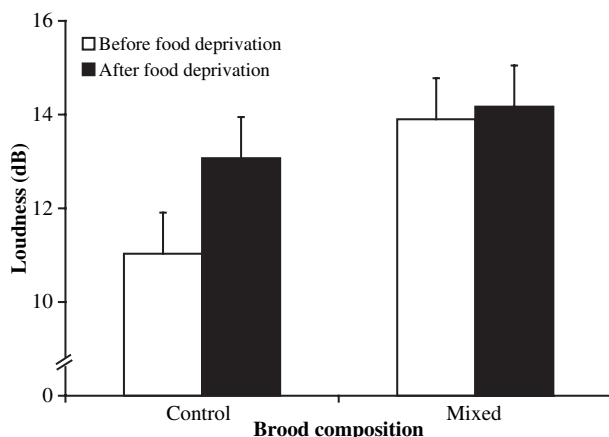


Fig. 1 Mean (\pm SE) loudness of collective begging calls of mixed or control broods before and after a food deprivation period.

$P = 0.289$). In addition, no significant variation in relation to origin was found for peak amplitude frequency or amplitude of the calls (all $P > 0.05$, details not shown). Analyses of variance showed repeatability within individuals for all the sonographic variables based on up to eight consecutive calls recorded for each individual (syllable duration: $F_{129,716} = 26.37$, $P < 0.001$, $R^2 = 0.83$; peak amplitude frequency: $F_{129,714} = 3.30$, $P < 0.001$, $R^2 = 0.37$; call amplitude: $F_{129,711} = 6.61$, $P < 0.001$, $R^2 = 0.55$). However, syllable duration was more repeatable than the other variables in an analysis of effect sizes [Q-test for heterogeneity (Hedges & Olkin, 1985), syllable duration vs peak frequency: $\chi^2 = 43.47$, $P < 0.001$; syllable duration vs. call amplitude: $\chi^2 = 21.33$, $P < 0.001$]. Call amplitude did not vary between resident and transferred nestlings ($F_{1,101} = 0.01$, $P = 0.93$).

Discussion

We found that under normal satiation conditions barn swallow broods of experimentally mixed origin beg more loudly than unmanipulated broods. Because food is limiting to nestlings and loudness of individual begging calls increases as food availability declines, functioning to attract parental food provisioning (see Introduction), present results suggest that under normal food provisioning scramble competition for food is more intense when relatedness among nestmates is experimentally reduced.

An increase in begging loudness after food deprivation was observed in control but not in mixed broods. This suggests that nestlings in mixed broods may display at nearly maximum level for this species already before food deprivation, given the physiological constraints on the intensity of vocalizations that nestlings can produce. The nonsignificant difference in the loudness of begging after food deprivation between mixed and control broods may suggest that the increase of loudness in food-deprived control broods led to a nearly maximal level of scramble competition even when relatedness among nestmates was unmanipulated. The differences in begging loudness caused by brood manipulation and food deprivation (Fig. 1) can be discriminated by birds (Dooling, 2004), and similar variations in begging loudness of individual calls (c. 2 dB after 2 h of food deprivation, $n = 86$ nestlings) result in an increase of food intake of individual nestlings (Boncoraglio *et al.*, 2007). In mixed broods, phenotype was not affected by the nestling being resident or transferred, and the mean and variance in offspring phenotype did not differ between control and mixed broods, suggesting that parents did not discriminate among offspring according to relatedness. However, survival was lower in mixed than in control broods, probably due to starvation of the less competitive nestlings caused by exaggerated monopolization of parental resources operated by their competitively supe-

rior broodmates (reviewed in Mock & Parker, 1997), rather than to increased predation for louder begging calls. In fact, brood predation is very rare in our study area (our unpublished data). Thus, increased competition in mixed broods under normal conditions should have resulted in an unfavourable rearing environment and, ultimately, in reduced chances of survival of individual chicks.

We considered alternative interpretations of the causes of the observed effects of brood manipulation. For example, swapping of randomly chosen eggs may have produced clutches with either more or, conversely, less eggs of low laying order. If egg composition (e.g. androgen levels) varies with laying order and affects offspring behaviour, this could result in altered brood competitive behaviour in mixed broods. However, because an increase in the proportion of e.g. first eggs in a clutch automatically results in a decrease in its cross-fostered counterpart, these opposite effects should have cancelled out in each pair of mixed broods. Moreover, the lack of significant difference in hatching spread, as well as in the within-brood variance between mixed and control broods, suggest that experimental manipulation did not disrupt the normal hierarchy among broodmates (e.g. Saino *et al.*, 2001). Finally, higher begging intensity and increased mortality in mixed broods could also have depended on reduced parental investment in mixed compared to control broods. Admittedly, we cannot completely dismiss this hypothesis because we cannot provide any correlational data on parental feeding intensity in these two groups. However, brood composition and nestling origin did not affect offspring morphology or immunocompetence in the present study, although there is strong evidence for barn swallows that lower parental investment with respect to brood demands should result in depressed phenotypic quality of the offspring, as reflected by worse general conditions of the nestlings reared in experimentally enlarged compared to reduced broods (e.g. Saino *et al.*, 1997b, 2000). Similar findings have been found in a large number of correlative studies showing a negative relationship between offspring phenotypic values and brood size in Birds (reviewed in Stearns, 1992). In addition, parental feeding rate in partially cross-fostered broods of barn swallows does not vary depending on whether parents are feeding pairs of only resident, only transferred, or half resident and half transferred nestlings (G. Boncoraglio and N. Saino, unpublished work). Thus, we are convinced that differences in feeding rates between mixed and control broods are unlikely to have occurred.

Variation in nestling behaviour according to brood composition raises the question of which evolutionary pathways could lead to a condition where offspring discriminate among broodmates according to relatedness whereas parents apparently do not, and, at a different level, which mechanism(s) might allow kin recognition among the offspring. Apparently non-adaptive adoption

behaviour of unrelated conspecific offspring occurs in several bird species (e.g. Saino *et al.*, 1994), as is the case for provisioning of depreciable care to unrelated extra-pair offspring by cuckolded fathers in species with sperm competition (Wright, 1998). Provisioning of alloparental care entails parents with fitness costs arising for example from denying care to related offspring. However, selection acting on parents to discriminate non-kin may be weaker than selection acting on offspring to circumvent parental kin-recognition mechanisms because failure in obtaining care from unrelated parents has higher fitness costs for the offspring than providing alloparental care has for the adults. On the other hand, selection acting on the offspring for recognition of kin among the nestmates may be strong because prevailing over nestmates in competition for limiting parental resources may result in marked reduction of their survival prospects. Thus, since the direct fitness benefit of obtaining more food rapidly decreases with increasing satiation (Parker & Macnair, 1979), the indirect fitness cost paid by a particular offspring in terms of starvation of non-recognized, closely related nestmates would be only partly counterbalanced by food provision by the parents to that offspring.

Vertebrates can discriminate nonkin via self-referent phenotype matching as mediated by acoustic cues (Hauber & Sherman, 2001; Nakagawa & Waas, 2004). Syllable length, a prominent feature of begging calls, varied among nestlings in mixed broods according to their origin, consistent with previous findings showing that the sonographic quality of begging calls of cliff swallows (*Petrochelidon pyrrhonota*), as well as the duration of calls of nestling barn swallows, vary in relation to parentage (Medvin *et al.*, 1992). In addition, this variable showed very strong repeatability within the individuals included in our data set, possibly serving as a cue for self-referent phenotype matching in mixed broods. If the variation we observed was indeed due to genetic effects and not to maternal effects via egg quality, differences would also be likely to occur between half-siblings, allowing nestlings to modulate their begging behaviour according to paternity of their broodmates. However, kin recognition, if any, could also have occurred via visual or chemical cues (Bonadonna & Nevitt, 2004; see Nakagawa & Waas, 2004).

This is the first experimental study of birds we are aware of where the prediction based on kin selection theory that offspring increase their competitive behaviour when relatedness to nestmates is low is verified. Because of practical limitations (see also above), we altered average relatedness among broodmates by partially cross-fostering clutches rather than by manipulating extra-pair paternity. However, present findings are consistent with those of a comparative study where begging call loudness of different species increased with the frequency of extra-pair paternity (Briskie *et al.*, 1994) and with an intraspecific study of a parasitoid wasp species (Giron *et al.*, 2004). Sperm competition and other mechanisms (e.g. intra-specific brood parasitism) that

inflate the variance in relatedness among offspring in a family are frequent in birds and other taxa (Birkhead & Møller, 1998). Kin recognition and actual genetic relatedness may therefore be important determinants of communication among offspring and parents, parental decisions on resource allocation among the progeny and, ultimately, offspring viability.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Supporting Online Methods

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