Sense and sensitivity: responsiveness to offspring signals varies with the parents' potential to breed again

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How sensitive should parents be to the demands of their young? Offspring are under selection to seek more investment than is optimal for parents to supply, which makes parents vulnerable to losing future fitness by responding to manipulative displays. Yet, parents cannot afford to ignore begging and risk allocating resources inefficiently. Here, we show that parents may solve this problem by adjusting their sensitivity to begging behaviour in relation to their own likelihood of breeding again, a factor largely neglected in previous analyses of parent–offspring interactions. In two carotenoid-supplementation experiments on a New Zealand passerine, the hihi Notiomystis cincta, we supplemented adults to enhance their propensity to breed again, and supplemented entire broods to increase their mouth colour, thus enhancing their solicitation display. We found that adults that attempted two breeding attempts a season were largely insensitive to the experimentally carotenoid-rich gapes of their brood, whereas those that bred just once responded by increasing their rate of provisioning at the nest. Our results show that parents can strategically vary their sensitivity to begging in relation to their future reproductive potential. By restricting opportunities for offspring to influence provisioning decisions, parents greatly limit the potential for offspring to win parent–offspring conflict.

Keywords: reproductive value; parent–offspring conflict; signals; carotenoids; phenotypic plasticity

1. INTRODUCTION

A well-substantiated prediction from a life-history theory is that natural selection favours parents that strike the optimal balance between investment in current and future reproduction. In many taxa, including insects, amphibia, mammals and especially birds, this trade-off is potentially influenced by dependent young, who have evolved complex and elaborate solicitation displays [1] to elicit care from their parents [2–4]. When the intensity of display is an honest advertisement, offspring provide a useful source of information to parents about where to direct investment efficiently among their brood and end up producing lower quality offspring as a result [6]. Parents, therefore, have much to gain by attending to offspring displays, and can lose fitness by ignoring offspring begging entirely.

Nevertheless, there are potential future fitness costs for parents that rely too heavily on their offspring’s begging behaviour to determine the extent of current parental investment. Natural selection favours offspring that can attract investment at a greater level than is optimal for parents, and this generates parent–offspring conflict over the provision of parental investment [2]. The offspring’s key weapon in this evolutionary conflict of interest is information [7,8]. Offspring have private information about their own quality or condition, which parents are keen to know and which offspring can exaggerate to their own advantage [2,3]. Parents are thus placed in an evolutionary dilemma: they rely on begging behaviour to allocate resources efficiently to their brood, but their dependence on offspring begging makes them vulnerable to losing future fitness to exploitative current young.

Here, we consider a novel solution to this evolutionary dilemma, which was first implied in the initial theoretical analyses of genetic adaptations for parent–offspring conflict [3], but which has been largely neglected ever since (but see [6]). This is the idea that individual parents protect themselves from exploitation by their young by exhibiting plasticity in their responsiveness to begging, to the extent that they are sometimes strategically insensitive to their offspring’s demands [3]. In the years since this idea was first implied, the collective results of many empirical studies have shown that parents exhibit a spectrum of sensitivities to offspring solicitation behaviour, both among species, and among populations within species (see [9,10]). However, it is unclear precisely what influences the degree of parental sensitivity to offspring displays. One candidate factor is the parent’s potential for future reproduction [11]. Parents with high-residual reproductive value, such as those in better condition [12], have more to lose when exposed to potentially manipulative begging displays, all else being equal. Parents that are likely to breed again should therefore be more inclined to defend themselves against exploitation by reducing their sensitivity to their current offspring’s demands (e.g. [7,13,14]).

Carotenoids provide a useful experimental tool for testing this prediction because they can potentially influence parental behaviour as well as offspring signals. Previous work suggests that they can influence how parents allocate investment between current and future...
breeding attempts [15,16], with supplementation biasing investment towards future reproduction in birds (e.g. [17]). Furthermore, since they cannot be synthesized de novo by animals [18], circulating carotenoid levels can readily be manipulated through dietary supplementation, even in free-living birds. Adult birds exposed to dietary carotenoid supplementation in this way should therefore show a greater capacity to breed again than control individuals. In addition, carotenoids are the molecules responsible for pigmenting nestling mouths [19] and other colourful offspring traits (e.g. [20]), which may signal information regarding nestlings’ health and fitness (e.g. [21–26]). Carotenoids, however, are unlikely to convey information about hunger [27], or increase detectability in dark nest environments [28]. Offspring fed on a carotenoid-supplemented diet therefore exhibit a solicitation display of increased intensity [19,29,30], which parents sometimes respond to [24,29,30]. By analysing how parents respond to carotenoid-supplemented nestlings, we can assess parental sensitivity to nestling begging intensity.

The hihi Notiomystis cincta, a passerine bird endemic to New Zealand, is particularly amenable for experiments involving carotenoid supplementation. Nectar is a key food source for this species [31], and adults will take sugar water laced with variable concentrations of carotenoids from hummingbird-style feeders positioned close to the nest (e.g. [32]). These birds are also territorial [31], making it possible to target diet manipulations to specific marked breeding pairs. In addition, broods can be supplemented with carotenoids independently from their parents, by hand-feeding. By independently manipulating the carotenoids supplemented to adults and to nestlings, we created an experiment with three treatments in all: adults and nestlings both supplemented (A∗N∗), neither adults nor nestlings supplemented (A∗N−) and only nestlings supplemented (A+N−). A fourth treatment (A+N∗) was not possible because carotenoids ingested by adults were always passed on to their dependent young [32,33].

We used these manipulations to investigate how a parent’s capacity to breed again influenced its sensitivity to nestling begging displays, focusing specifically on the parent’s capacity for future reproduction within the same breeding season. We have previously shown that the nestlings involved in this experiment showed a high concentration of blood plasma carotenoids when supplemented (figure 1) [19], and that this intensified the pigmentation of the gape and rictal flanges [19]. Using a between-brood experimental design, here we predict that: (i) parents on a carotenoid-supplemented diet should show greater inclination to breed again than control parents and (ii) parents with a greater likelihood of breeding again should be less sensitive to their offspring’s begging displays. We measure sensitivity to begging as the rate of provisioning to broods with experimentally intensified gape pigmentation [19]: the higher the rate of provisioning when gapes are experimentally intensified, the more sensitive are parents.

2. MATERIAL AND METHODS  
(a) Study population  
We studied a reintroduced population of hihi on Tiritiri Matangi Island, New Zealand (36°36’ S, 174°53’ E) where all ca 150 individuals are identifiable by coloured leg ring combinations, and their ages are known. The hihi feeds predominantly on nectar, fruit and invertebrates, regurgitating all three food types to their young. To promote the conservation of this vulnerable species, supplementary sugar water (20% by weight) is provided ad libitum throughout the year at five fixed feeding locations. Males defend the paired female during her fertile period, and defend their territory throughout breeding. Females incubate clutches of 3–5 eggs, and perform the majority of provisioning visits to nestlings during the 30 day nesting period [34]. We monitored all nesting attempts (in wooden nestboxes) during the 2006–2007 breeding season. We recorded initiation of nest building, clutch size, date of completion and day of hatching (day = 0), and then recorded whether pairs re-nested, and if so the clutch size, hatching success and number of fledglings produced from second clutches to measure the investment in future reproduction. In this experiment, all pairs remained together throughout the breeding season.

(b) Carotenoid supplementation  
The experiment was designed to enhance carotenoid-based nestling displays, while minimizing any potential confounding effects of carotenoid-related effects on general chick quality [16]. We used carotenoids to manipulate these displays to investigate parental responses in a biologically relevant context, and to allow that parents may not respond to large differences in colour, per se, but other aspects of the carotenoid-based signal. Therefore, supplementation was restricted to just part of the nesting period. At 4 days of age, all first clutches containing at least three nestlings were assigned to one of three supplementation groups (as
described previously [19]). Broods did not differ among treatments in mean mass, and parents did not differ in age or circulating plasma carotenoid levels when assigned to the three experimental groups (for details see [19]).

Briefly, in each treatment, adults were provided with sugar water ad libitum, in hummingbird-type feeders familiar to the birds and placed 10 m from the nest, until the cessation of the experiment at day 13 (with the exception of day 11, see [19]). Nestlings in all treatments were hand-fed sugar water (same as that available to control parents) to satiation once daily, until day 12 after hatching. In the A\(^{-}\)N\(^{+}\) treatment (n = 10 nests), the sugar water was laced with the carotenoids lutein and zeaxanthin to supplement the adult’s diet (for further details of the carotenoids and dosage used, see [19,32]). Chicks in this treatment were supplemented with carotenoids indirectly by ingesting their parents’ carotenoid-enhanced diet during brood provisioning (R. Thorogood 2004–2006, personal observation), but were hand-fed with plain sugar water as a control. In the A\(^{-}\)N\(^{+}\) treatment (n = 11 nests), the feeders were filled with plain sugar water and nestlings were hand-fed plain sugar water. In the A\(^{-}\)N\(^{+}\) treatment (n = 10 nests), nestlings were hand-fed to satiation daily with the carotenoid-enhanced sugar solution while adults received plain sugar water in their feeders. Although adults may actively choose carotenoid supplements [35], adult hūi do not visit carotenoid-laden feeders differently to those presented with plain sugar water, nor do they use feeders in other pairs’ territories [24]. Providing hūi with sugar water close to their nests does not increase reproductive output (R. Thorogood 2004, unpublished data), and our main manipulation of sugar water and carotenoids was for a limited part of the breeding season (10 days of the 30 day nestling period). Our study population is free-living, but does receive supplemental food year round, on which the hūi’s survival is thought to depend [36]. Therefore, our manipulations are unlikely to produce markedly different parental responses than those to be expected from a completely non-manipulated population.

To measure the effects of carotenoids on parents, we sampled circulating carotenoid levels and morphometrics of parents during nest building, and again on day 14 using the techniques explained elsewhere [19]. In brief, adults were caught in temporary cage traps, body mass (0.01 g accuracy) and tarsus length (0.1 mm accuracy) were measured, and a small blood sample (ca 150 µl) was taken via brachial venipuncture. This was then immediately centrifuged and the plasma stored at -20 °C before subsequent carotenoid analyses were performed using high-performance liquid chromatography to extract total carotenoid concentration of each sample (for further details see [19,32]).

(c) Provisioning behaviour
The behaviour of parents at the nest was filmed using miniature infrared nest-box cameras (Henry’s Electronics Ltd) when nestlings were 13 days old. Cameras were installed the day prior to filming, and recordings were made to portable hard disc recorders (Archos AV700). Upon installation of the camera, parents inspected the camera and cables, but quickly resumed normal feeding (R. Thorogood 2006, personal observation). Each brood was filmed for 3 h, between 09.00 and 12.00 h with the first 15 min discarded for data collection, to allow parents to recover from the brief disturbance at the nest. For each feeding visit, the sex of the parent and the number of regurgitations given to the brood were recorded. These data were then used to calculate a visit rate (visits per hour) and regurgitation rate (regurgitations per hour) for each brood, and for each parent. As hūi parents can feed multiple offspring in a given visit, regurgitation rate is a better measure of parental attentiveness than the more commonly used nest visit rate. During observations of parental provisioning, the duration each nestling begged (moving from a resting position to when they relaxed, 0.01 s accuracy) was also recorded to calculate an average begging intensity for the brood. This allowed us to assess the effects of carotenoid supplementation on other aspects of the begging display than only colour.

(d) Statistical analyses
All statistics were performed using R v. 2.7.1 [37]. For analyses of parental carotenoid levels, we used linear mixed effects (LME) models with nest identity entered as a random intercept to control for the non-independence associated with the nesting territory and pair formation. A Fisher’s exact test was used to test propensities for re-nesting. Parental provisioning data were analysed with three different approaches using general linear models containing the fixed factor of carotenoid treatment, and its interaction with repeat breeding for two of these analyses. LME models were used to test for effects of parental sex and its interaction with treatment. The covariates of date during the season, average brood mass (0.01 g, as measured on day 11 as part of another experiment [19]), brood size and year were also entered where appropriate. We also included parental age in models because provisioning rules could be affected by age, with the current brood hypothesized to become of greater importance as parents senesce and reach their terminal investment [38,39]. In addition, maternal age can determine the breeding success in hūi [40]. All models were simplified using a backwards stepwise method until only terms that contributed significantly to the model remained. The validity of assumptions of normality and homoscedasticity was checked by visual inspection of residuals and normal probability plots, and where necessary response variables were log-transformed to meet these assumptions. Sample sizes varied between analyses when either not all data were collected for all parents, or when males did not feed (two nests, both A\(^{-}\)N\(^{+}\), but males were observed to feed outside the data collection period).

3. RESULTS
(a) Effect of carotenoid supplementation on adults
Supplementation to parents increased the concentration of carotenoids circulating in the plasma (figure 1), and to a similar degree in each sex (LME: treatment, F\(_{2,26}\) = 26.57, p < 0.0001; sex, F\(_{1,24}\) = 0.55, p = 0.47; sex × treatment, F\(_{2,22}\) = 0.43, p = 0.66). To test prediction (i), we investigated whether carotenoid supplementation influenced the likelihood that adults might breed again. Previous work has shown that naturally breeding hūi will sometimes attempt a second clutch during the breeding season, depending on environmental conditions and the timing of first clutches [40]. Few second clutches successfully yield fledglings, but those offspring that do survive to fledge are highly likely to recruit to the breeding population the following year [40]. Laying a second clutch is therefore a little like buying a ticket in a lottery, because it offers a low chance of a high-reproductive reward.
We found that supplementing adults with carotenoids increased the likelihood that they would lay a second clutch. In the year of our experiment, seven of the 10 pairs supplemented with carotenoids started to breed again, but only five of the 21 pairs supplemented only with sugar water laid a second clutch (Fisher's exact test, \( p = 0.02 \)). Here, a second clutch is defined as the nest-building and completion of a new clutch after a successful first breeding attempt. The greater inclination to breed again cannot be explained by adult mass during chick rearing, because this was unrelated to carotenoid supplementation (LME: treatment, \( F_{2,23} = 0.72, p = 0.50 \); sex, \( F_{1,14} = 178.12, p < 0.0001 \); sex \& treatment, \( F_{2,12} = 1.05, p = 0.38 \)). Nor is it related to parental age as this covariate was not significant to any model and was removed. However, because our study population has skewed age demography (R. Thorogood \& J. G. Ewen 2005, unpublished data), there was low replication of ages. This may provide an interesting avenue for future research. Unfortunately, our data are also too few to assess whether carotenoid supplementation increased the success of second clutches. Only two of the second clutches initiated by supplemented adults fledged young while just one pair of control adults produced a successful second brood.

(b) Effect of parental capacity to breed again on sensitivity to offspring begging

We investigated whether the parents’ capacity to breed again influenced their sensitivity to begging in three different ways.

(i) Probability of breeding again and sensitivity to offspring begging

First, we used our original experimental design to group parents by the probability that they would breed again. In other words, based on the results above, we regarded A⁻ parents as more likely to breed again than A⁺ parents. The advantage of this approach is that it groups parents by experimental treatment, with any intrinsic differences in parental quality being spread randomly across the treatments. The disadvantage is that the grouping is probabilistic: not all parents in the A⁻ treatment actually did breed again, and some parents in the A⁺ treatment did attempt a second brood.

(ii) Double-clutching and sensitivity to offspring begging

In our next analysis, we grouped parents by whether they actually did breed again or not (A⁻ parents laid a second clutch, A⁺ parents did not), irrespective of whether...
parents were themselves supplemented with carotenoids. We then compared responses of these parents with either their control (N−) or carotenoid-enhanced broods (N+). The advantage of this approach is that it tells us directly whether breeding twice in a season is correlated with provisioning decisions at the first brood. The disadvantage is that it is not possible to tell whether breeding twice in a season itself causes any differences in the sensitivity of parents to their first brood’s begging display because breeding twice is confounded with intrinsic differences in parental quality. Furthermore, because the birds effectively sorted themselves among the groupings in this analysis, our sample sizes are unevenly spread across treatment groups (2−N− = 9 nests, 2−N+ = 8, 2+N− = 2, 2+N+ = 8). Nevertheless, our results remain consistent with prediction (ii) (figure 3a). Birds that did not attempt a second clutch were as responsive to their brood’s begging display as parents that did attempt a second clutch, but only when the brood’s begging display was enhanced (carotenoid treatment × second clutch, F1,22 = 6.10, p = 0.02). Again, regurgitations declined during the season (F1,22 = 6.01, p = 0.02), but were not affected by the brood size (F1,20 = 0.80, p = 0.38) or parental age (F1,21 = 0.77, p = 0.39).

(iii) Double-clutching and sensitivity to offspring begging across different years
To be certain that the results of the analysis in §3b(ii) were not driven by artefacts of the low sample sizes in some treatments, we expanded our dataset (2−N− = 14 nests, 2−N+ = 13, 2+N− = 15, 2+N+ = 19) by including data from a previous experiment on the same population [24].

The earlier study measured parental response to begging using nest visit rate, rather than regurgitations to offspring, so to compare the two studies directly we used this measure as our index of parental sensitivity. After controlling for year, effects on parental provisioning (F1,56 = 27.54, p < 0.001), our results were once again in line with prediction (ii) (figure 3b, carotenoid treatment × second clutch: F1,56 = 6.42, p = 0.01). Importantly, parents responded in a similar way to the experimental treatment in different years (carotenoid treatment × second clutch × year: F1,51 = 0.15, p = 0.70). Neither date during season nor brood size contributed significantly to the model (date: F1,54 = 0.03, p = 0.86, brood size: F1,55 = 1.12, p = 0.30).

A further motivation for this analysis was that the results of this earlier work seemed superficially to be at odds with our experimental results, because they showed that carotenoid-supplemented parents were just as sensitive to their offspring’s carotenoid-enhanced displays (i.e. A−N+) as parents who had not received carotenoid supplementation and neither had their brood (i.e. A−N+). However, this study and that of Ewen et al. [24] are in agreement in showing that a reduced sensitivity to begging is correlated with attempting to breed twice in a single season. Where they differ is in how carotenoid supplementation to parents changes the likelihood of breeding twice, and this stems from a key methodological difference between the two studies. Unlike the experiment we report here, the earlier study involved prolonged supplementation with sugar water, from before egg-laying to fledging. The effects of the sugar water on the likelihood of re-nesting swamped any effects of carotenoid supplementation. Birds given sugar water were more likely to lay a second clutch that season than birds not given sugar water (table 2). Among the pairs given sugar water, there was no significant difference in the likelihood of relaying when adults were supplemented with carotenoids (table 2).

4. DISCUSSION
A substantial body of work shows the extent of parental investment in the current brood is limited by a high potential for future parental reproduction (reviewed by [41–43]). A similarly large literature also shows that current parental investment levels can be increased by intense offspring solicitation (reviewed by [7]). Our study provides a rare link between these two areas of work by showing that parents are less sensitive to their offspring’s displays when there is a high chance of breeding again. By highlighting the influence of cryptic variation in future reproductive potential, our results potentially explain why parents vary so much in their sensitivity to

Figure 3. Mean estimates of overall parental (a) regurgitation rates and (b) nest visit rates to control broods (N−) or broods enhanced with carotenoids (N+), depending on whether parents attempted a second clutch that season (2+) or not (2−). Data for (b) come from this experiment combined with data from reference [24]. See text for details of significance of the interaction terms. (a,b) Filled circles with solid line, 2+; open circles with dashed line, 2−.
numerous studies have considered how parental resources before in the parental care literature, although perhaps responsiveness to offspring displays has been documented to be determined. Carotenoid-related signals of food abundance remains condition) or context-dependent (i.e. driven by indirect, carotenoid availability [52]. Whether these changes in whatever the precise change in parental behaviour, our results show generally that parental responses to begging behaviour vary with respect to environmental conditions, in much the same way as female preferences for male sexual displays vary (reviewed by [51]), especially those that depend on carotenoid availability [52]. Whether these changes in provisioning were condition-dependent (i.e. driven by a direct, carotenoid-induced improvement in parental condition) or context-dependent (i.e. driven by indirect, carotenoid-related signals of food abundance) remains to be determined.

The condition- or context-dependency of parental responsiveness to offspring displays has been documented before in the parental care literature, although perhaps not always by using this terminology. For example, numerous studies have considered how parental resources are divided among the current brood, and how these decisions are related to environmental conditions or parental quality [4,53,54]. Condition- or context-dependent food allocation within broods is expected because parents pay a cost for supplying investment but the benefits of preferentially feeding some classes of offspring vary with the prevailing ecological conditions (reviewed by [4,55]). Our study complements this previous body of work by differing in three key respects. First, unlike the earlier research, we consider interactions between parents and the brood as a collective, rather than the way that resources are partitioned to individual offspring. In other words, we focus on the scope for interbrood conflict, rather than intrabrood conflict [7]. Second, since previous work has focused on the division of investment within broods, in many instances, it has not always been possible to discern whether experimentally induced changes in provisioning result from changes in the intensity of nestling competition (such as barging or jostling behaviour) or modulation of the parents' response to begging displays ([55], but see e.g. [56]). By contrast, in the experiments we present here, we can be certain that parents are controlling changes in provisioning behaviour. Finally, in much of the previous work, parental or environmental conditions have been inferred through correlations with food availability (e.g. [57]) or the hunger of the brood (e.g. [56]), meaning that it has not always been easy to determine causality (cf. [51]). Here, we have manipulated environmental conditions directly, by supplementing the parents' intake of dietary carotenoids, and we have shown that this has direct downstream consequences on parental provisioning decisions.

The striking begging displays used by young birds to solicit food have long been regarded a key behaviour determining the outcome of parent–offspring conflict over provisioning (e.g. [2,3,58,59]). Recent research has focused particularly on how the condition-dependence of these displays might influence conflict resolution [1,7,9,60,61], but has rather neglected individual variation in the way that parents react to these solicitation displays. Early theoretical analyses of parent–offspring conflict investigated how parental insensitivity to offspring begging might influence the outcome of parent–offspring conflict over provisioning [3]. The key conclusion was that parents could win this conflict by becoming insensitive to their offspring's demands, but only if this incurred no associated costs [3]. Otherwise, the outcome would be an evolutionary chase with no stable resolution [3]. Since then, experimental work has demonstrated that ignoring nestling begging is costly [62], so does this mean that parent–offspring conflict has no stable resolution in hihi? The original theoretical models assumed that parental insensitivity was genetically determined [3], whereas our work shows that it is phenotypically plastic, varying with parental condition or context. Flexible provisioning rules have recently been demonstrated in a small mammal [11], and residual reproductive value can limit the amount of investment parents are willing to give in a beetle species [63], suggesting that individual variation in parental responsiveness is widespread in nature.

Our study suggests that parents strategically balance the costs of ignoring their current brood's demands against the costs of losing future fitness through manipulative begging. By restricting the opportunities for offspring to influence provisioning decisions, parents...
can greatly reduce the scope for parent–offspring conflict (i.e. interbrood conflict) and therefore presumably supply investment at, or close to, their optimum. According to this view, parents ‘win’ parent–offspring conflict simply by virtue of their authority over their young, much as originally suggested by Alexander [64]. In future work, it will be interesting to determine just how common this pattern is, whether such flexible provisioning rules are determined by parental condition or context, and whether such phenotypic plasticity has directly influenced the evolution and elaboration of offspring begging displays.

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