

Species divergence in offspring begging intensity: difference in need or manipulation of parents?

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Conflicts over the delivery and sharing of food among family members are expected to lead to evolution of exaggerated offspring begging for food. Coevolution between offspring begging intensity and parent response depends on the genetic architecture of the traits involved. Given a genetic correlation between offspring begging intensity and parental response, there may be fast and arbitrary divergence in these behaviours between populations. However, there is limited knowledge about the genetic basis of offspring solicitation and parental response and whether these traits are genetically correlated. In this study, we performed a partial cross-fostering experiment of young between pied and collared flycatchers (*Ficedula hypoleuca* and *Ficedula albicollis*) and recorded the behaviour of individual offspring and their (foster)parents. We found that nestling collared flycatchers reached a higher phenotypic quality, estimated both as mass at fledging and as intensity of their T-lymphocyte-mediated immune response when raised by heterospecific foster parents. However, although collared flycatchers begged relatively more intensively, we found no evidence of corresponding higher resistance (i.e. lower feeding rate) of adult collared flycatchers than of adult pied flycatchers. Thus, the difference in offspring begging intensity between the two species seems not to be a result of a difference in escalation of the parent–offspring conflict. Instead, the species' divergence in exaggeration of offspring begging intensity 'honestly' matches a difference between the species in offspring need. This interpretation is strengthened by the fact that the difference in begging intensity between the two species increased as the season progressed, coinciding with the higher sensitivity of nestling collared flycatchers to the seasonal decline in food availability. Thus, the behavioural differentiation appears to be a direct consequence of a life-history differentiation (offspring growth patterns).

Keywords: parent–offspring conflict; sibling competition; collared flycatcher; pied flycatcher; interspecific competition; life-history trade-off

1. INTRODUCTION

In many species, the phenotypes of offspring are affected not only by the genotype of the parents, but also by the phenotype of the parents, i.e. through maternal and paternal effects. When maternal and paternal effects have a genetic component, the 'parental environment' and the offspring phenotype will coevolve (Mousseau & Fox 1998; Wolf & Brodie 1998). Parents are expected to evolve a wide range of adaptations that enhance the fitness of their young. Such adaptations may include providing their offspring with appropriate food items and being able to accurately respond to their signals of need. However, parents and their offspring are unlikely to have identical fitness interests. The evolution of exaggerated solicitation for food by offspring is partly attributed to conflicts between parents and offspring (Trivers 1974; Parker & Macnair 1979; Godfray 1991) and among offspring (Godfray 1995; Rodriguez-Gironés 1999; Mock & Parker 1997) over the delivery and distribution of food items. While a parent is selected to provide and distribute resources between siblings in a way that maximizes the

parent's own fitness, any particular offspring is selected to demand a larger share. The resolution to this parent–offspring conflict (i.e. when costs and benefits of begging for food are balanced) has been extensively modelled. Whether this resolution is shifted in favour of the parents (e.g. Parker & Macnair 1979), the offspring (Parker & Macnair 1978) or represents honest signalling by the young (Godfray 1991; Johnstone 1996; Godfray & Johnstone 2000) depends on the underlying assumptions of the model. Empirical studies testing the assumptions regarding behavioural interactions between family members are much more common than studies investigating assumptions on the genetic basis of the traits involved (Kölliker & Richner 2001; Kölliker *et al.* 2005). As for coevolutionary arms races in general, there may be a rapid genetic divergence between populations in communication between parents and offspring (Kölliker & Richner 2001). Moreover, the resolution of conflicts is expected to vary across environments, because the costs of both parental care and begging display strongly depend on environmental factors (Parker & Macnair 1978).

Genetic divergence between populations in communication between parents and offspring is difficult to demonstrate empirically. Since individuals belonging to genetically diverged populations often provide their

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offspring with different types of food items, experiments using a classical cross-fostering design might be impossible to perform. A possible way to avoid this problem is to cross-foster young between breeds or strains (reviewed by Kölliker & Richner 2001), but caution is needed when interpreting the results from such studies because breeds and strains are generally highly inbred and adapted to artificial environments. In this study, we cross-fostered young between two closely related species of birds. Pied and collared flycatchers (*Ficedula hypoleuca* and *Ficedula albicollis*) co-occur throughout central and eastern Europe and on the two Swedish islands of Öland & Gotland, where they occasionally hybridize. The two species are clearly genetically differentiated (Sætre *et al.* 2003), but their habitat preference and feeding mode are similar (Lundberg & Alatalo 1992), which is an important prerequisite for cross-fostering young between the two species. In this study, we partially cross-fostered young between the two species (i.e. created nests containing young of both species), recorded the behaviour of individual offspring and their (foster)parents and estimated the phenotypic quality of the young. Our two main aims were: (i) to examine whether there is a species' divergence in offspring begging intensity and parents' responses to offspring begging and (ii) to compare the phenotypic quality of siblings raised by their own versus foster parents. If the two species have diverged in communication between parents and offspring, we expect that young, which solicit most intensely, will experience an increased phenotypic quality when fostered by less resistant parents of the other species.

2. MATERIAL AND METHODS

The partial cross-fostering experiment was performed in box breeding populations of collared and pied flycatchers on Öland (57°10' N, 16°58' E), Sweden in 2003 and 2004. We recorded the date of the onset of egg laying, the total number of eggs laid and the number of offspring hatched and exchanged approximately half of each brood between nests of pied and collared flycatchers with the same hatching dates and brood sizes. This was done when nestlings were 3 days old. By dividing the broods, we could compare both (i) the behaviour of nestlings of the two different species while controlling for social and environmental effects and (ii) the behaviour of the adult birds of the two different species when exposed to a standardized composition of nestlings (i.e. controlling for differences in nestlings' begging intensity). In addition, the experiment resulted in sibling groups being exposed to two different treatments: (i) reared by their biological parents and (ii) reared by heterospecific foster parents. We individually marked all nestlings in experimental broods by clipping their toenails and subsequently measured and ringed them using standard protocols (Qvarnström *et al.* 2005). Since there is a positive correlation between mass at fledging and survival probability (Lindén *et al.* 1992), we used mass as an estimate of phenotypic quality. In a sub-sample of experimental nests, we also tested the immune response of nestlings to a novel antigen, phytohaemagglutinin (PHA). When nestlings were 10 days old, 70 µl PHA solution was injected into the webbing on their left wing. The thickness of the skin at the point of injection was measured immediately prior to injection and 24 h afterwards. The non-injected wing was measured at the same time and the immune response was

estimated as the increase in thickness on the injected wing, relative to the increase on the other wing. We controlled for consistent differences in the measurements taken by two persons by correcting each response by the mean immune response measured by either person. In total, we measured mass at fledging of 454 nestlings that were raised in 77 experimental broods and the immune response of 236 nestlings that were raised in 39 experimental broods. Since our data were unbalanced (as a consequence of naturally occurring mortality, such as predation of whole broods), we utilized Bayesian inference (Gelman *et al.* 2003) to examine the effect ($\mu_{0(ab)}$) of any given combination of species of nestling and parent on an individual nestling's immune response and weight. This is equivalent to a model with main effects of nestling and parental species and the interaction between the two factors. To control for the effects of the original nest (common genes) and rearing nest (common environment), we include these factors in the model as random effects, i.e. assuming they followed normal distributions with mean zero. Taking a Bayesian approach requires input of prior assumptions about the probability distribution of the model parameters, and these are updated using the likelihood of the data to yield the posterior probability distributions of each parameter in the model. We assigned uninformative priors for $\mu_{0(ab)}$ (mean = 0, variance = 0.00001), and for the variances of the random effects (inverse gamma distributions with a shape and scale of 0.00001). The model was fitted to the data using MCMC methods, as implemented by the WINBUGS package (Spiegelhalter *et al.* 2004). Three chains were run and, after a burn-in of 4000 iterations, we used the values taken from the next 6000 iterations. The parameter estimates were summarized through their posterior mode (i.e. the most probable value, equivalent to a maximum-likelihood estimate) and their 95% highest posterior density interval (HPDI). These are confidence intervals in which 95% of the distribution with the highest density is contained.

In 2003, the feeding rates, i.e. number of visits to the nest, of males and females to 19 experimental nests were measured for two 1 h periods on two consecutive mornings when nestlings were 8–10 days old. Observers were placed 30–35 m from the nest. In 2004, we recorded the behaviour of offspring and responses of adults using IR-light cameras (YOKO model YK-3045B, $f=3.6$ mm broad lens) that we placed inside the nest boxes. These cameras were connected to digital video cameras (JVC GR-D30), which were placed outside the nest-box. Nestlings were individually marked with water-soluble white out and recordings were made during 1 h periods. We used a digital videocassette recorder (Panasonic, DVCPRO model AJ-D230) to analyse the videotapes. The begging behaviour of nestlings and the responses of adults were recorded in 61 nests, 28 attended by collared flycatchers and 33 by pied flycatchers. In total, 1825 feeding events were scored. In 80 of these cases, two nestlings were fed during the same feeding event and, in one case, three were fed during the same feeding event. For each feeding event, all nestlings were assigned a begging rank depending on the order in which they started to beg for food and we noted which nestling the parent fed. We then calculated the mean begging rank for each individual nestling and the total number of times it got food. The difference in mean begging rank between nestlings of the two species is used as an estimate of their relative intensity of begging within any particular nest.

Table 1. Effects on (a) weight at fledging and (b) immune response of nestling flycatchers caused by nest of origin (common genes) and rearing nest (common environment). (Variance components are estimated as the mode of posterior variance component distributions from Markov Chan Monte Carlo simulations, and confidence intervals (CI) as the central 95% of the posterior distributions. The rearing nests consisted of approximately equal numbers of nestling collared and pied flycatchers.)

source	variance component	CI
<i>(a) weight at fledging</i>		
residual	0.4237	0.33–0.52
rearing nest	0.4706	0.33–0.60
nest of origin	0.1057	0.02–0.23
<i>(b) immune response of nestling</i>		
residual	0.623	0.51–0.77
rearing nest	0.396	0.22–0.75
nest of origin	0.0225	0–0.119

3. RESULTS

(a) Phenotypic quality of nestlings of the two species

Bayesian models indicated that a large proportion of the total variation caused by random effects in the nestlings' weight at fledging and immune response was attributed to the nest environment in which they were reared, while box of origin only explained a small amount of this variation (table 1). The models revealed that there were small but significant fixed effects of both the species of nestling and the species of the attending parent on the phenotypic quality of the nestlings. Nestling collared flycatchers outperformed their congeners in nests attended by pied flycatchers, but there was no significant difference between nestling collared and pied flycatchers in nests attended by collared flycatchers (figure 1a,b). Thus, nestling collared flycatchers experienced a growth advantage when reared by heterospecific foster parents, while nestling pied flycatchers did not.

(b) Offspring begging behaviour and parental response

A pairwise comparison between the mean begging rank of nestlings of the two species that were sharing the rearing nest revealed that nestling collared flycatchers on average started to beg relatively faster than their pied flycatcher foster siblings ($N=61$, $t=3.65$, $p=0.0005$). This difference in begging rank between nestling collared and pied flycatchers increased as the season progressed (ANCOVA: $F_{1,58}=4.35$, $p=0.04$; figure 2), but did not depend on the species of the attending parents (ANCOVA: $F_{1,58}=0.77$, $p=0.34$).

A general mixed linear model with rearing nest as a random factor revealed that an individual nestling's mean begging rank ($F_{1,60}=4.71$, $p=0.03$) rather than species' identity ($F_{1,60}=1.76$, $p=0.53$) predicted how many times it was fed by the parents. How many times a nestling was fed by the parents predicted the nestling's mass at fledging (general linear model, $F_{1,57}=3.79$, $p=0.05$) and tended to be related to its immune response (general linear model, $F_{1,21}=3.29$, $p=0.07$) when controlling for species.

We investigated whether adult pied and collared flycatchers responded differently to the begging nestlings. First, we analysed whether there were any differences

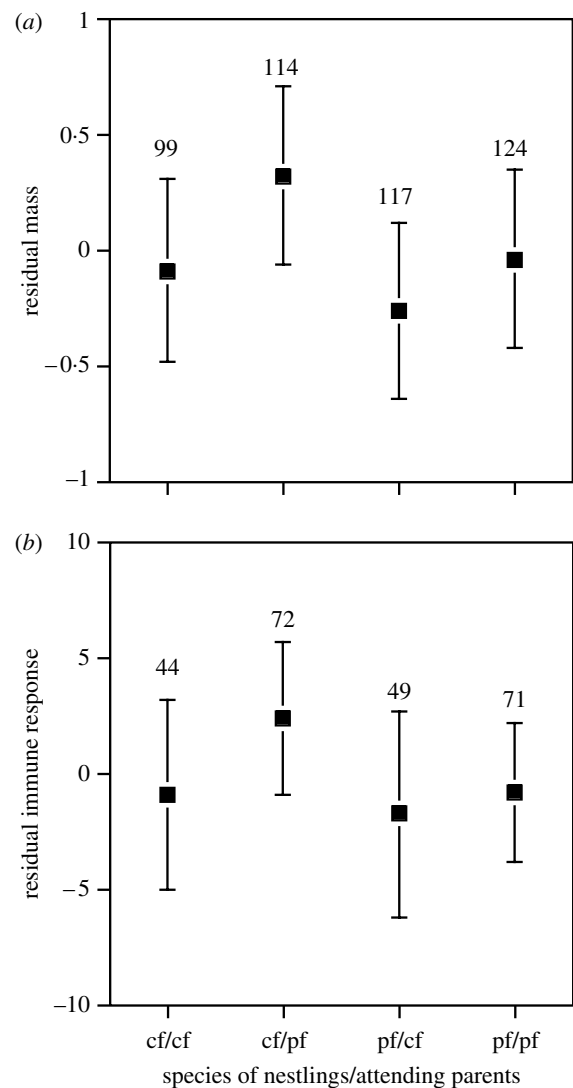


Figure 1. Mean effect of the species of the nestling and the rearing parent on a nestling's (a) weight at fledging and (b) residual immune response. Error bars indicate 95% confidence calculated using Bayesian inference with 'original nest' and 'rear nest' as random factors, and species of the nestling and the rearing parent as fixed factors. cf, collared flycatchers and pf, pied flycatchers.

between the species in the proportion of food deliveries that were allocated to either the first-begging young or the collared flycatcher young using generalized linear models (logit link) with the software package GLMSTAT 5.7.7. The proportion of feeding events, where the first-begging nestling was fed, did not differ depending on the species of the attending parents ($Z=0.015$, $p=0.99$, d.f.=63) nor did the proportion of all food deliveries that were provided to nestling collared flycatchers ($Z=0.6985$, $p=0.48$, d.f.=63). The data were overdispersed and the scaling parameters were therefore altered to 1.492 and 3.524, respectively. Within pairs, the male's feeding rate was a good predictor of the female's feeding rate (ANCOVA: $F_{3,76}=73.89$, $p<0.0001$) in both species (i.e. there was no significant interaction between male feeding rate and species on female feeding rate; ANCOVA: $F_{3,76}=0.51$, $p=0.48$). The overall feeding frequency of experimental broods ($N=80$, $t=0.62$, $p=0.54$, mean 28.9 ± 2.2 and 26.9 ± 2.2 for collared and pied flycatchers, respectively) did not differ significantly depending on the species of the

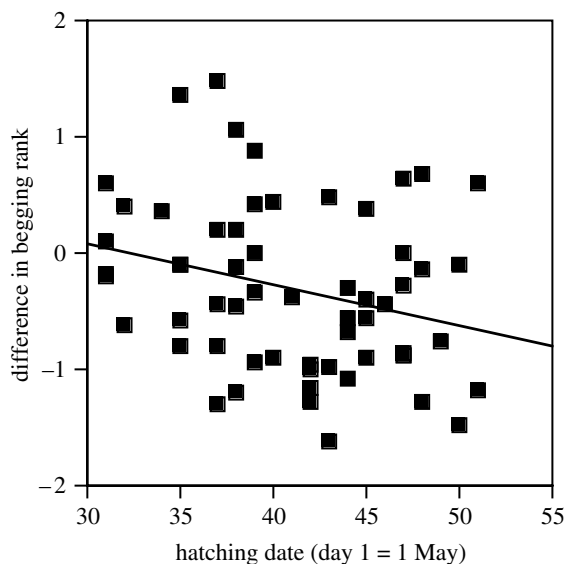


Figure 2. Difference in mean begging rank between nestling collared and pied flycatchers being raised in the same experimental nests in relation to timing of breeding (i.e. hatching date, where day 1 = 1 May). A relatively low begging rank means that offspring are relatively fast at starting begging. Nestling collared flycatchers on average increase their begging aggressiveness relatively more, as the season is progressing and food availability is getting lower.

attending parents. Thus, adult pied and collared flycatchers appear not to use different strategies in terms of their likelihood of feeding the first begging young nor do they appear to differ in their degree of resistance against a standardized composition of begging nestlings.

4. DISCUSSION

We cross-fostered pied and collared flycatcher nestlings and found that the parental environment was an important determinant of the phenotypic quality of the young. As much as 40% of variation in general condition and health (estimated as weight at fledging and intensity of T-lymphocyte-mediated immune responsiveness) was explained by 'rearing nest' (i.e. common environment), while only a small proportion, less than 10%, of variation was caused by 'nest of origin' (i.e. common genes). This is a small genetic component of variation considering that the young represent two different species. In these experimental nests, which consist of young of both species, nestling collared flycatchers begged more intensively for food than did nestling pied flycatchers. Furthermore, nestling collared flycatchers experienced a growth advantage (estimated as mass at fledging) when reared by heterospecific foster parents. However, we found no evidence suggesting that the latter result was a consequence of adult pied flycatchers being less resistant in terms of feeding intensively begging nestlings at a higher rate. Moreover, the difference between the species in begging intensiveness did not differ between experimental nests that were attended by collared or pied flycatchers, but increased as the season progressed, coinciding with the higher sensitivity of nestling collared flycatchers to the seasonal decline in food availability (Qvarnström *et al.* 2005).

The growth advantages experienced by nestling collared flycatchers reared by heterospecific foster parents contrast

with previous studies on laboratory mice (*Mus musculus*; Hager & Johnstone 2003) and burying beetles (*Nicrophorus vespilloides*; Lock *et al.* 2004). In these previous studies, cross-fostering experiments were performed between individuals belonging to the same species and the results provided evidence for positive genetic correlations between the parental environment and the offspring need, such that offspring experienced an advantage when reared by their genetic relatives. By contrast, our study appears to support a partially antagonistic coevolution between the parental environment and the offspring phenotype. The fact that nestling collared flycatchers begged more aggressively for food (when environmental and social factors were being controlled for) than nestling pied flycatchers is in line with a further evolutionary escalation of the parent-offspring conflict over food deliveries in collared flycatchers. However, the absence of evidence for a corresponding stronger resistance against begging nestlings of adult collared flycatchers implies that an alternative explanation is more probable. Since nestling collared flycatchers have a relatively higher intrinsic growth potential under favourable conditions, but are less robust to harsh conditions (Qvarnström *et al.* 2005), we instead suggest that the observed difference in begging intensity between the young of the two species honestly reflects a genetic difference in need, which the adults of both species responded to. This latter interpretation is supported by the fact that we found a difference in how the young of the two species changed their behaviour as the season was progressing. Nestling collared flycatchers increased their begging intensity relatively more as the season was progressing, matching their relatively higher sensitivity to the seasonal decline in food availability. Thus, the difference in begging behaviour between the two species seems to honestly indicate an intrinsic difference in offspring's physiological response to changes in the environment. Previous studies on great tits (*Parus major*; Kölliker *et al.* 2000) and burying beetles (Lock *et al.* 2004) have found positive correlations between offspring begging behaviour and parental response, i.e. parents with more demanding young have a stronger response. By contrast, a study on burrower bugs (*Sehirus cinctus*; Agrawal *et al.* 2001) found a negative correlation between offspring begging behaviour and parental response. Our study suggests that adult flycatchers of the two species use a very similar decision rule when they respond to nestlings' signalling of need and that most of the variation in response is determined by external factors.

One may argue that our experimental design makes it easier for us to detect genetically based differences in begging rate between nestlings of the two species than to detect genetic differences in response of the parents. This is because although the parents are responding to the same social composition of nestlings, we have not controlled for possible differences in external conditions (e.g. territory quality). The possibility to investigate differences between parents of the two species under the same environmental conditions arises from a regular occurrence of heterospecific pairings. In another study (Wiley *et al.* in press), we investigate possible species differences in parental care to test whether there are possible direct benefits from heterospecific pairing. We found that adult birds of the two different species provided similar food types to their offspring and that there were no differences in how the workload was shared between the sexes.

Apart from an exploitation of less resistant foster parents, a possible explanation for the observed advantage experienced by nestling collared flycatchers in hetero-specific nests is that pied flycatchers on average provide a better rearing environment and that nestling collared flycatchers are better able to exploit this due to a greater sensitivity to environmental conditions. Pied flycatchers appear not to feed young at a higher rate than collared flycatchers, but this does not rule out the possibility that adult pied flycatchers breed in better territories. Collared flycatchers have only been present in Sweden for the last 150 years. It is therefore probable that they are less adapted to predict and deal with local fluctuations in availability of different food items. We have indeed identified 'access to seasonally stable territories' as a direct benefit to female collared flycatchers from pairing with male pied flycatchers late in the season (Wiley *et al.* in press). Thus, although our experiment indeed demonstrates that the two species of flycatchers are 'ecologically similar' (they provide each others' offspring with suitable food), feed offspring at a similar rate and use similar allocation rules; pied flycatchers appear to be better able to choose optimal breeding territories under certain conditions.

In accordance with a previous study on food allocation in collared flycatchers (Rosivall *et al.* 2005), we found that individual young that begged more intensively indeed were fed more often. Offspring that were fed more often were in better general condition and health than the ones fed less often. One may then question why nestling pied flycatchers have not evolved a higher begging intensity? Should we interpret our results as nestling collared flycatchers, in fact, being better pre-adapted to the parental environment provided by pied flycatchers than nestling pied flycatchers? It is important to keep in mind that the reward (i.e. likelihood of being fed) in relation to an individual's begging intensity strongly depends on the behaviour of the whole brood. In a natural brood, consisting of only nestling pied flycatchers, less aggressive begging behaviour is likely to have a higher reward compared with the same behaviour in a brood partly comprising nestling collared flycatchers. The evolution of exaggerated begging display is limited by the costs imposed on the offspring through increased predation risk and energy expenditure (Macnair & Parker 1979; Mock & Parker 1997). Experimentally increased begging intensity has been demonstrated to result in both increased predation risk (Haskell 1994) and growth costs (Kilner 2001). Some costs involved with exaggerated begging behaviour may be mediated through increased testosterone levels, which is associated with begging behaviour in pied flycatchers (Goodship & Bachanan 2006). The crucial question then rather becomes why nestling collared flycatchers do not agree to reduce their overall effort spent on begging. However, conflicts among siblings may complicate the matter. Although a high begging frequency may on average be more costly, any particular nestling is selected to ensure its own fitness and try to obtain a larger share, leading to escalation of begging intensity above the optimum for the whole brood. A brood-size-manipulation experiment in great tits showed that begging intensity increased with increased clutch size, while the condition of offspring deteriorated despite full parental compensation (Neuenschwander

et al. 2003). By extension, a high begging rate could reduce the optimal brood size. Female collared flycatchers indeed lay smaller clutch sizes than female pied flycatchers (Qvarnström *et al.* 2005). Although individual collared flycatchers are relatively more demanding, an average natural brood of collared flycatchers may demand a similar total amount of food as a brood of pied flycatchers. Thus, the begging intensity of individual offspring is probably tightly linked with evolution of life-history traits in both young (e.g. development and growth) and parents (e.g. optimal litter/clutch size). Our findings illustrate that the evolution of offspring signals and parental response may be tightly integrated with the evolution of life-history traits. A plausible scenario being that an initial species divergence in nestling growth strategy in response to different selection pressures in allopatric populations has led to a difference in recourse need of individual nestlings of the two species. A greater need is in turn associated with stronger sibling competition that may have further reinforced the difference in need (since begging is in itself costly). Given that each individual nestling collared flycatcher is energetically more demanding, a higher parental provisioning rate and/or a smaller clutch size are to be expected.

In summary, we have shown that nestling collared flycatchers beg more intensively than pied flycatchers, when social and physical environmental conditions are being controlled for. We argue that the species divergence in this behaviour is caused by the underlying differences in life-history strategies (i.e. nestling collared flycatchers have a higher growth potential under good conditions, but are more prone to starvation under poor conditions) rather than by an arbitrary divergence in a coevolutionary arms race between parents and their offspring. It is important to note that our conclusion focuses on the evolution of the *difference* in nestling behaviour between the two species and that we do not claim that parent-offspring conflicts are irrelevant for the evolution of offspring behaviour and parental response in these two species.

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