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Parentally biased favouritism in relation to offspring sex in zebra finches

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Abstract Family conflicts over parental care result in offspring attempting to exert control using solicitation behaviours, whilst the parents are potentially able to retaliate through provisioning rules. However, the evolutionary interests of one parent may not necessarily support the evolutionary interests of the other parent, and such conflicts of interest may be expressed in how the two parents allocate the same form of parental care to individual offspring. Theory suggests that such parentally biased favouritism is a universally predicted outcome of evolutionary conflicts of interest, and empirical evidence suggests that parentally biased favouritism occurs in relation to offspring size and solicitation behaviours. However, unequivocal empirical evidence of parentally biased favouritism in relation to offspring sex is absent, due to being strongly confounded by sex differences in size and solicitation behaviours. Here, we present strong evidence for parentally biased favouritism in relation to offspring sex in zebra finches (*Taeniopygia guttata*), independent of the effects of chick size and begging intensity. Mothers preferentially provisioned sons over daughters, whilst fathers showed no bias, meaning that sons received more food than daughters. Parentally biased favouritism in relation to offspring sex facilitates parental control over evolutionary conflicts of interest and is probably more widespread than previously realised.

Keywords Parental care • Parentally biased favouritism • Offspring sex • Chick begging • Hatching asynchrony • Zebra finch

Introduction

Family conflicts over the amount and distribution of parental care (Trivers 1974) result in avian female parents attempting to exert control by determining brood sizes and hatching patterns, whilst offspring growth rates and begging behaviours are potential retaliatory mechanisms (Stoleson and Beissinger 1995; Mock and Parker 1997). For example, a parent arriving at the nest with food results in chicks revealing brightly coloured gapes, begging loudly and engaging in scramble competition to occupy the best position within the nest (Mock and Parker 1997; Kilner and Johnstone 1997; Budden and Wright 2001; Kilner 2002a). Such excessive begging is usually attributed to individual chicks attempting to influence provisioning behaviour, either by increasing their current individual chances of being fed (Mock and Parker 1997; Budden and Wright 2001), or by increasing the longer term provisioning rate of the parents (Mock and Parker 1997; Kilner 2002a). Traditionally, each offspring was expected to respond to the begging of rivals by increasing their own begging intensity in a selfish way. However, recent studies have demonstrated that kin selection strongly affects begging strategies, with the intensity of solicitation behaviours being inversely related with relatedness (Bell 2007; Boncoraglio and Saino 2008; Boncoraglio et al. 2008a, 2008b). For example, a recent study demonstrated that in communally breeding banded mongooses (*Mungus mungo*), potential rivals gain direct benefits from begging by littermates, so that begging behaviour becomes a collective enterprise (Bell 2007). Such a scenario is likely to be suboptimal for parents as the total brood demand increases, and as brood requirement is not absolute, additional food consumption contributes incrementally to offspring fitness

at a diminishing rate. Parent-offspring conflict over the amount and distribution of parental care results in parents attempting to exert control, for example, by determining the number of offspring and the extent of competitive hierarchies. Offspring can also influence the outcome of family conflict, through mechanisms such as siblicide, solicitation behaviours or changes to growth rates (Trivers 1974; Mock and Parker 1997; Royle et al. 1999, 2002; Budden and Wright 2001; Kilner 2002a; Lessells 2002a).

Parents are potentially able to retaliate against nestling begging behaviours through provisioning rules, yet the evolutionary interests of one parent may not necessarily support the evolutionary interests of its reproductive partner (Clutton-Brock 1991). Each parent will prefer their partner to invest more than they do themselves and this evolutionary conflict of interest may be expressed in how the two parents allocate the same form of parental care to individual chicks. Such parentally biased favouritism occurs when the two parents deviate from the other by preferentially feeding offspring in relation to their size, begging behaviours, or other attributes (Lessells 1998, 2002a, 2002b). Theoretical models suggest that parentally biased favouritism towards different types of offspring is the universally predicted outcome of evolutionary conflicts of interest, especially when the offspring are confined within the same nursery (Lessells 2002a). For example, hatching asynchrony, whereby the brood hatches out over a number of days, results in size differences between chicks (Magrath 1990; Stoleson and Beissinger 1995) and a number of studies have demonstrated that smaller chicks are preferentially provisioned by mothers (Stamps et al. 1987; Leonard and Horn 1996; Krebs et al. 1999; Dickens and Hartley 2007; Wiebe and Slagsvold 2009) and fathers (Westneat et al. 1995, but see Shiao et al. 2009). Despite several studies being unable to

detect any evidence of parentally biased favouritism in relation to offspring size (Weatherhead and McRae 1990; Malacarne et al. 1994; Slagsvold 1997; Smiseth et al. 1998; Tanner et al. 2008), the general pattern is of mothers feeding the smallest chicks preferentially (Lessells 2002a). Alternatively, chick begging intensity can influence parental provisioning rules (Mock and Parker 1997; Budden and Wright 2001; Lessells, 2002b) and a recent study showed that whilst canary (*Serinus canaria*) mothers paid decreasing attention to begging behaviours as chicks aged, the fathers' responsiveness remained constant (Kilner 2002b). While there is empirical support for favouritism in relation to offspring size and solicitation behaviours, there is no unequivocal evidence of favouritism in relation to offspring sex (Teather 1992; Leonard et al. 1994; Michler et al. 2010).

There is one report of parentally biased favouritism in relation to chick sex (Gowaty & Droge 1991), but in that study, sex is confounded to some extent by chick size and begging behaviour. Several other studies were unable to detect bias in relation to chick sex (Stamps et al. 1987; Teather 1992; Westneat et al. 1995; Michler et al. 2010), which is surprising as offspring sex plays an important role in parental fitness (Stamps 1990; Lessell 2002b). Even in the absence of sexual size dimorphism, parentally biased favouritism in relation to chick sex should be expected as the sexes differ in their competitive abilities and/or physiological requirements (Boncoraglio et al. 2008; Michler et al. 2010). Therefore, we should expect selection to favour those parents that discriminate directly on the basis of offspring sex, rather than a trait that variably may correlate with it, such as size or behaviour. Additionally, in the absence of size or

behavioural differences in offspring, which may correlate with sex, we should expect to find direct sexual discrimination by provisioning parents.

Here, we describe an experiment that simultaneously controlled zebra finch (*Taeniopygia guttata*) brood sizes and manipulated hatching synchrony, which allowed us to compare parental provisioning patterns and chick begging behaviours within broods that exhibited varying age and size differences between the chicks (Mainwaring et al. 2010). Theory suggests that parental fitness is maximised by a more equitable distribution of food than which maximises the fitness of individual offspring (Trivers 1974; Mock and Parker 1997; Parker et al. 2002). We predict that there will be parentally biased favouritism in relation to chick size and begging intensity in broods which exhibit high variation in age and size differences between chicks and parentally biased favouritism in relation to chick sex in broods which exhibit low variation in age and size differences between chicks.

Materials and methods

Manipulation of hatching patterns

Individual breeding females were placed into one half of a partitioned breeding cage (120 x 45 x 40 cm), and an arbitrarily selected, unrelated male was placed in the other half of the cage, but behind a partition so that neither bird could see the other. Before removal of the partition (pairing), each bird was weighed and had their head-bill length recorded. Pairs were randomly assigned to the asynchronous (n = 16) or synchronous (n = 12)

hatching regime, and nestboxes were checked each morning, when fresh eggs were made individually identifiable with a non-toxic indelible marker pen. In synchronous broods, eggs were removed on the day they were laid and replaced with an artificial egg, and returned on the day following clutch completion, in order to establish hatching synchrony. Eggs were kept in small, tissue lined bowls designed to closely match the nest conditions and all eggs were turned daily to prevent the yolk from settling. Overall hatching success was 94.5%: the manipulation of hatching patterns had no effect on the hatching success of synchronous and asynchronous clutches (t-test; $t = 0.852$, $d.f = 26$, $p = 0.871$). Parent birds at synchronously hatched nests had their incubation period extended by one day, because their eggs were returned on the day following clutch completion, which was not the case for parents at asynchronously hatched nests. Given that incubation is costly (Reid et al. 2002), and is likely to lower the body condition of the parent birds at synchronously hatched nests, the mass and head-bill length of each adult was recorded on the day following clutch completion. Consequently, we were able to examine changes in body condition between the day prior to the partition being removed at the beginning of the reproductive event and on the day following clutch completion. Reassuringly, there were no differences in changes in the body condition (as indicated by a composite index of mass in relation to head-bill length) of males (GLM; $F_{1,26} = 4.365$, $P = 0.652$) or females ($F_{1,26} = 5.835$, $P = 0.739$) with respect to hatching pattern. All of the synchronous broods hatched within a 24 hour interval and with the difference in hatching weight within broods not exceeding 0.5 grams (following Skagen 1988; Mainwaring et al. 2010). In all nests, brood sizes were maintained at four, either by the addition of extra

foster nestlings from other broods, or through fostering nestlings to other broods as necessary (following Royle et al. 2006).

Quantifying parental care and chick begging behaviours

Parental care and chick begging were assessed using video cameras recording through a hole in the back of each nestbox, which was covered when not recording. Videos were recorded in the mornings, beginning between 0900 and 1000, and all nests were filmed for three hours. Videos were recorded when chicks were 8-13 days old. Videos were not recorded either side of this period because parents tended to stand on the chicks when they were feeding them at a young age, thereby obscuring them from view, and after this period due to the risk of premature fledging (Royle et al. 2006). The mass of the chicks was recorded immediately prior to filming in order to analyse the effect of hatching patterns on the within-brood competitive hierarchy. There were no differences in the mean mass of the chicks in asynchronous and synchronous broods (t-test; $t = 0.650$, $d.f = 26$, $p = 0.522$) although the coefficient of variation in chick mass suggested that the mass of chicks was more variable in asynchronous than in synchronous broods (Levene's test for equality of variances; $F = 4.518$, $p < 0.001$). Birds were familiarised with the camera and tripod over a 24 hour period before recording (Royle et al. 2006).

Zebra finch parents regurgitate food for their chicks several times during a single feeding visit and chicks display some unusual begging behaviours, which involve tongue wagging and squirming away from, rather than towards, the feeding parent when begging is most intense (Royle et al. 2006), as opposed to the majority of other passerine

chicks (Budden and Wright 2001). Every parental feeding visit and associated chick begging behaviours during the three hours of filming were included in this study. Chicks were individually marked with white correction fluid on the head before videoing and all of the markings remained visible for the full duration of the videos, meaning that chicks were individually identifiable throughout. For each regurgitation event we recorded the sex of the provisioning parent, which chick received the food and the begging intensity of each chick. Parents were scored as having fed a chick when they inserted their bill into the chicks gaping mouth and they could be seen regurgitating, with characteristic heaves of their bodies, and chick begging was scored on a four point scale as follows: 0: no begging; 1: mouth open and slight movements of the tongue; 2: mouth open, more regular tongue movements and ‘rolling’ of the head and neck; 3: mouth open, rapid tongue movements, exaggerated head rolling and body ‘squirming’ (Royle et al. 2006). The experiment was conducted under the required conditions of ultraviolet, full spectrum, lighting (Bennett et al. 1996). The sex of the chicks was determined when they were 35 days old and had acquired sex-specific adult plumages (Zann 1996).

Statistical analyses

Models were fitted with the lme4 package (Bates, D. Maechler, M. & Dai, D. lme4: Linear mixed-effects models using Eigen and S4 classes, 2008.) in the R statistical programming environment (R Development Core Team 2006). Whether a chick received food or not upon each regurgitation event was considered a binary response, and the initial models were fitted using ‘hatching pattern’, ‘begging intensity’, ‘chick weight’, ‘chick sex’, and

‘parent sex’ as fixed effects. Random effects allowed the models to account for repeated measures for related data, and in this case, ‘parental pair’, ‘chick identity’, ‘chick weight’, and the interaction between ‘chick weight’ and ‘parental pair’ (Browne et al. 2007) were all fitted as nested random terms in each of the models. For each of the models, ‘chick weight’ was nested within ‘chick identity’, both of which were nested within ‘parental pair’ and those three effects were nested within the interaction between ‘chick weight’ and ‘parental pair’ (Browne et al. 2007). It quickly became apparent that of the above, ‘begging behaviour’ was the dominant effect and that the other terms were small by comparison. As interest lay in the finer structure of the relationships between these fixed effects it was decided to condition upon ‘begging intensity’, and, in effect, fit four separate models, one for each of the four begging intensities. Fixed terms in each of the full models were ‘hatching pattern’, ‘chick weight’, ‘chick sex’, and ‘parent sex’. Once again, ‘parental pair’, ‘chick identity’, ‘chick weight’, and the interaction between ‘chick weight’ and ‘parental pair’ (Browne et al. 2007) were all fitted as nested random terms in each of the models, as described above. Note that the interaction between ‘chick weight’ and ‘parental pair’ is a covariate and so was defined as a random slope in the models. For each of the models each random effect was sequentially removed from the model if its value was zero. Note that the lme4 package uses a Lapacian approximation to calculate p-values for its parameters. This involves using the second derivative of the function describing the parameter about the most likely value of that parameter to calculate a corresponding Gaussian. That Gaussian is then used to calculate the p-value for the parameter being zero. Consequently, the Gaussian does not have degrees of freedom as a parameter, and so it is not reported here. The use of likelihood information

based criteria meant that models could not be evaluated between levels of begging behaviour, but models were compared and evaluated within the same level of begging behaviour. The Akaike Information Criterion (AIC) was selected as the main criterion for model selection (Burnham and Anderson 2002), and a significance level of $\alpha = 0.05$ was adopted throughout.

Results

The initial model showed that the probability of individual chicks being fed increased markedly with increased begging intensity (Fig. 1). Meanwhile, hatching pattern was one of the effects examined, but was removed as it had no significant effect on the probability of individual chicks being fed (Table 1). As interest lay in the other covariates, a binary outcome model was conditioned on each of the four begging intensities from 0 (lowest) to 3 (highest). The probability of chicks receiving food whilst begging at intensity levels 0 and 1 was <0.5% and ~5% respectively (Table 1; Fig. 1), and at these low begging intensities, the optimal models included only the intercept as a fixed effect, meaning that no other covariates influenced the probability of chicks receiving food (Table 1; Fig. 1). At higher levels of begging intensity (scores 2 and 3), individual chicks had a higher probability of being fed (Fig. 1), and the optimal models indicated that ‘chick sex’, ‘parent sex’ and their interaction were significantly important. Mothers preferentially fed sons over daughters, while fathers showed no bias, meaning that on average, sons were more likely to receive food than were daughters (Table 1; Fig. 2). These patterns were

more pronounced at higher begging intensities, as chick weight became an increasingly important determinant of begging success (Table 1; Fig. 2).

The random effects from the optimal models indicate a large amount of variation in the log Odds of being fed between chicks, but apart from at begging level 2, there was very little variation between pairs of adults. This suggests that the probability of being fed did not vary greatly between breeding pairs, but the significant interaction between chick weight and pair indicates that chick weight within a brood has differing effects on the probability of being fed in different broods.

Discussion

We found that the probability of chicks being fed increased with chick weight and begging intensity, which is consistent with several other studies that have found that nestlings which are larger and begging more intensely have a higher probability of successfully soliciting food from their parents (Stamps et al. 1987; Westneat et al. 1995; Leonard and Horn 1996; Krebs et al. 1999; Budden and Wright 2001; Lessells 2002a). However, parentally-biased favouritism can take forms other than nestling size, and we found strong evidence that parents biased their provisioning efforts in relation to nestling sex. When chicks begged intensely, mothers were more likely to feed sons over daughters, while fathers showed no such bias, meaning that on average sons were more likely to receive food than were daughters. This supports predictions from theoretical models which predict that parentally biased favouritism is favoured by selection and

should be more intense and more widespread than is actually observed in birds (Lessells 2002a).

Meanwhile, we found no evidence to support the original prediction of parentally biased favouritism in relation to chick size and begging intensity in asynchronous broods and favouritism in relation to chick sex in synchronous broods. This is surprising as theory suggests that parentally biased favouritism is the universally predicted outcome of evolutionary conflicts of interest (Clutton-Brock 1991; Lessells 2002a). Parentally biased favouritism should therefore occur in relation to the size hierarchies created by hatching asynchrony within asynchronous broods (Glasse and Forbes 2002), whilst biases in relation to nestling sex are not expected to override the size differences. Consequently, we should only expect allocation rules to be based upon sex differences in synchronous broods, when the size hierarchies have been (experimentally) removed (Boncoraglio et al. 2008; Michler et al. 2010). It is unclear why parental provisioning rules did not differ between hatching regimes, although the strong evidence for parentally biased favouritism in relation to chick sex observed in our study may be due to parental trade-offs between the time needed for discrimination of chick sexes and foraging time being relaxed in domestic environments. In the wild, the benefits of discrimination are unlikely to outweigh the resulting lower foraging yield (Boncoraglio et al. 2008; Michler et al. 2010), whilst the provision of *ad libitum* food in our study may have increased the benefits of discrimination for the parents.

Differential investment in sons and daughters should result when the fitness returns per unit investment are higher for one sex than for the other (Lessells 2002a, 2002b). Whilst sex-specific parental provisioning behaviour has been widely

demonstrated in highly size dimorphic mammals where sons have higher energy requirements than daughters (Clutton-Brock et al. 1981), differential provisioning in relation to chick sex within the nest has only once been reported previously (Lessells 2002a). In contrast to our study, Eastern bluebird (*Sialia sialis*) fathers were more likely to provision daughters whilst mothers showed no bias (Gowaty and Droge 1991). There are two possible reasons why the two studies report different findings. First, in contrast to our study, the study of Eastern bluebirds never statistically controlled for chick size and begging behaviours, meaning that male Eastern bluebirds may have provisioned their daughters because they were begging more intensely. Second, the potential fitness returns for parents per unit investment may be higher for sons in zebra finches and for daughters in Eastern bluebirds (Lessells 2002a, 2002b). However, drawing firm conclusions from two studies is rather difficult and further studies of parentally biased favouritism in relation to offspring sex are required before generalisations are made.

Other studies report sex-biased provisioning of fledglings (Stamps et al. 1987; Price et al. 1987; Yasukawa et al. 1990; Byle et al. 1990; Teather 1992; Vega et al. 2007) resulting from brood division, when the acquisition of adult plumage also means that offspring gender is easily distinguishable to parents (Lessells 2002b), although other studies have found no evidence of sex-biased favouritism by provisioning parents (Leonard et al. 1994; Lessells 2002a). The parentally biased favouritism in relation to chick sex observed in our study may be due to parental trade-offs between the time needed for discrimination of chick sexes and foraging time being relaxed in domestic environments. The provision of *ad libitum* food in our study may have increased the benefits of discrimination for the parents, whilst the benefits of discriminating the gender

of individual chicks is unlikely to outweigh the resulting lower foraging yield in the wild (Boncoraglio et al. 2008; Michler et al. 2010). It is generally thought that parents are unable to discriminate the sex of individual offspring prior to them attaining adult plumage. However, a recent study showed that the two sexes differ in their begging behaviours and parents reacted to this difference by adjusting their provisioning rules (Boncoraglio et al. 2008). The mechanisms which allow parent zebra finches to discriminate the sex of individual chicks are currently unknown and further work could usefully examine how parents are able to identify offspring gender. Also, given that parent-offspring conflict is a co-evolutionary arms race, it may be surprising that female chicks do not try to match the appearance of their male siblings. Whilst it is likely to be impossible for individual offspring to conceal their sex in species with pronounced levels of sexual size dimorphism, it would presumably be easier in size monomorphic species such as zebra finches (Lessells 2002a, 2002b). Alternatively, it may be that the less favoured sex may actually be selected to be distinguishable from their siblings, as although their own direct fitness may be reduced, they are likely to be compensated by the inclusive fitness gained through their siblings (Lessells 2002b).

The evolution of parentally biased favouritism is fairly readily understood when more than one form of parental care is provided by two parents that show morphological, physiological or behavioural specialisations or differences (Lessells 2002a). For example, male and female parents commonly differ in the cost of reproduction, which results in the parent investing the least, favouring the most valuable offspring. Males and females may also differ in the benefits they receive from investment in different offspring, and for example, males are likely to invest less in offspring that may have resulted from extra-

pair copulations. Finally, parent-offspring conflict selects for the male and female parents to each feed a subset of their offspring so that dominant offspring do not determine parental provisioning rules (Lessells 2002a). However, the mechanisms and advantages of such a strategy are harder to understand in species where care appears to be provided only in one form (Lessells 2002a), as is the case in zebra finches (Zann 1996). There is likely to be positive selection for parental favouritism in relation to chick sex, as parental fitness is potentially maximised by a more equitable distribution of food than that which maximises the fitness of individual offspring, and chicks faced with parents using different provisioning rules may be less likely to be able to manipulate the parent-offspring conflict outcome in their favour (Lessells 2002a). However, sex biased provisioning may also evolve if offspring differ in their energy requirements or if advantages result from an association occurring between a parent and offspring of the opposite sexes (Stamps et al. 1987; Lessells 1998, 2002a). Such an association would allow for kin recognition to be reinforced, for the possibility of future inbreeding to be avoided and investment in the sex most likely to eventually compete for mates and territories to be avoided (Price et al. 1987; Yasukawa et al. 1990; Byle et al. 1990; Lessells 2002a; Vega et al. 2007). However, if a parent invests in offspring of the opposite sex in order to reduce current competition and gain a future benefit, then it is difficult to understand why the other parent does not also invest in offspring of the opposite sex. In our study, female parents favoured male offspring, but why male parents did not respond by favouring female offspring is unclear.

However, parent-offspring conflict is a co-evolutionary arms race and a single provisioning event involves interactions between parents and at least one chick (Trivers

1974; Mock and Parker 1997). Consequently, an alternative explanation for our findings is that parental provisioning patterns are controlled by one or more of the chicks, rather than the adults (Mock and Parker 1997; Kilner 2002a; Lessells 2002a). Unfortunately, our experimental design meant that we were unable to disentangle the relative influences of parents and their chicks in controlling provisioning rules. However, an experiment involving specific choice tests whereby parents are offered the opportunity to feed chicks, experimentally matched for size, begging strategy, brood size, brood sex ratio and hunger, and differing only in sex, would be very informative. Further work could usefully examine the proximate mechanisms underlying such sex-specific favouritism, with a view to determining how parents are able to identify the sex of individual offspring. For example, the results from specific choice tests in which an adult is offered the opportunity to feed matched chicks, differing only in sex, may prove illuminating. Further work should also examine the long-term consequences of parentally biased favouritism.

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Table 1 Summary of Generalised Linear Mixed Models examining parental provisioning rules at varying offspring begging intensities. The fixed and random terms of those models selected as the ‘best fit’ are shown, although for those models for begging levels 0 and 1, the ‘optimal’ model was the *null* model. For all models with parent and chick sex as significant terms, the reference categories were female and all fixed effects terms in these models are significant at $\alpha = 0.05$. Note that for random terms, the same ‘pair’ of birds sometimes bred both asynchronously and synchronously and so had two ‘nests’ included in the data set

Begging level	Fixed terms	Coefficients	Z value	P value	Random terms	Variance	AIC (null)
0	intercept	-7.69	-3.941	8.12×10^{-5}	chick	31.02	66.73
1	intercept	-2.90	-12.51	2×10^{-16}	chick Nest weight pair	0.50 0.51 0.002	1120
2	intercept parent (m) chick sex (m) parent:chick sex (m:m) weight	-1.87 0.14 0.27 -0.33 0.07	-7.927 2.168 2.229 -3.793 2.789	2.21×10^{-5} 0.03 0.02 0.00015 0.0052	chick	0.28	15728 (15743)
3	intercept parent (m) chick sex (m) parent:chick sex (m:m) weight	-2.37 0.36 0.67 -0.76 0.19	-7.58 2.51 3.73 -3.92 5.36	3.5×10^{-14} 0.012 0.00019 8.75×10^{-5} 8.01×10^{-8}	chick pair weight pair	0.15 0.03 0.001	3098 (3132)

Figure 1 Parental provisioning patterns in relation to chick begging intensity. Error bars represent 95% confidence intervals calculated from the fixed effects only. At begging intensity levels 0 and 1 no other effects were significant, thus the model for both of these levels of begging intensity takes the form of a single point. Model values are shown in Table 1

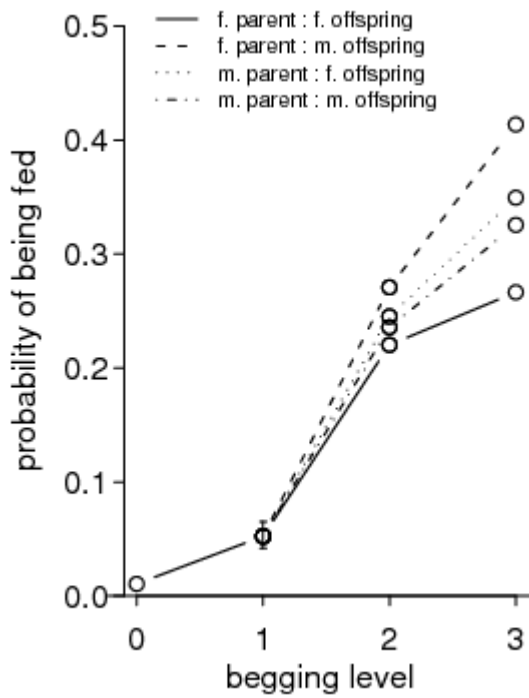


Figure 2 Parental provisioning patterns in relation to chick weight. Error bars are for guidance only and are calculated for chick weights 8, 9, 10 and 11 grams from the fixed effects at 95% confidence. Note that the inclusion of uncertainty from the random effects would increase the span of each bar and the log-odds calculated from the models have been translated to the probability scale, and explains the non-linearity in the response with weight. Model values are shown in Table 1

