Detectability matters: conspicuous nestling mouth colours make prey transfer easier for parents in a cavity nesting bird

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An often underappreciated function of signals is to notify receivers of the presence and position of senders. The colours that ornament the mouthparts of nestling birds, for example, have been hypothesized to evolve via selective pressure generated by parents’ inability to efficiently detect and feed nestlings without such visually conspicuous targets. This proposed mechanism has primarily been evaluated with comparative studies and experimental tests for parental allocation bias, leaving untested the central assumption of this detectability hypothesis, that provisioning offspring is a visually challenging task for avian parents and conspicuous mouths help. To test this assumption, I manipulated the mouths of nestling house sparrows to appear minimally and maximally conspicuous, and quantified prey transfer difficulty as the total duration of a feeding event and the number of transfer attempts required. Prey transfer to inconspicuous nestlings was, as predicted, more difficult. While this suggests that detectability constraints could shape nestling mouth colour evolution, even minimally conspicuous nestlings were not prohibitively difficult for parents to feed, indicating that a more nuanced explanation for interspecific diversity in this trait is needed.

1. Introduction

Signals vary both in the extent to which they are detectable by receivers and in the extent to which, once detected, they elicit a desirable response [1]. Variation in either signal function can drive variation in sender fitness, with the relative importance of each reflecting numerous social and environmental factors [1,2]. While the most easily detected signal sometimes also effects the most favourable response, this positive relationship is not a necessary one. These signal properties might be independent or even trade-off against one another [2–5]. A key component of explaining and predicting signal diversity is, then, understanding the circumstances under which the fitness benefits of signals arise from variation in their detectability versus variation in the response of receivers that have detected them.

The colourful mouthparts of nestling birds are traits hypothesized to have evolved both because they signal qualitative information (e.g. quality) and because, when highly conspicuous, they aid parents in food delivery [6–12]. As originally framed, the latter ‘detectability hypothesis’ was built on the proposition that, for avian parents, transferring prey to offspring is a visually challenging task that can be made easier by conspicuous nestling mouths [6]. Two indirect lines of evidence are consistent with this hypothesis. First, parents respond differently to experimental manipulations of nestling mouth colour with relatively high and relatively low ambient light at the nest [11–13]. Second, the rictal flanges outlining nestling mouths are brighter (reflect more total light) in species that use dim nests (e.g. cavities) than in those that use more well-lit nests (e.g. open cups [7–9]).
Parental allocation bias towards conspicuous nestlings has been interpreted as evidence that parents have difficulty feeding inconspicuous mouths [11–13], but this design does not distinguish detectability constraints from active parental preferences for colours [4]. Furthermore, while the detectability hypothesis cannot be used to predict the magnitude of allocation biases arising from reduced detection, parents do successfully provision nesting mouths manipulated to the lower limits of detectability [13], suggesting that the assumed visual constraint underlying the detectability hypothesis warrants further scrutiny.

I tested the key assumption of the detectability hypothesis, that parents have difficulty feeding nestlings with inconspicuous mouth colours, by manipulating the conspicuousness of nestling house sparrow (Passer domesticus) mouths and observing parental prey transfer. I manipulated nestling mouths so as to either minimize or maximize achromatic conspicuousness, the feature of colour most likely to mediate detectability in dark nests [4,14] and the one that is more intense in dark-nesting species [8,9]. I observed the parents feeding these nestlings and quantified two proxies for the difficulty of prey transfer: the total time required for transfer, and number of feeding attempts required before offspring consumed prey. Unlike parental allocation patterns [11–13], these parameters should primarily reflect parental ability to provision nestlings independently of any active preferences for colour [10–12]. If prey transfer is indeed a task made easier by visually conspicuous mouthparts, parents should more easily transfer food to conspicuous nestlings.

2. Material and methods

(a) Study animals

I studied a free-living population of house sparrows breeding in nest-boxes in Norman, OK, USA [4,10,15]. Early in the 14 day nestling period, when broods were 5 to 6 days old (mean ± s.d. = 5.4 ± 0.7 days), I weighed all members of 16 broods to the nearest 0.01 g and selected the two most similar individuals for this experiment. Pre-treatment mass of experimental broodmates did not differ (paired t15 = 0.1, p = 0.989). These two nestlings were removed for 10–15 min, with the remainder of the brood left in the nest. Experimental chicks were then returned to the nest and non-participating brood members removed and cared for during the 90 min trial. I recorded parent–offspring interactions with cameras inside the nest-box (electronic supplementary material, appendix S1). Although I did not score begging intensity, parents provisioned experimental nestlings similarly during trials (paired t15 = 0.341, p = 0.738), suggesting no treatment differences in mean satiety.

(b) Manipulation of achromatic conspicuousness

I manipulated nestling conspicuousness by altering rictal flange colour. When nestling house sparrows beg, their naturally yellow flanges are juxtaposed by a red gape and a background that might include nesting material and the integument of that nestling or its broodmates [3,7–9]. To control the background against which flanges appeared, I fitted nestlings with black felt collars, like those worn by pets after surgery (electronic supplementary material, figure S1). I painted flanges with acrylic paints [10]: a white paint (no. 02505, Delta Creative, City of Industry, CA, USA) maximized the difference in total light reflected (achromatic contrast) between the flange, background and gape, whereas a grey paint (no. 02436, Delta Creative) minimized contrast (figure 1 and electronic supplementary material, figure S1). After trials, I removed paints and returned all chicks to the nest.

I quantified two proxies for prey transfer difficulty at each feeding event. First, I measured total duration of the feeding event as the time, to the nearest second, between the parent’s bill crossing the portal threshold and the last contact between the parent’s bill and the offspring’s mouth. If neither nestling was gaping when the parent entered, I defined the initiation of gaping as the beginning of the event, and if the parent exited and re-entered the box before feeding, I considered the time of final re-entry as the start. Second, I counted transfer attempts, defined as the parent’s bill coming into and then breaking contact with the nestling’s mouth (see electronic supplementary material, videos S1 and S2 for examples). These variables were positively correlated (r = 0.69, n = 162, p < 0.001). While it is possible that total event duration could have captured parental latency associated with encountering unfamiliar or non-preferred nestling colours [13], this potential alternative to the interpretation of ‘transfer difficulty’ seems particularly unlikely to explain any treatment effect on food transfer attempts. To ensure the isolation of treatment effects, I excluded from analysis events (n = 17) in which prey items were split or initially offered to one nestling but eventually consumed by the other. Following previous work in this population [15], I scored prey size as ‘tiny’ (greater than 0.6 cm), ‘medium’ (ca 1 cm) or ‘enormous’ (greater than 2 cm), hereafter T, M and E, respectively.

(c) Statistical analyses

Across all feeding events (n = 162 from 16 broods), I used a linear‐mixed model to compare total feed duration between treatments, and a generalized linear mixed model with Poisson error distribution to compare the number of feeding attempts. Both models included the fixed effects of treatment (conspicuous or inconspicuous), prey size (T, M, E), nestling mass and all interactions, and the random effects of nest and chick and parent identity within nest. I sequentially removed non‐significant fixed effects but retained all random effects. Total feed duration was log10 transformed to meet the assumption of normality. Degrees-of‐freedom for fixed effects were estimated using the Kenward–Rogers correction. I used SAS v. 9.2 for all analyses (SAS Institute, Cary, NC, USA).

3. Results

Feedings to inconspicuous nestlings were longer in duration (F1,152 = 8.5, p = 0.004; figure 2a) and required more
feeding attempts ($F_{1,157} = 26.7$, $p < 0.001$; figure 2b). The effect of nestling mass was negative on both feed duration ($F_{2,15.9} = 7.2$, $p = 0.016$, $\beta \pm$ s.e. = $-0.03 \pm 0.01$) and the number of feeding attempts per event ($F_{1,15.5} = 6.8$, $p = 0.020$, $\beta \pm$ s.e. = $-0.07 \pm 0.03$), meaning that food was delivered more easily to heavier nestlings. Larger prey items took longer to transfer ($F_{2,157} = 5.43$, $p = 0.005$; figure 2c), but did not require significantly more transfer attempts ($p = 0.139$; figure 2d).

4. Discussion

Parent house sparrows took approximately 30% longer to transfer prey to nestlings with minimally conspicuous mouths than to those with maximally conspicuous mouths, and feedings to inconspicuous offspring required approximately 19% more transfer attempts. These patterns demonstrate that prey transfer in dim cavity nests is made more efficient by conspicuous mouth coloration, confirming the underlying assumption of a long-standing functional hypothesis for these nestling colours [6–9]. Regardless of nestling conspicuousness, parents took longer to transfer larger food items, with the largest prey taking twice as long to transfer as the smallest. Although the benefits of large prey almost certainly outweigh this cost [15], this pattern, along with the increased difficulty of transferring prey to smaller nestlings, more broadly supports the hypothesis that prey transfer is subject to physical constraints and thus an interaction for which behavioural and morphological adaptations might evolve [16].

The detectability hypothesis neither explicitly nor necessarily predicts active parental preferences for conspicuous mouths [6]. When conspicuous mouths make parental care more efficient, offspring can recoup any signal production costs via indirect benefits accrued through saved parental time/effort later invested in genetic relatives, and/or via direct benefits if parents use savings to increase current delivery rates. Interestingly, a manipulation of ambient light revealed a marginal increase in parental deliveries under higher light [12]. Nonetheless, several studies have revealed proximate evidence that parents allocate more resources to conspicuous nestlings [11–13]. Such biases might result from parents simply failing to detect inconspicuous offspring as often, as predicted by the detectability hypothesis. However, the performance of house sparrow parents in the current study suggests that this explanation merits skepticism; any minimum threshold for detectability is reached by mouths far less conspicuous than those naturally expressed by nestlings [8–13]. Alternatively, parents may detect the full range of colours, but actively favour conspicuous mouths. Because conspicuous nestlings take less effort to feed, they should, ceteris paribus, offer higher net fitness returns and thus be favoured by parents. This selective scenario, however, is quite distinct from one in which parental responses are constrained by their visual systems, and if conspicuous colour elements also signal condition, it would be...
difficult to attribute active preferences to detectability benefits per se [4].

Despite the potential benefits of a conspicuous mouth, nestlings of most species are not maximally conspicuous (i.e. not white) [6–9]. This could be because there is no increase in efficacy [1], or functional advantage, of conspicuously above some threshold of detectability. Behavioural assays along a colour gradient would be invaluable to the interpretation of the visual models commonly used to compare detectability of signals [4,9]. Even when conspicuousness offers a benefit, this feature of a colourful tissue can trade-off with other components that signal individual quality; carotenoid pigments often colour nestling mouths, and can decrease visual conspicuousness [3,4]. The brighter and whiter flanges of cavity nesters [6–9] could reflect an increased relative importance of detectability in cavity nests. Alternatively, a more detectable mouth may not be any more valuable at a dark nest, but a pigment-rich (i.e. more colourful, less white) mouth may be less valuable if low ambient light restricts parents’ ability to perceive variation in coloration that is costly to produce [4,11,14,17].

Advances in perceptual modelling have offered novel insights into the evolution of visual traits, but behavioural assays of receiver response remain fundamental to understanding the function and fitness consequences of these traits. Nestling mouth coloration should prove an excellent model system for studying visual signal evolution: colours vary within and among species and are used in simple light environments [4,7–9], and intended receivers are obvious and their responses straightforward to quantify [10–13]. Future work can test hypotheses drawn from comparative work with focused experiments, offering insights not just into how pressures to cooperate and compete shape signal expression in families, but also into how the diverse functions of signals shape their expression and evolution.

References