

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

Rose Thorogood, John G. Ewen and Rebecca M. Kilner

*Proc. R. Soc. B* 2011 **278**, 2638-2645 first published online 26 January 2011  
doi: 10.1098/rspb.2010.2594

---

### **References**

**This article cites 55 articles, 18 of which can be accessed free**

<http://rsjb.royalsocietypublishing.org/content/278/1718/2638.full.html#ref-list-1>

**Article cited in:**

<http://rsjb.royalsocietypublishing.org/content/278/1718/2638.full.html#related-urls>

### **Subject collections**

Articles on similar topics can be found in the following collections

[behaviour](#) (2188 articles)

[ecology](#) (2598 articles)

[evolution](#) (2875 articles)

### **Email alerting service**

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

---

To subscribe to *Proc. R. Soc. B* go to: <http://rsjb.royalsocietypublishing.org/subscriptions>

---

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

Rose Thorogood<sup>1,\*</sup>, John G. Ewen<sup>2</sup> and Rebecca M. Kilner<sup>1</sup>

<sup>1</sup>Department of Zoology, Downing Street, Cambridge CB2 3EJ, UK

<sup>2</sup>Institute of Zoology, Zoological Society of London, Regents Park, NW1 4RY London, UK

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 to secure the greatest fitness returns (e.g. [3–5]). Experimental work has shown that parents that are then insensitive to the needs of their young allocate resources inefficiently 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

\* Author for correspondence ([rt303@cam.ac.uk](mailto:rt303@cam.ac.uk)).

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 ( $36^{\circ}36' S$ ,  $174^{\circ}53' E$ ) where

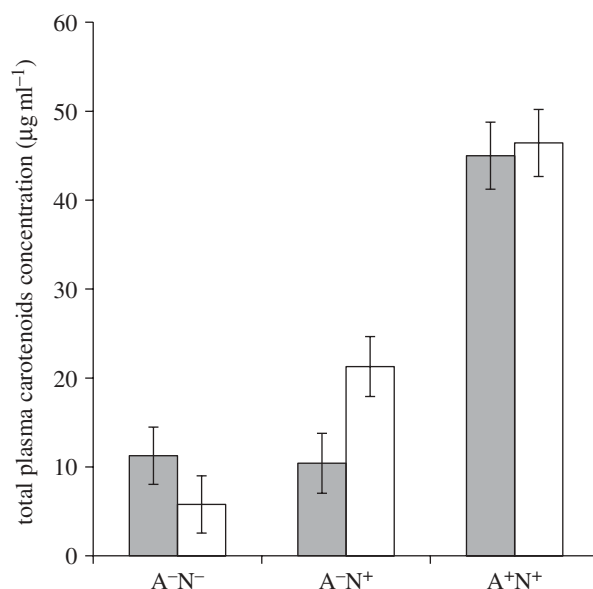


Figure 1. The effect of carotenoid supplementation on mean ( $\pm$  s.e., LME model estimates) concentration of total carotenoids circulating in the plasma of parents (grey bars) and their nestlings (open bars) in control broods ( $A^-N^-$ ), broods where only nestlings were supplemented with carotenoids ( $A^-N^+$ ), and broods where both parents and nestlings were carotenoid-enhanced ( $A^+N^+$ ). Only supplemented parents showed a significant increase in carotenoids, whereas both groups of supplemented nestlings were significantly greater than controls. Data for nestlings from reference [19].

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 nestling 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 nestling 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<sup>+</sup>N<sup>+</sup> 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<sup>-</sup>N<sup>-</sup> treatment ( $n = 11$  nests), the feeders were filled with plain sugar water and nestlings were hand-fed plain sugar water. In the A<sup>-</sup>N<sup>+</sup> 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 hihi 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 hihi 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 hihi'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  $\mu$ l) was taken via brachial venipuncture. This was then immediately centrifuged and the plasma stored at  $-20^{\circ}\text{C}$  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 hihi 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 hihi [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<sup>+</sup>N<sup>+</sup>, 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  $\times$  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 hihi 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.

Table 1. Effect of carotenoid treatment and covariates of average nestling mass per brood, date relative to first nest hatched, brood size and combined parental age of male and female on regurgitation rates. See figure 2 for statistical contrasts between the three carotenoid treatment groups ( $A^-N^-$ ,  $A^-N^+$  and  $A^+N^+$ ).

	$\beta$	d.f.	$F$	$p$
<i>final model</i>				
carotenoid treatment		222	11.29	0.0004
average nestling mass	$0.03 \pm 0.01$	122	9.73	0.005
date during season	$-0.01 \pm 0.004$	122	9.32	0.004
<i>covariates removed</i>				
brood size		120	0.27	0.61
parental age		121	1.36	0.24

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  $\times$  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.

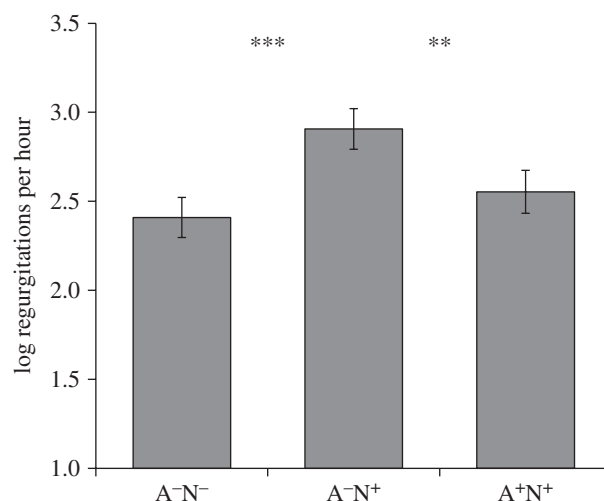


Figure 2. Mean estimates of overall parental regurgitation rates to control broods ( $A^-N^-$ ), broods where only nestlings were supplemented with carotenoids ( $A^-N^+$ ), and broods where both adults and nestlings were carotenoid-enhanced ( $A^+N^+$ ). Significance levels from *a priori* treatment contrasts are presented as  $0.001 > p < 0.01$  (\*\*), and  $0.0001 < p < 0.001$  (\*\*\*). There was no significant difference between  $A^-N^-$  and  $A^+N^+$  parents (see text).

Despite these caveats, the results matched prediction (ii). We found a significant difference between treatment groups in the rate at which parents regurgitated food to their brood (table 1, carotenoid treatment,  $F_{2,22} = 11.29$ ,  $p = 0.0004$ ). Supplemented broods, which displayed more richly pigmented gapes (see [19]), attracted more regurgitations (figure 2) but only when tended by control parents ( $A^-N^+$  versus  $A^-N^-$ : effect size =  $3.14 \pm 0.87$  regurgitations per hour,  $t$ -difference of model contrasts = 4.68,  $p = 0.0001$ ;  $A^-N^+$  versus  $A^+N^+$ : effect size =  $2.25 \pm 0.73$  regurgitations per hour,  $t$ -difference = 2.89,  $p = 0.009$ ). In other words, parents that were less likely to breed again were highly sensitive to the begging intensity of their brood. By contrast, parents more likely to breed again were largely insensitive to the carotenoid-induced changes in the begging display. Carotenoid-supplemented parents ( $A^+N^+$ ) regurgitated food at a similar rate to control parents ( $A^+N^+$  versus  $A^-N^-$ ; effect size =  $0.72 \pm 0.23$  regurgitations per hour,  $t$ -difference = 1.21,  $p = 0.24$ ; figure 2), even though their offspring begged with intensely coloured mouths that were more richly pigmented than those displayed by the hand-fed nestlings to control parents [19]). This change in parental behaviour is unlikely to be explained by differences among treatments in other components of the nestling begging display as chicks in the different carotenoid treatments did not differ in their begging intensity ( $A^-N^- = 18.00s \pm 1.73$ ,  $A^-N^+ = 19.71 \pm 2.11$ ,  $A^+N^+ = 23.74 \pm 2.75$ , GLM: treatment,  $F_{2,22} = 1.85$ ,  $p = 0.18$ ). Each sex changed their sensitivity to begging in a similar way (sex  $\times$  carotenoid treatment,  $F_{2,24} = 1.91$ ,  $p = 0.17$ ) although overall, females provided more food to the brood than males (LME: sex,  $F_{1,26} = 54.47$ ,  $p < 0.0001$ ).

#### (ii) Double-clutching and sensitivity to offspring begging

In our next analysis, we grouped parents by whether they actually did breed again or not ( $2^+$  parents laid a second clutch,  $2^-$  parents did not), irrespective of whether

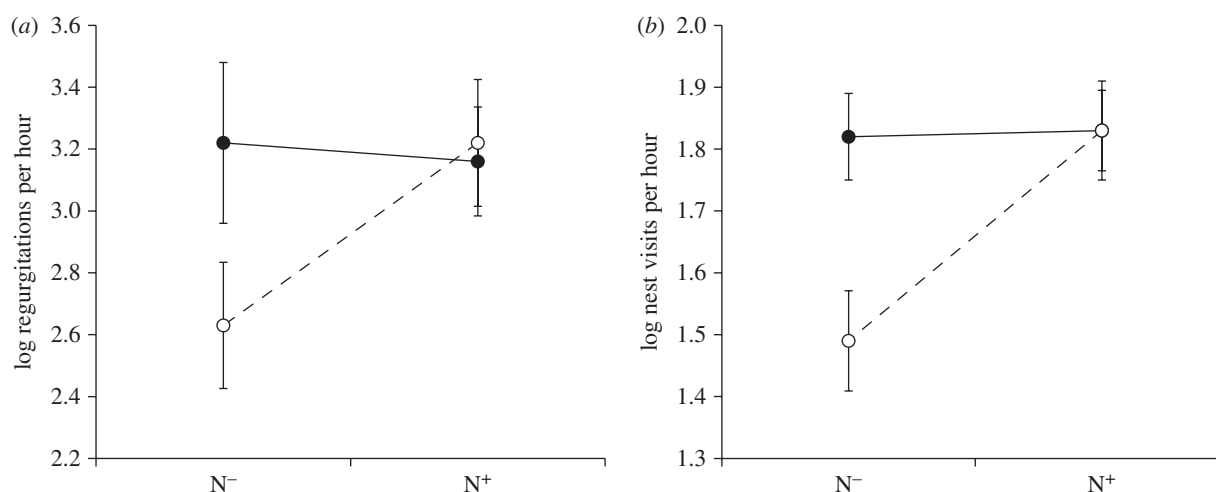


Figure 3. Mean estimates of overall parental (a) regurgitation rates and (b) nest visit rates to control broods (N<sup>-</sup>) or broods enhanced with carotenoids (N<sup>+</sup>), depending on whether parents attempted a second clutch that season (2<sup>+</sup>) or not (2<sup>-</sup>). Data for (b) 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<sup>+</sup>; open circles with dashed line, 2<sup>-</sup>.

parents were themselves supplemented with carotenoids. We then compared responses of these parents with either their control (N<sup>-</sup>) or carotenoid-enhanced broods (N<sup>+</sup>). 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<sup>-</sup>N<sup>-</sup> = 9 nests, 2<sup>-</sup>N<sup>+</sup> = 8, 2<sup>+</sup>N<sup>-</sup> = 2, 2<sup>+</sup>N<sup>+</sup> = 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,  $F_{1,22} = 6.10$ ,  $p = 0.02$ ). Again, regurgitations declined during the season ( $F_{1,22} = 6.01$ ,  $p = 0.02$ ), but were not affected by the brood size ( $F_{1,20} = 0.80$ ,  $p = 0.38$ ) or parental age ( $F_{1,21} = 0.77$ ,  $p = 0.39$ ).

### (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<sup>-</sup>N<sup>-</sup> = 14 nests, 2<sup>-</sup>N<sup>+</sup> = 13, 2<sup>+</sup>N<sup>-</sup> = 15, 2<sup>+</sup>N<sup>+</sup> = 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 ( $F_{1,56} = 27.54$ ,  $p < 0.001$ ), our results were once again in line with prediction (ii) (figure 3b, carotenoid treatment × second clutch:  $F_{1,56} = 6.42$ ,  $p = 0.01$ ). Importantly, parents responded in a similar way to the experimental treatment in different years (carotenoid treatment ×

second clutch × year:  $F_{1,51} = 0.15$ ,  $p = 0.70$ ). Neither date during season nor brood size contributed significantly to the model (date:  $F_{1,54} = 0.03$ ,  $p = 0.86$ , brood size:  $F_{1,55} = 1.12$ ,  $p = 0.30$ ).

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<sup>+</sup>N<sup>+</sup>) as parents who had not received carotenoid supplementation and neither had their brood (i.e. A<sup>-</sup>N<sup>-</sup>). 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

Table 2. In a previous study with our population of hihi [24], pairs supplemented with (a) food of any kind throughout laying and chick-rearing were more likely to lay a second clutch that season (Fisher's exact,  $p = 0.03$ ), but those supplemented with (b) carotenoids throughout laying and chick-rearing were no more likely to lay a second clutch that season than birds supplemented with plain sugar water, presented in an identical fashion (Fisher's exact,  $p = 0.73$ ). Note that provisioning data were unavailable for seven nests included in this analysis.

diet supplement	no. of pairs	
	attempted second clutch	did not attempt
(a) any additional food		
none	1	4
supplied	30	10
(b) carotenoids		
none	13	5
supplied	17	5

begging, both within and between species (reviewed in [10] and e.g. [21,24,25,27,29,44–50]). In our experiment, carotenoid-supplemented nestlings were not always fed more according to the intensity of their display—it depended on the future reproductive potential of their parents. Our results, therefore, provide one potential explanation for other anomalies in the literature, for example, by explaining why carotenoid-supplemented nestlings sometimes attract extra provisioning (e.g. [24,30,49]) and sometimes do not (e.g. [25,29,44,50]).

In our experiments, parent hihi appeared to be strategically insensitive to nestling begging, adjusting the extent of their sensitivity in relation to the fitness they stood to lose through exploitation by their current brood. However, we cannot tell from our results whether parents became equally insensitive to all aspects of the solicitation display, and ignored begging completely, or whether they simply ceased to respond to nestling mouth colour. Perhaps, some components of the begging display cannot convincingly exaggerate the brood's true needs, and these are the aspects that parents choose to ignore when defending their future reproduction. 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.

We thank the New Zealand Department of Conservation for permission to work on a conservation estate, the Supporters of Tiritiri Matangi Island for logistical support, Renske Kwikkel, Rebecca Gribble and Patricia Brekke for assistance in the field, and the Bird Behavioural Ecology Group, University of Cambridge for advice, support and helpful discussion. Kemin Industries donated carotenoids and Filiz Karadas instructed carotenoid extraction in the laboratory of the Department of Pharmacy, Yüzüncü Yıl University Research Hospital, Turkey. Animal ethics permission was granted by the Zoological Society of London. R.T. was supported by doctoral grants from the John Stanley Gardiner Fund, Benson Carslaw Fund, and the Cambridge Commonwealth Trust, J.G.E. was supported by a RCUK fellowship and Royal Society Research Grant, and R.M.K. was supported by a Royal Society University Fellowship. R.T. designed and performed experiments, analysed the data, and wrote the paper, J.G.E. provided data and comments on the manuscript, and R.M.K. co-wrote the paper. We are grateful to Sheena Cotter, Matt Bell, Uri Grodzinski, Camilla Hinde, Mathias Kölliker and Janine Wong for comments on drafts of this manuscript, and to Phill Cassey for statistical advice.

## REFERENCES

- Kilner, R. & Johnstone, R. A. 1997 Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.* **12**, 11–15. (doi:10.1016/S0169-5347(96)10061-6)
- Trivers, R. L. 1974 Parent–offspring conflict. *Am. Zool.* **14**, 249–264.
- Parker, G. A. & Macnair, M. R. 1979 Models of parent–offspring conflict. IV. Suppression: evolutionary retaliation by the parent. *Anim. Behav.* **27**, 1210–1235. (doi:10.1016/0003-3472(79)90068-X)
- Mock, D. W. & Parker, G. A. 1997 *The evolution of sibling rivalry*. Oxford, UK: Oxford University Press.
- Godfray, H. C. J. 1995 Signaling of need between parents and young: parent–offspring conflict and sibling rivalry. *Am. Nat.* **146**, 1–24. (doi:10.1086/285784)
- Grodzinski, U. & Lotem, A. 2007 The adaptive value of parental responsiveness to nestling begging. *Proc. R. Soc. B* **274**, 2449–2456. (doi:10.1098/rspb.2007.0658)
- Kilner, R. M. & Hinde, C. A. 2008 Information warfare and parent–offspring conflict. *Adv. Stud. Behav.* **38**, 283–336. (doi:10.1016/S0065-3454(08)00006-5)
- Hinde, C. A., Johnstone, R. A. & Kilner, R. M. 2010 Parent–offspring conflict and coadaptation. *Science* **327**, 1373–1376. (doi:10.1126/science.1186056)
- Royle, N. J., Hartley, I. R. & Parker, G. A. 2002 Begging for control: when are offspring solicitation behaviours honest? *Trends Ecol. Evol.* **17**, 434–440. (doi:10.1016/S0169-5347(02)02565-X)
- Hinde, C. & Kilner, R. M. 2007 Negotiations within the family over the supply of parental care. *Proc. R. Soc. B* **274**, 53–60. (doi:10.1098/rspb.2006.3692)
- Naguib, M., Kobera, M. & Trillmich, F. 2010 Mother is not like mother: concurrent pregnancy reduces lactating guinea pigs’ responsiveness to pup calls. *Behav. Process.* **83**, 79–81. (doi:10.1016/j.beproc.2009.10.005)
- McNamara, J. M., Houston, A. I., Barta, Z., Scheuerlein, A. & Fromhage, L. 2009 Deterioration, death and the evolution of reproductive restraint in late life. *Proc. R. Soc. B* **276**, 4061–4066. (doi:10.1098/rspb.2009.0959)
- Kölliker, M., Brodie III, E. D. & Moore, A. J. 2005 The coadaptation of parental supply and offspring demand. *Am. Nat.* **166**, 506–516. (doi:10.1086/491687)
- Hatchwell, B. J. 1999 Investment strategies of breeders in avian cooperative breeding systems. *Am. Nat.* **154**, 205–219. (doi:10.1086/303227)
- Pike, T. W., Blount, J. D., Lindström, J. & Metcalfe, N. B. 2007 Dietary carotenoid availability influences a male’s ability to provide parental care. *Behav. Ecol.* **18**, 1100–1105. (doi:10.1093/beheco/arm084)
- Blount, J. D. 2004 Carotenoids and life-history evolution in animals. *Arch. Biochem. Biophys.* **430**, 10–15. (doi:10.1016/j.abb.2004.03.039)
- Blount, J. D., Houston, D. C., Surai, P. F. & Møller, A. P. 2004 Egg-laying capacity is limited by carotenoid pigment availability in wild gulls *Larus fuscus*. *Proc. R. Soc. Lond. B* **271**, S79–S81. (doi:10.1098/rspb.2003.0104)
- Fox, D. L. 1979 *Biochromy: natural coloration of living things*. Berkeley, CA: University of California Press.
- Thorogood, R., Kilner, R., Karadas, F. & Ewen, J. G. 2008 Spectral mouth colour of nestlings changes with carotenoid availability. *Funct. Ecol.* **22**, 1044–1051. (doi:10.1111/j.1365-2435.2008.01455.x)
- Fitze, P. S., Tschirren, B. & Richner, H. 2003 Carotenoid-based colour expression is determined early in nestling life. *Oecologia* **137**, 148–152. (doi:10.1007/s00442-003-1323-3)
- Saino, N., Ninni, P., Calza, S., Martinelli, R., De Bernardi, F. & Møller, A. P. 2000 Better red than dead: carotenoid-based mouth coloration reveals infection in barn swallow nestlings. *Proc. R. Soc. Lond. B* **267**, 57–61. (doi:10.1098/rspb.2000.0966)
- Saino, N., Ambrosini, R., Martinelli, R., Ninni, P. & Møller, A. P. 2003 Gape coloration reliably reflects immunocompetence of barn swallow *Hirundo rustica* nestlings. *Behav. Ecol.* **14**, 16–22. (doi:10.1093/beheco/14.1.16)
- Berthouly, A., Helfenstein, F. & Richner, H. 2007 Cellular immune response, stress resistance and competitiveness in nestling great tits in relation to maternally transmitted carotenoids. *Funct. Ecol.* **21**, 335–343. (doi:10.1111/j.1365-2435.2006.01236.x)
- Ewen, J. G., Thorogood, R., Karadas, F. & Cassey, P. 2008 Condition dependence of nestling mouth colour and the effect of supplementing carotenoids on parental behaviour in the hihi *Notiomystis cincta*. *Oecologia* **157**, 361–368. (doi:10.1007/s00442-008-1073-3)
- O’Brien, E. L. & Dawson, R. D. 2008 Parasite-mediated growth patterns and nutritional constraints in a cavity-nesting bird. *J. Anim. Ecol.* **77**, 127–134. (doi:10.1111/j.1365-2656.2007.01315.x)
- Ewen, J. G., Thorogood, R., Brekke, P., Cassey, P., Karadas, F. & Armstrong, D. P. 2009 Maternally invested carotenoids compensate costly ectoparasitism in the hihi. *Proc. Natl Acad. Sci. USA* **106**, 12 798–12 802. (doi:10.1073/pnas.0902575106)
- Kilner, R. M. 1997 Mouth colour is a reliable signal of need in begging canary nestlings. *Proc. R. Soc. Lond. B* **264**, 963–968. (doi:10.1098/rspb.1997.0133)
- Dugas, M. B. & Rosenthal, G. G. 2010 Carotenoid-rich mouth colors influence conspicuousness of nestling birds.

- Behav. Ecol. Sociobiol.* **64**, 455–462. (doi:10.1007/s00265-009-0861-z)
- 29 Loiseau, C., Fellous, S., Haussy, C., Chastel, O. & Sorci, G. 2008 Condition-dependent effects of corticosterone on a carotenoid-based begging signal in house sparrows. *Horm. Behav.* **53**, 266–273. (doi:10.1016/j.yhbeh.2007.10.006)
- 30 Helfenstein, F., Berthouly, A., Tanner, M., Karadas, F. & Richner, H. 2008 Nestling begging intensity and parental effort in relation to prelaying carotenoid availability. *Behav. Ecol.* **19**, 108–115. (doi:10.1093/beheco/arm103)
- 31 Higgins, P. J., Peter, J. M. & Steele, W. K. 2001 *Handbook of Australian, New Zealand & Antarctic birds*. Melbourne, Australia: Oxford University Press.
- 32 Ewen, J. G., Thorogood, R., Karadas, F., Pappas, A. C. & Surai, P. F. 2006 Influences of carotenoid supplementation on the integrated antioxidant system of a free living endangered passerine, the hihi *Notiomystis cincta*. *Comp. Biol. Physiol. A* **143**, 149–154. (doi:10.1016/j.cbpa.2005.11.006)
- 33 Blount, J. D., Houston, D. C. & Møller, A. P. 2000 Why egg yolk is yellow. *Trends Ecol. Evol.* **15**, 47–49. (doi:10.1016/S0169-5347(99)01774-7)
- 34 Ewen, J. G. & Armstrong, D. P. 2000 Male provisioning is negatively correlated with attempted extrapair copulation frequency in the stitchbird or hihi. *Anim. Behav.* **60**, 429–433. (doi:10.1006/anbe.2000.1485)
- 35 Senar, J. C., Moller, A. P., Ruiz, I., Negro, J. J., Broggi, J. & Hohtola, E. 2010 Specific appetite for carotenoids in a colorful bird. *PLoS ONE* **5**, e10716. (doi:10.1371/journal.pone.0010716)
- 36 Armstrong, D. P. & Ewen, J. G. 2001 Testing for food limitation in reintroduced hihi populations: contrasting results for two islands. *Pac. Conserv. Biol.* **7**, 87–92.
- 37 R Development Core Team. 2010 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.R-project.org>.
- 38 Clutton-Brock, T. H. 1984 Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* **123**, 212–229. (doi:10.1086/284198)
- 39 Velando, A., Drummond, H. & Torres, R. 2006 Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. *Proc. R. Soc. B* **273**, 1443–1448. (doi:10.1098/rspb.2006.3480)
- 40 Low, M., Pärt, T. & Forslund, P. 2007 Age-specific variation in reproduction is largely explained by the timing of territory establishment in the New Zealand stitchbird *Notiomystis cincta*. *J. Anim. Ecol.* **76**, 459–470. (doi:10.1111/j.1365-2656.2007.01234.x)
- 41 Stearns, S. C. 1990 *The evolution of life histories*. New York, NY: Oxford University Press.
- 42 Lessells, C. M. 1991 The evolution of life histories. In *Behavioural ecology: an evolutionary approach* (eds J. R. Krebs & N. B. Davies), pp. 32–68. 3rd edn. Oxford, UK: Blackwell Scientific Publications.
- 43 Székely, T., Webb, J. N., Houston, A. I. & McNamara, J. M. 1996 An evolutionary approach to offspring desertion in birds. *Curr. Ornithol.* **13**, 271–330.
- 44 Biard, C., Surai, P. F. & Møller, A. P. 2005 Effects of carotenoid availability during laying on reproduction in the blue tit. *Oecologia* **144**, 32–44. (doi:10.1007/s00442-005-0048-x)
- 45 Kilner, R. M., Noble, D. G. & Davies, N. B. 1999 Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature* **397**, 667–672. (doi:10.1038/17746)
- 46 Götmark, F. & Ahlström, M. 1997 Parental preference for red mouth of chicks in a songbird. *Proc. R. Soc. Lond. B* **264**, 959–962. (doi:10.1098/rspb.1997.0132)
- 47 Heeb, P., Schwander, T. & Faoro, S. 2003 Nestling detectability affects parental feeding preferences in a cavity-nesting bird. *Anim. Behav.* **66**, 637–642. (doi:10.1006/anbe.2003.2238)
- 48 Dugas, M. B. 2009 House sparrow, *Passer domesticus*, parents preferentially feed nestlings with mouth colours that appear carotenoid-rich. *Anim. Behav.* **78**, 767–772. (doi:10.1016/j.anbehav.2009.07.009)
- 49 Remeš, V., Krist, M., Bertacche, V. & Stradi, R. 2007 Maternal carotenoid supplementation does not affect breeding performance in the great tit *Parus major*. *Funct. Ecol.* **21**, 776–783.
- 50 Tschirren, B., Fitze, P. S. & Richner, H. 2005 Carotenoid-based nestling colouration and parental favouritism in the great tit. *Oecologia* **143**, 477–482. (doi:10.1007/s00442-004-1812-z)
- 51 Cotton, S., Small, J. & Pomiankowski, A. 2006 Sexual selection and condition-dependent mate preferences. *Curr. Biol.* **16**, R755–R765. (doi:10.1016/j.cub.2006.08.022)
- 52 Grether, G. F., Kolluru, G. R., Rodd, F. H., De La Cerda, J. & Shimazaki, K. 2005 Carotenoid availability affects the development of a colour-based mate preference and the sensory bias to which it is genetically linked. *Proc. R. Soc. B* **272**, 2181–2188. (doi:10.1098/rspb.2005.3197)
- 53 Forbes, S. & Mock, D. W. 2000 A tale of two strategies: life-history aspects of family strife. *Condor* **102**, 23–34. (doi:10.1650/0010-5422(2000)102[0023:ATOTSL]2.0.CO;2)
- 54 Magrath, R. D. 1990 Hatching asynchrony in altricial birds. *Biol. Rev.* **65**, 587–622. (doi:10.1111/j.1469-185X.1990.tb01239.x)
- 55 Clutton-Brock, T. H. 1991 *The evolution of parental care*. Princeton, NJ: Princeton University Press.
- 56 Kilner, R. M. 2002 Sex differences in canary *Serinus canaria* provisioning rules. *Behav. Ecol. Sociobiol.* **52**, 400–407. (doi:10.1007/s00265-002-0533-8)
- 57 Magrath, R. D. 1989 Hatching asynchrony and reproductive success in the blackbird. *Nature* **339**, 536–538. (doi:10.1038/339536a0)
- 58 Dawkins, R. 1976 *The selfish gene*. Oxford, UK: Oxford University Press.
- 59 Zahavi, A. 1977 Reliability in communication systems and the evolution of altruism. In *Evolutionary ecology* (eds B. Stonehouse & C. M. Perrins), pp. 253–259. London, UK: MacMillan.
- 60 Parker, G. A., Royle, N. J. & Hartley, I. R. 2002 Intrafamilial conflict and parental investment: a synthesis. *Phil. Trans. R. Soc. Lond. B* **357**, 295–307. (doi:10.1098/rstb.2001.0950)
- 61 Godfray, H. C. J. & Johnstone, R. A. 2000 Begging and bleating: the evolution of parent–offspring signalling. *Phil. Trans. R. Soc. Lond. B* **355**, 1581–1591. (doi:10.1098/rstb.2000.0719)
- 62 Grodzinski, U., Erev, I. & Lotem, A. 2008 Can hungry nestlings be trained to reduce their begging? *Behav. Ecol.* **19**, 116–125. (doi:10.1093/beheco/arm107)
- 63 Ward, R. J. S., Cotter, S. C. & Kilner, R. M. 2009 Current brood size and residual reproductive value predict offspring desertion in the burying beetle *Nicrophorus vespilloides*. *Behav. Ecol.* **20**, 1274–1281. (doi:10.1093/beheco/arp132)
- 64 Alexander, R. D. 1974 The evolution of social behaviour. *Ann. Rev. Ecol. Syst.* **5**, 325–383. (doi:10.1146/annurev.es.05.110174.001545)