Surprising flexibility in parental care revealed by experimental changes in offspring demand

Katherine Pelletier¹, Chelsey Oedewaldt², and David F. Westneat³

Department of Biology and

Center for Ecology, Evolution, and Behavior

101 Morgan Building

University of Kentucky

Lexington, KY 40506-0225

1. Current address: 2 Prospect Court, #4, Northampton, MA 01060; katepell33@gmail.com

2. Current address: 220 Tacoma Ave S, Apt 910, Tacoma, Washington 98402;
chelseyloedewaldt@gmail.com

3. Corresponding author. E-mail: david.westneat@uky.edu

Word Count: 7122

Running Head: Rapid plasticity in parental care

Parental behaviour often exhibits plasticity to factors expected to affect the benefits or costs of care. For example, parent songbirds typically increase their provisioning behaviour as nestlings mature. Several mechanisms exist that could allow parents to track nestling age and provide appropriate care. We performed a short-term experiment on house sparrows (*Passer domesticus*), in which offspring of different ages were exchanged, to assess the level of flexibility parents exhibit and the likely cues they use. We found that a pair's rate of food delivery, an individual parent's visit rate to the nest, the duration of a foraging trip, and both the time a parent was in the nest and how long they perched near the nest after emerging from feeding nestlings changed according to the age of the offspring at the time. This shift in parenting was evident by the second visit after the swap. The amount of food brought per trip did not change with either natural or manipulated age. While females spent more time in the nest than males, there were no sex differences in the responses to the experiment. Food delivery rate increased nestling mass gain during each phase of the experiment, suggesting that parental plasticity in delivery was beneficial to offspring. However, there was an additional effect of the experiment on nestling weight gain, suggesting possible effects of food type brought during each phase of the experiment. Parent sparrows appear to use cues of offspring age over a time span that differs greatly from the natural time course of changes in nestling demand. This extension of plasticity into unnatural conditions has implications for understanding individual differences in plasticity and how at least some organisms might adjust to rapid and unusual environmental change.

Keywords: phenotypic plasticity, parent-offspring interactions, house sparrow, *Passer domesticus*, provisioning, plasticity cues, nestling demand, rapid environmental change

50

51 **INTRODUCTION**

52 The care that parents provide to offspring often exhibits fundamental properties with
53 general implications. An example is that most forms of care are part of a life-history trade-off
54 between the impact of care on offspring and the costs of providing care to the parent's ability to
55 produce more offspring (Clutton-Brock, 1991; Klug & Bonsall, 2010; Trivers, 1972; Winkler &
56 Wilkinson, 1988). Because both the benefits to offspring and the costs to parents depend on the
57 environmental context, selection on parental care is tightly tied to ecology. Many of the
58 ecological factors that could influence selection on parental care are spatially and temporally
59 variable, usually on a scale that favours the evolution of phenotypic plasticity (Pigliucci, 2001;
60 Scheiner, 1993). Indeed, flexibility in expression of care is another general property exhibited by
61 parents in most species that have evolved parental care. Across a wide array of organisms,
62 individual parents adjust their care to a variety of conditions, such as the number of offspring
63 (e.g., Gow & Wiebe, 2014), the availability of new mates (Muldal et al., 1986), the value of
64 resources needed for offspring (Trumbo, 1991), the potential risks of care to either the parents
65 (Ghalambor et al., 2013) or to the offspring (Eggers et al., 2005). Such flexibility is predicted by
66 both life history theory about parental care (e.g., Clutton-Brock, 1991; Winkler, 1987) and theory
67 on phenotypic plasticity (e.g., Moran, 1992; Scheiner, 1993).

68 The evolution of plasticity requires that the factors that influence the fitness
69 consequences of a particular trait value are variable and also predictable by the individual
70 organism (e.g., Chevin & Lande, 2015; Getty, 1996; Tufto, 2000). To be plastic, organisms must
71 assess, either directly or indirectly, the environmental factor that affects fitness (Chevin & Lande
72 2015). For example, many birds begin breeding by using indirect cues to predict the peak of

insect emergence, with highest fitness being obtained when that peak coincides with the peak of nestling growth (e.g., Lack 1968; Charmantier et al. 2008; Nussey et al. 2005). Adaptive plasticity is facilitated by cues that are easier to assess (Getty 1996) and more strongly correlated with the fitness-affecting aspect of the environment (Chevin & Lande 2015). In general, this means such cues are appropriately linked in time and space with the factor that affects fitness.

In birds, species that provision dependent offspring adjust levels of provisioning in response to many potential cues of offspring need (Budden & Wright, 2001). For example, parents respond to changes in the colour of the mouth (Heeb et al., 2003), or the posture of the nestlings (Redondo & Castro, 1992) or aural sounds such as begging calls (Kilner et al., 1999; Leonard & Horn, 2006). In food deprivation experiments, nestlings increased the intensity of their begging with hunger, and increased begging elevated parental feeding rates (e.g., Dor & Lotem, 2010; Leonard & Horn, 2006; Whittingham & Robertson, 1993). Parents also increased or decreased provisioning in response to brood size manipulations (reviewed in Gow & Wiebe, 2014). These results indicate that parents are attentive to changes in nestling attributes (because parents may attend to stimuli that might or might not have evolved to provide information, we generally use the word “cue” instead of “signal” when we focus on the parents’ perspective; e.g., Maynard Smith & Harper 2003), and alter their behaviour according to changes in these attributes and other aspects of the environment.

It is not clear, however, over what time scales these cues may exert their influence, and investigation of age-related changes in behaviour may reveal more complex sets of cues than studies of begging or brood size alone. Here, we focus on the plasticity that parents exhibit with respect to offspring age. This form of plasticity is intriguing because there are multiple potential cues to offspring age, but offspring get older in only one direction and the change in demand due

to maturation of offspring is on an intermediate time scale (a day or two rather than either minutes or a week). The unidirectional nature of the change in demand plus the time scale could have shaped what cues are used and how. Previous work provides a mix of results. In a cross-fostering experiment, zebra finches (*Taeniopygia guttata*) were found to extend the length of the nestling care and post-fledging care when presented with offspring younger than their own, and to reduce the length of care in the reciprocal swap (Rehling et al., 2012), suggesting use of a bidirectional cue arising from the offspring but with uncertain timing. Yasukawa et al. (1993) found rapid adjustment of parental care in red-winged blackbirds (*Agelaius phoeniceus*) following a temporary exchange of broods differing in age, suggesting that parents use a short-term cue such as begging intensity despite the fact that age-related changes in nestling demand occur over days. However, in a similar cross-fostering experiment with Atlantic Puffins (*Fratercula arctica*), chicks of different ages were exchanged, and parents were found to continue age-appropriate provisioning as if there had been no manipulation, instead of adjusting to the age of their foster chick (Hudson, 1979). This suggests use of a cue independent of the nestlings and related instead to the time since hatching (e.g., a long-term cue). Similarly, parent blue tits (*Cyanistes caeruleus*) and pied flycatchers (*Ficedula hypoleuca*) did not adjust the size of prey brought to the nest after experimental swaps of broods differing in age (Wiebe & Slagsvold, 2014), also suggesting a mismatch between cues and the experiment. This mix of results could indicate either different magnitudes of plasticity between species, or plasticity in some elements of provisioning behaviour and not others, perhaps accompanied by use of cues that change over different time courses.

To investigate age-related plasticity in more detail, we measured parental behaviour before, during, and after temporary cross-fostering of house sparrow (*Passer domesticus*) broods differing in nestling age. We assessed if parents would adjust to sudden changes in cues to

offspring age and if so, how quickly. House sparrows are non-migratory songbirds native to Europe and introduced to North America, and are common in both urban and rural environments. Males and females form socially monogamous pairs and exhibit biparental care (Anderson, 2006; Summers-Smith, 1963). Prior studies of parental care in this species have shown that parents generally increase the rate of trips to the nest as nestlings age, typically from 1 day to 10 days of age (Anderson, 2006; Ringsby et al., 2009; Westneat et al., 2011). The short-term swap of nestlings differing in age allows a test of whether parents use cues obtained on recent visits (short-term) or cues that change over days (long-term) and if they exhibited flexibility in response to unnatural changes in the age of their offspring.

We made the following a priori predictions. If parents use cues independent of the offspring (such as counting days since hatching) to adjust provisioning as nestlings get older, we expected a significant main effect of treatment (which captures the age of the parents' natural offspring) and no effect of the interaction between the stage in the experiment and treatment. The same result was expected if parents used a cue with an intermediate timing, such as the average level of begging the previous day, to assess changes in demand as offspring age. If parents use cues provided by nestlings that are assessed during the most recent visits, then we expected a treatment by stage interaction and no main effect of treatment. A disruptive effect of the swap itself would produce a significant stage effect. If any of the interactions with sex were significant, that would imply different mechanisms of plasticity for the two sexes. Because provisioning behaviour consists of several timing variables, such as the length of the foraging trip and the time spent on or near the nest between trips, and also the load of food carried back on each trip, we tested if the manipulation affected each of these. We also analysed brood mass changes during the experiment for three reasons: 1) to confirm that fostering offspring was not harmful to the swapped nestlings, 2) to establish that any behavioural changes during the

experiment improved offspring mass and reflected potentially adaptive responses to changes in demand by nestlings as they aged, and 3) to assess if there might be effects of the experiment on otherwise unmeasured aspects of provisioning behaviour affecting nestling condition.

METHODS

We conducted this study in a free-living population of house sparrows at the University of Kentucky's Agricultural Experimental Research Station, in Lexington, Kentucky which has been monitored since 1992 (Westneat et al., 2009, 2011). We performed temporary cross-foster experiments with birds breeding in nest boxes in April - July of 2013 and 2014. Starting in April in both years, we visited boxes every other day and checked the contents of the nest. Once a clutch was complete, determined by no new eggs appearing on two successive visits, we estimated when hatching was likely to begin using an 11-day incubation period from the day the last egg was laid as day 1. We then checked boxes every day around the day of hatching to determine hatch date and hence obtain an estimate of nestling age in days, with 0 days being the day of hatch of the majority of nestlings. After hatching was complete, pairs of boxes were identified that had the same brood size and were 2-5 days apart in age. When two boxes met those criteria, they were paired as a dyad, and targeted for a swap when both nests were between 2 and 8 days of age. The age difference between nests within dyads averaged 3.6 days and included: two dyads with nests differing by two days in age, eight dyads with a three-day difference, eight with four-day difference, and three with a five-day difference.

On the day of the swap, we visited both nests, counted nestlings and weighed the brood, and started a digital video camera (standard definition), which was aimed at the opening of the box and mounted inside a wooden box designed to house a camera or on a tripod nearby. We

recorded parental behaviour for a 90 min (2013) or 120 min (2014) pre-swap period (labelled as the “Pre” stage, which served as an internal control). We then weighed the brood again, simultaneously at both boxes in a dyad, and exchanged all nestlings between boxes by transporting them to their foster nest and placing the new brood in each nest at the same time. During the transfer, both boxes were empty simultaneously and equally for no more than 15 min. The swapped broods remained in their foster nests for approximately two hours, during which time video was again recorded (labelled as the “Swap” stage). After two hours, we removed the brood, re-weighed it, and returned all nestlings to their original nests simultaneously. Either 90 min (2013) or 120 min (2014) of video was taken of the parents’ post-swap behaviour (labelled as the “Post” stage, which formed another internal control for the disruption of the swapping procedure). At the end of this taping session, we weighed the brood a final time.

Video files were viewed using VLC player (Videolan.org), and parental provisioning was scored without knowledge of the starting age of the nestlings in the focal box. Scorers recorded the time either parent arrived at the box, the size of the load in comparison to the volume of the bill (e.g., Schwagmeyer et. al., 2002) scored to tenths, a brief description of the type of food brought, the time of entry into the box, time of emergence from the box, and time of departure. There was no systematic bias among scorers in load size ($F_{5,84.3} = 1.6$, $P = 0.16$). We assessed the repeatability of load size scores from 321 visits extracted from videos taken on five nests chosen arbitrarily from both seasons, across all three stages of the experiment, and originally scored by five different people. These were rescored blindly by a second scorer; inter-observer repeatability was 0.69 and was highly significant (likelihood ratio test, $X^2 = 88.1$, $df = 1$, $p < 0.0001$). From the scored information, we extracted for each visit the length of time between departure at the last visit and arrival to the current visit (trip time), the amount of time spent inside the nest box, the time spent on the box after emerging, and load size in cubic mm using

218 cubic mm as the mean bill volume (calculated from the equation $V = \pi r^2 L / 3$ where $r = 4.02$ mm, the radius at the nostril of the average bill in this population, and $L = 12.90$ mm, the mean bill length from base of bill to tip). Time variables were log-transformed to provide a better fit to a normal distribution. We calculated the rate of visits per hour for both parents individually and for the pair together. For some visits the load size could not be scored either because of the angle of arrival, the speed with which the parent entered the box, or because the camera malfunctioned or was disturbed (other birds occasionally tried to enter the camera box and moved some cameras). We calculated two measures of “delivery,” the rate of food brought to the nest. First, we summed the load sizes per hour for those visits that we could score for each parent (observed delivery) and second, because this metric is sensitive to missing information, we also generated an estimated delivery based on average load per trip for scored trips times the total number of trips (which assumes load size scores were missing at random with respect to load size).

Statistical Analysis

We performed a total of 10 swap trials in 2013 and 13 trials in 2014. We omitted 1 trial (the first) in 2013 because of procedural issues, and 1 trial in 2014 because the parents at one nest of a dyad had disappeared just prior to or during the pre-manipulation period. The final sample size thus involved 21 dyads and 42 boxes. In two dyads 1 box was omitted because of problems with the camera. At two other boxes, only 1 parent was present during the entire experiment. Finally, because 81% of parents were individually marked, we knew that seven individuals were involved in two and one was recorded in three separate swaps. All of this meant we collected data from 69 unique individuals who experienced the manipulation. One additional dyad was missing the pre-trial video due to problems storing the video files. The full dataset consisted of 4469 visits, of which 3594 (80%) could be scored for load size.

We used linear mixed models (LMM), which we performed in SAS 9.4 (SAS, Inc). LMM is well-suited for hierarchically structured data such as those collected in this experiment, especially when repeated measures may differ in number between units (as is the case for visits to the nest by parents) or some data is missing. Three datasets were analysed. One set consisted of the parental pair's observed or estimated delivery of food per hour. The random effects structure of this model included dyad identity and box within dyad. The fixed effects structure in these analyses included stage, treatment, and the stage by treatment interaction, with the latter being the term of focus for the statistical null hypothesis that parents would not respond to the experimental change in age of the nestlings.

The second dataset consisted of each individual's measures of trip rate and estimated delivery per individual per hour for each stage. The models of these data had a nested random effects structure of dyad identity, box within dyad, and individual within box. Fixed effects again included sex, stage, and treatment along with all interactions.

Finally, we constructed a dataset consisting of each trip that each individual made to the nest. This dataset included timing variables from each visit and the load for that visit if it could be scored. We used a model with a random effects structure of dyad identity, box nested within dyad, individual parent identity nested within box, and stage in the experiment nested within individual. In the fixed effects portion, we included sex, the stage in the experiment, the treatment (swapped to older or swapped to younger) and all interactions. In all models, we calculated denominator degrees of freedom using the Kenward-Roger's method which adjusts degrees of freedom for the random effects structure (Kenward & Roger 1997). All tests were two-tailed using a $p = 0.05$ criteria.

Ethical Note

We took several steps to ensure that the experiment did not cause any undue harm to nestlings. During the first 3 trials in 2013, we observed parents using binoculars during the experiment to assess if the swap caused any major disruptions to their parental behaviour. We only swapped nestlings that were between 2 days old and 8 days old; any younger and we worried that the disruption might affect thermoregulation, and any older the nestlings or parents might have begun recognizing each other (which occurs at 9-10 days of age; Sloane and Westneat, unpublished data). Nestling mass was taken before and after each taping session, and we would have stopped the experiment if there had been massive weight loss or any evidence either directly or indirectly (wounding of nestlings) that parents were attacking the swapped nestlings. We checked nests on subsequent days and found no evidence of abnormal nestling loss that suggested parents reacted poorly to the experiment. These experiments were conducted under a Master Banding permit (#22183) to DFW from the U.S. Fish and Wildlife Service and an animal care protocol (2012-0948) approved by the University of Kentucky IACUC.

RESULTS

The experimental alteration of nestling age that resulted from temporarily swapping whole broods of different ages resulted in several distinct changes in parental behaviour. The estimated delivery by the pair was influenced by an interaction between the treatment (swap to older versus swap to younger) and the stage (Pre, Swap, or Post) of the experiment (Fig. 1A; $F_{2,74.5} = 7.2$, $P < 0.001$). In the “Pre” stage, estimated delivery by the pair was higher at nests with older nestlings. During the “Swap,” parents switched their behaviour; pairs with younger nestlings increased their estimated delivery when faced with older nestlings and pairs with older nestlings decreased delivery when attending younger nestlings (Fig. 1A). These patterns reverted to the natural state when nestlings were restored to their original nest (“Post”; Fig. 1A). A priori

contrasts comparing natural and foster parent behaviour either from before the swap or after the swap showed no evidence of effects of the swap procedure on estimated delivery (all $P > 0.59$, Table S1). Analysis of observed delivery revealed the same pattern (Table S2), as did an analysis using the difference in age between swapped nests in place of the categorical Treatment variable (Table S3). In an analysis of estimated delivery separately for each parent, the stage by treatment interaction was also highly significant ($F_{2,152} = 26.3$, $P < 0.0001$); we found no differences between the sexes either overall ($F_{1,32.7} = 2.1$, $P = 0.15$) or in their response to the experiment ($F_{2,152} = 0.1$, $P = 0.9$, Table S4).

The delivery of food may be a function of the number of visits made to the nest per hour. Visit rate per parent was affected by the interaction between treatment and stage in the experiment (Fig. 1B; $F_{2,156} = 50.7$, $P < 0.0001$, Table S5), with a higher rate occurring when nestlings were older in each stage regardless of the age of the parents' actual nestlings. We found no effect of sex on either overall trip rate ($F_{1,38.1} = 0.01$, $P = 0.93$) or in the response to stage by treatment interaction ($F_{2,157} = 0.2$, $P = 0.84$).

Figure 1. Box plots showing (A) estimated total food delivered (cubic cm) per h by the pair ($n = 42$) of house sparrow parents and (B) visits per hour per parent ($n = 78$) over the three stages of the experiment. Open boxes represent the behaviours exhibited by parents to younger nestlings. Shaded boxes indicate behaviour exhibited by parents to older nestlings. For both (A) and (B), the interaction between stage and treatment was highly significant (see text). Each box contains the median (heavy horizontal line), indicates the upper and lower quartile of the data (box), whiskers indicating the max or min point within the range of 1.5 times the inter-quartile range (R-default), and open circles indicate outlier points.

Parents can change visit rate by adjusting the timing of several different elements of provisioning behaviour. First, visit rate can increase if the time per trip away from and back to the nest decreases. Indeed, we found that the length of individual trips decreased when older nestlings were in the nest at each stage of the experiment (Fig. 2A) and was affected by the interaction between stage and treatment ($F_{2,248} = 21.3$, $P < 0.0001$). The sexes did not differ in

trip time over all conditions ($F_{1,63.9} = 3.6$, $p = 0.06$) nor in their reaction to the experiment (sex by stage by treatment, $F_{2,259} = 1.3$, $P = 0.27$).

Visit rate could also be influenced by time spent at the nest. We analysed two elements of time at the nest: the time the parent spent inside the nest box on each trip and the time they spent perched on the nest box after feeding and before leaving for the next foraging trip. Time in the box was affected by the interaction between stage and treatment (Fig. 2B, $F_{2,344} = 139$, $P < 0.0001$), with parents attending younger nestlings regardless of stage in the experiment spending more time in the box than parents attending older nestlings. Females spent longer (76 ± 13 s) than males ($F_{1,60.4} = 45.3$, $P < 0.0001$) in the box regardless of treatment and stage, but females responded similarly to males to the stage by treatment interaction ($F_{2,344} = 0.6$, $P = 0.58$). The experiment also affected the time parents spent at the box after emerging from feeding nestlings (stage by treatment interaction: $F_{2,131} = 7.3$, $p < 0.001$), with parents attending younger nestlings spending more time on the box. There was no effect of sex ($F_{1,50.4} = 0.6$, $P = 0.42$) or the sex by stage by treatment interaction ($F_{2,131} = 1.4$, $P = 0.25$) on time spent at the box after emerging.

Besides the various effects of timing on visit rate, the delivery of food to nestlings could also be affected by the load size per trip. We found no effect of the stage by treatment interaction (Fig. 2C, $F_{2,197} = 0.03$, $P = 0.97$) or sex ($F_{1,57.2} = 1.8$, $P = 0.19$) on load size per trip. Load size was also not influenced by treatment ($F_{1,58.5} = 0.5$, $P = 0.48$), suggesting that parents in this population did not differ in load size with the age of their nestlings.

Figure 2. Box plots (A) trip time (log seconds), (B) the time in the box per trip (log seconds), and (C) the load size measured on each trip (in mm³) for parent house sparrows by treatment type (parents of younger nestlings on left, parents of older nestlings on right), with open boxes representing behaviour directed to younger nestlings and shaded boxes indicating behaviour directed to older nestlings. There was a significant stage by treatment interaction for trip time and time in box but not for load size (see text). Plots indicate the median (heavy horizontal line), the upper and lower quartile (box), the max or min point within the 1.5 time the inter-quartile range (whiskers), and outliers (points).

A striking feature of the parental response to this experiment was how quickly they shifted their behaviour after the manipulated change in offspring age. We analysed just the behaviour of each parent on the second visit to the nest in each stage, which for stages “Swap”

and “Post” is the trip immediately following the first visit to the nest after the manipulation. We found stage by treatment interactions for trip time ($F_{2,157} = 4.4$, $P = 0.01$) and the time spent in the box ($F_{2,143} = 11.6$, $P < 0.0001$). Both trip time and in box time were shorter when nestlings were older than when younger, at all stages. Females spent longer in the nest than males on the second visit ($F_{1,32.5} = 21.0$, $P < 0.0001$) and overall took less time to return to the nest following the first visit ($F_{1,45.1} = 10.6$, $P = 0.002$) but otherwise there were no sex effects.

Anecdotally, some parents initially reacted to the swap with abnormal behaviour, although whether this was from the disruption of the swap itself or the sudden change in appearance of the nestlings is not clear. Some individuals entered the box with food and exited without feeding the nestlings. However, these occasional instances of disruption had no general statistical influence, as there was no effect of stage on latency to arrive on the first visit ($F_{2,158} = 0.1$, $P = 0.88$) or the number of entrances into the box without feeding nestlings in the first 15 minutes after the swap ($F_{2,207} = 1.0$, $P = 0.37$). Only nine broods lost mass during a stage; two lost mass during the Pre, three during the Swap, and four during the Post.

The rapid and symmetrical response by parents to the experimental change in nestling age had consequences for offspring mass changes. In a model with stage, treatment, and the stage by treatment interaction, brood mass gains per hour were influenced by the stage by treatment interaction ($F_{2,94.7} = 10.9$, $P < 0.0001$), with older broods gaining more mass regardless of who was caring for them (Figure 3, Table S6). Contrast analysis revealed no evidence that younger nestlings fostered with parents of older nestlings gained a different amount than they did with their natural parents (-0.4 ± 0.2 g; $t_{1,96} = 1.5$, $P = 0.13$). Older nestlings fostered with parents of younger nestlings gained essentially the same mass (0.002 ± 0.2 g/brood; $t_{1,96.7} = 0.01$, $P = 0.99$)

as with their natural parents. However, older nestlings gained significantly less mass (0.6 ± 0.2 g/brood; $t_{1,96} = 2.4$, $P = 0.02$) when returned to their natural parents.

Figure 3. Box plot of the brood mass changes per hour of younger (left) and older (right) nestlings during each stage of the experiment. Open boxes represent the mass changes of broods attended by parents whose natural broods were of younger nestlings. Shaded boxes indicate broods attended by parents whose natural broods were composed of older nestlings and who received younger nestlings during the swap (swap to younger). The stage by treatment interaction was significant (Table 1); younger nestling tended to gain more weight after being returned from foster parents to their natural parents and older nestlings gained less weight upon being returned to their natural parents (see text).

Brood mass changes were negatively associated with brood starting weight and strongly positively associated with estimated delivery brought by the pair (Table 1). Including these two variables along with the stage by treatment interaction revealed that despite the fact that the interaction term strongly affected estimated delivery (Figure 1A), adding delivery did not

eliminate the effect of the interaction term on brood mass changes (Table 1), indicating that the experiment influenced nestling mass changes beyond its effect on parental delivery of food.

Table 1. Results from the fixed factor portion of a linear mixed model (random factors of dyad identity and box were included) of brood mass change (g) per hour experienced by experimental broods of nestling house sparrows that were part of the age swap experiment.

Factor	Effect size (SE)	F-value	DF	Pr > F
Brood starting weight	-0.01 ± 0.005	4.1	1,105	0.046
Brood size	0.14 ± 0.08	3.4	1,44.7	0.07
Estimated load per hr per pair (mm ³)	0.0003 ± 0.00006	33.0	1,108	< 0.0001
Stage	-	1.2	2,74.2	0.31
Treatment	-	0.4	1,41.8	0.53
Stage by Treatment	-	8.3	2,88.3	0.0005

We compared mass changes of foster broods to their mass changes during the pre-swap period with their natural parents using a priori contrasts within the overall mixed model presented in Table 1. As in the simpler model reported above, younger nestlings gained 0.3 ± 0.2 g per h more with natural parents than foster, but this difference was not significant ($t_{1,108} = 1.5$, $P = 0.13$). Older nestlings gained essentially the same with their foster parents as with natural parents (Natural = 0.07 ± 0.2 g per h more; $t_{1,108} = 0.3$, $P = 0.75$). Once younger nestlings were returned to their natural parents, they gained 0.5 ± 0.2 g per h more than with their foster parents, a significant difference ($t_{1,108} = 2.2$, $P = 0.03$), and older nestlings gained 0.5 ± 0.2 g per h less upon returning to their natural parents than they did with their foster parents ($t_{1,108} = 2.3$, $P = 0.03$).

DISCUSSION

Our cross-fostering experiment revealed striking flexibility in provisioning behaviour, with parents adjusting nearly immediately to our manipulation in the age of the nestlings present

in their nest. Parents of both sexes either shortened (when the nestlings were suddenly older) or lengthened (when the nestlings were suddenly younger) the time they spent away from the nest between visits, inside the nest on each trip, and at the nest after feeding the nestlings. These changes in time devoted to particular activities altered both the rate of trips to the nest and the rate of food delivery to the broods in ways that make sense given the age of the nestlings at that point in time. This rapid flexibility was symmetrical—parents whose own nestlings were younger switched immediately to the appropriate behaviour when confronted with nestlings that were 2-5 days older, and parents whose own nestlings were older switched immediately to providing appropriate care to offspring that were 2-5 days younger. This symmetrical behaviour existed for all elements of provisioning involving time. Conversely, there was no evidence that the age of nestlings, whether natural or manipulated, affected how much food parents collected on each trip.

Our results eliminate two classes of cues parents might use for assessing and responding to the increasing demand that likely occurs as nestling mature. First, parents are clearly not employing cues of the time since hatching separately from the attributes of the nestlings; if they were, then their behaviour should not have changed during the swap. House sparrows thus appear to differ from puffins (Hudson, 1979), blue tits, and pied flycatchers (Wiebe & Slagsvold, 2014) in the mechanism for plasticity in provisioning behaviour. We wondered going into the experiment if parents might integrate cues over an intermediate time frame. Since the changes in demand as nestlings grow older accumulate slowly over days, it seemed reasonable that parents might use cues that change over the same time period, such as assessing the average behaviour of the brood the previous day. Our results suggest this also is unlikely.

Parents might use cues that change over intermediate time periods but are somehow able to extrapolate (e.g., Sih et al., 2011) to the sudden change in nestling age in the manipulation, an unnatural shift in those cues. In the case of sparrows, this could occur in two ways. First, in most birds, older nestlings differ from younger nestlings in multiple ways; they are bigger (in many of our swaps, the older nestlings weighed twice as much as the younger), their feathers are more developed and their gapes have changed colour (unpublished data), and they likely produce aural cues that differ in amplitude and other spectral components than those produced by younger nestlings. None of these attributes change naturally on a time scale that overlaps the rapidity with which they changed in our experiment and with which parents responded. If parents are using these types of cues under natural conditions, they are employing a mechanism that assesses them over just a few visits, which is more temporally fine-grained than it needs to be to assess age-related changes in demand.

An alternative possibility is that parents use short-term cues for both short-term and longer-term changes in offspring demand (Kitamura et al., 2011; Wright et al., 2002). A likely candidate is the visual or aural elements of nestling begging displays. Correlational studies (e.g., Kitamura et al., 2011), experimental manipulations of nestling hunger (Dor & Lotem, 2010; Grieco, 2001; Tanner et al., 2008; Whittingham & Robertson, 1993), and playbacks of begging calls (Burford et al., 1998; MacGregor & Cockburn 2002; Ottosson et al., 1997; Wright et al., 2010b) have provided strong evidence that parents adjust their provisioning behaviour, typically over a short time scale (minutes), in response to begging intensity. Begging appears to be an all-purpose signal of nestling hunger, influencing how parents allocate feedings within a nest (Kitamura et al., 2011; Redondo & Castro, 1992; Tanner et al., 2008; Whittingham et al., 2003), possibly for making decisions on the scale of minutes to hours that affects the intermediate-term rate of food delivery to the nest (Kitamura et al., 2011), and potentially for responding to the

steady increase in demand over days as nestlings age. This would help explain how quickly parent house sparrows responded in the present study.

However, for a single cue to be useful at providing information about offspring hunger and possibly underlying need throughout the entire nestling period, several relationships must exist (Mock et al., 2011). An important one is that begging must contain effective information at all ages. Leonard and Horn (2006) demonstrated experimentally that begging reflects offspring hunger across a wide range of nestling ages in tree swallows (*Tachycineta bicolor*). However, for two reasons this is not sufficient for begging to be used for both short-term and long-term assessments of offspring condition. First, short-term hunger is not the same thing as fitness-affecting condition, which is a more salient definition of need (Mock et al., 2011), and parental use of the same cue to assess both may lead to mistakes in providing appropriate care. Second, changes in the absolute intensity of begging must mean the same thing at all ages. However, Leonard and Horn's (2006) data also show that as nestlings are deprived for longer, most aspects of begging increase in both mean and variance differently at different nestling ages. It is possible the same length of deprivation causes a larger increase in hunger in older nestlings than younger, but if not, then hunger appears scaled to variance in begging within an age but not across ages. If this is the case, then to appropriately make short-term decisions, parents would have to use a relative scale, such that they appropriately attend to changes in the intensity of begging within the range of begging exhibited by nestlings of that age. We do not know how parent sparrows reacted to variation in behaviour among foster nestlings. However, if sparrow parents use a scale that differs by age, it would seem they shifted that scale artificially quickly in our experiment. Studies of the ability of both aural and other senses to function in the face of changes in scale reveal that many organisms have difficulty discriminating different cues with a sudden change in the scale of the cue (e.g., Gross-Isseroff & Lancet, 1988; Hulse et al., 1990). Our results thus

suggest two possibilities: (1) either begging reflects nestling hunger and possibly need on the same absolute scale regardless of age such that parents adjust immediately and apparently appropriately to the magnitude of begging, or (2) parents are using some set of hierarchical cues (e.g., body size for age and begging for assessing variance in need within a particular age) but do so seemingly appropriately in circumstances that never exist in nature.

An unexpected result from the present experiment was the general lack of sex differences in response to manipulations of brood age. Previous work has uncovered differences in plasticity with respect to nestling age and brood size in this same population (Westneat et al., 2011) using data collected from 1998-2003. Because brood size was not altered in this experiment, it may be that the range of nestling ages fell within areas of the reaction norm where males and females are similar, and it is only later on, when nestlings are 9-11 days old, that sex differences emerge.

The adjustments parents made to offspring age had a significant positive impact on brood mass gains. Mass gain was correlated with the delivery rate of food (Table 1) independent of the number of offspring in the brood and their starting mass. Parental response would thus seem to be adaptive, at least from the brood's point of view, except that natural broods do not suddenly change by an average of 3.6 days in age. The experiment effectively sped up (in the case of the swap to older treatment) the natural progression, and if we extrapolate the responses to the sped-up treatment to the natural progression, this result suggests that parents who do adjust their delivery rates appropriately would gain higher benefits than those that do not (Klug & Bonsall, 2014).

We also found evidence of deviations in the mass change data from the behavioural data, producing some patterns that are not easy to explain. The stage by treatment interaction continued to be significant even when the estimated rate of food delivery was included the

model. If this result is real, it suggests some influence of the experiment on nestling mass change driven by a process other than the behavioural changes in the amount of food delivered. The contrast comparisons of particular groups refined our understanding of this extra effect and revealed a mixed story. Assuming there is no hidden bias in the data, young nestlings with foster parents gained a similar amount of weight as they did prior to the swap with their natural parents, but when returned to their natural parents after the swap they gained more than with their foster parents (Figure 3). House sparrow parents often process food items by removing legs and wings (unpublished data). We do not know if the level of processing changes with nestling age because it was difficult to score for most visits. If it does, parents of older nestlings might not have switched this behaviour when confronted with young nestlings. Unprocessed insects could be difficult for young nestlings to swallow or digest, such that young nestlings may have been hungrier when returned to their natural parents. While there is no evidence their natural parents compensated behaviourally, it is possible they did so either in the type of prey (e.g., Wright & Cuthill, 1990) or in the level of processing, neither of which we could assess, but which could have affected brood mass.

The effect on older nestlings is also puzzling; their mass gain during the swap was similar to that achieved with their natural parents in the “Pre” stage, but when they were returned to their natural parents after the swap, they gained significantly less than they achieved with their foster parents (Figure 3). Assuming that this is correct, one possible explanation is that older nestlings were more sensitive to the swap *per se*, but this is not consistent with the fact that they did so well with foster parents. There is some evidence that parents of young nestlings over-responded to the switch in age; there is a slight but non-significant increase in estimated load delivered to older nestlings by foster parents compared to natural parents (Figure 1; Table S1), and a larger but marginally non-significant increase in visits per hr (Figure 1; Table S3). If parents of young

nestlings did overshoot, the lower mass gain in the Post stage might be a carryover effect. Older nestlings, upon return to their natural parents, could have been more satiated than usual. Too much food in the digestive tract could slow digestion efficiency (Budden & Wright, 2008; Kasarov & Wright, 2002), which might have reduced assimilation of that food and reduced the visit rate by natural parents during the post stage (Fig. 1, Table S3). However, there are two problems with this explanation. First, the general links between food intake, digestion rate, and begging behaviour are not simple (e.g., Grodzinski & Lotem, 2007; Wright et al., 2010a), and we would need additional details about the food being brought and the begging of nestlings to assess this idea. Second, the evidence in our study for foster parents overshooting is not particularly strong.

In summary, parent house sparrows are sufficiently flexible in provisioning behaviour to adjust appropriately to sudden, unnatural changes in cues that may be used to assess offspring demand. This is similar to the type of plasticity that may allow organisms to adjust to other forms of rapid environmental change including those caused by human activities (Palumbi, 2001; Sih, 2013). An essential feature of such plasticity is that the mechanism driving the phenotypic response is sufficiently open-ended that it happens to work in unnatural conditions. We do not know exactly what form such mechanisms may take, but one possibility suggested by the present study is that some shifts in the timing of cues may allow rapid accommodation. This does not seem to be the case for the timing of breeding which in some birds is now off-kilter with the peak food supply (e.g., Both et al., 2006). However, in those cases, the main cue used to assess the timing of migration, and hence constraining the start of breeding, is day length, which is not the rapidly changing cue (temperature) used by the main insect prey to time emergence. Parent sparrows use more direct cues of offspring demand, which in this case were only shifted in their timing (early to late or vice-versa). Our unnatural shift in the timing of offspring demand may

have by chance revealed a level of plasticity that is merely a by-product of selection for plasticity within the normal range of changing nestling demands (Ghalambor et al., 2007). Alternatively, some more complex form of selection that favours flexibility in the timing of those cues may exist. Only more fine-grained studies of the mechanistic details of plasticity will provide us with an appropriate answer.

ACKNOWLEDGEMENTS

We thank the staff at the UK Agricultural Experimental Station for allowing us to use the farm for these studies. We are also indebted to David Moldoff, Annie Griggs, Lauren Loy and the rest of the sparrow crews in 2013 and 2014 for helping with data collection. Christopher Dudley and Laura Westneat helped score videos and Ariane Mutzel, Becky Fox, and Kat Sasser provided valuable feedback on analysis and interpretation. We also appreciate many suggestions from Doug Mock, Ariane Mutzel, Jon Wright, and two anonymous reviewers that greatly improved the manuscript. This project was funded by a regular NSF grant to DFW (IOS1257718) and a site-based Research Experience for Undergraduates (REU) summer program (Suburban Ecology and Invasive Species, DBI-1062890) which supported KP and CO during this research.

References

- Anderson, T. R. (2006). *Biology of the ubiquitous house sparrow: from genes to populations*. New York, U.S.: Oxford University Press.
- Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441(7089), 81-83.

- 543 Budden, A. E., & Wright, J. (2001). Begging in nestling birds. *Current Ornithology*, 16, 83-118.
- 544 Budden, A. E., & Wright, J. (2008). The effects of feeding frequency on nestling begging and
545 digestion. *Ibis*, 150(2), 234-241.
- 546 Burford, J. E., Friedrich, T. J., & Yasukawa, K. (1998). Response to playback of nestling
547 begging in the red-winged blackbird, *Agelaius phoeniceus*. *Animal Behaviour*, 56(3), 555-
548 561.
- 549 Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E., & Sheldon, B. C.
550 (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird
551 population. *Science*, 320(5877), 800–803.
- 552 Chevin, L-M., & Lande, R. (2015). Evolution of environmental cues for phenotypic plasticity.
553 *Evolution*, 69(107), 2767-2775.
- 554 Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ, U.S.: Princeton
555 University Press.
- 556 Dor, R. R., & Lotem, A. A. (2010). Parental effort and response to nestling begging in the house
557 sparrow: repeatability, heritability and parent–offspring co-evolution. *Journal of*
558 *Evolutionary Biology*, 23(8), 1605-1612.
- 559 Eggers, S., Griesser, M., & Ekman, J. (2005). Predator-induced plasticity in nest visitation rates
560 in the Siberian jay (*Perisoreus infaustus*). *Behavioral Ecology*, 16(1), 309-315.
- 561 Getty, T. (1996). The maintenance of phenotypic plasticity as a signal detection problem. *The*
562 *American Naturalist*, 148(2), 378-385.

- 563 Ghalambor C. K., McKay J. K., Carroll S. P., & Reznick D. N. (2007). Adaptive versus non-
564 adaptive phenotypic plasticity and the potential for contemporary adaptation in new
565 environments. *Functional Ecology*, 21(3), 394–407.
- 566 Ghalambor, C. K., Peluc, S. L., & Martin, T. E. (2013). Plasticity of parental care under the risk
567 of predation: how much should parents reduce care? *Biology Letters*, 9(4), 20130154.
- 568 Gow, E. A., & Wiebe, K. L. (2014). Responses by central-place foragers to manipulations of
569 brood size: parent flickers respond to proximate cues but do not increase work rate.
570 *Ethology*, 120(9), 881-892.
- 571 Grieco, F. (2001). Short-term regulation of food-provisioning rate and effect on prey size in blue
572 tits, *Parus caeruleus*. *Animal Behaviour*, 62(1), 107-116.
- 573 Grodzinski, U., & Lotem, A. (2007). The adaptive value of parental responsiveness to nestling
574 begging. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1624),
575 2449-2456.
- 576 Gross-Isseroff, R., & Lancet, D. (1988). Concentration-dependent changes of perceived odor
577 quality. *Chemical Senses*, 13(2), 191–204.
- 578 Heeb, P., Schwander, T., & Faoro, S. (2003). Nestling detectability affects parental feeding
579 preferences in a cavity-nesting bird. *Animal Behaviour*, 66(4), 637-642.
- 580 Hudson, P. J. (1979). The parent-chick feeding relationship of the puffin, *Fratercula arctica*.
581 *Journal of Animal Ecology*, 48(3), 889-898.
- 582 Hulse, S. H., Page, S. C., & Braaten, R. F. (1990). Frequency range size and the frequency range
583 constraint in auditory perception by European starlings (*Sturnus vulgaris*). *Animal Learning*
584 *& Behavior*, 18(3), 238-245.

- 585 Karasov, W. H., & Wright, J. (2002). Nestling digestive physiology and begging. In J. Wright, &
586 M. L. Leonard (Eds.), *The Evolution of Nestling Begging: Competition, Cooperation and*
587 *Communication* (pp. 199-219). Dordrecht, Netherlands.: Kluwer Academic Publishers.
- 588 Kenward, M. G. & Roger, J. H. (1997). Small Sample Inference for Fixed Effects from
589 Restricted Maximum Likelihood. *Biometrics* 53, 983-997.
- 590 Kilner, R., Noble, D., & Davies, N. (1999). Signals of need in parent-offspring communication
591 and their exploitation by the common cuckoo. *Nature*, 397(6721), 667-672.
- 592 Kitamura, W., Fujita, G., & Higuchi, H. (2011). Barn swallow (*Hirundo rustica*) parents use past
593 information on food provisioning to the brood, but not to decide on allocation within the
594 brood. *Journal of Ethology* 29(3), 409-417.
- 595 Klug, H., & Bonsall, M. B. (2010). Life history and the evolution of parental care. *Evolution*,
596 64(3), 823-835.
- 597 Klug, H., & Bonsall, M. B. (2014). What are the benefits of parental care? The importance of
598 parental effects on developmental rate. *Ecology and Evolution*, 4(12), 2330-2351.
- 599 Lack, D. (1968). *Ecological adaptations for breeding in birds*. London, UK: Methuen.
- 600 Leonard, M. L., & Horn, A. G. (2006). Age-related changes in signalling of need by nestling tree
601 swallows (*Tachycineta bicolor*). *Ethology*, 112(10), 1020-1026.
- 602 MacGregor, N. A., & Cockburn, A. (2002). Sex differences in parental response to begging
603 nestlings in superb fairy-wrens. *Animal Behaviour* 63(5), 923-932.
- 604 Maynard Smith, J. & Harper, D. (2003) *Animal Signals*. Oxford, UK: Oxford University Press.
- 605 Mock, D. W., Dugas, M. B., & Strickler, S. A. (2011). Honest begging: expanding from signal of
606 need. *Behavioral Ecology*, 22(5), 909-917.

- 607 Moran, N. A. (1992). The evolutionary maintenance of alternative phenotypes. *American*
608 *Naturalist*, 139(5), 971-989.
- 609 Muldal, A. M., Moffatt, J. D., & Robertson, R. J. (1986). Parental care of nestlings by male red-
610 winged blackbirds. *Behavioral Ecology and Sociobiology*, 19(2), 105-114.
- 611 Nussey, D. H., Postma, E., Gienapp, P. & Visser, M. E. (2005) Selection on heritable phenotypic
612 plasticity in a wild bird population. *Science*, 310(5746), 304–306.
- 613 Ottosson, U., Bäckman, J., and Smith, H. G. (1997). Begging affects parental effort in the pied
614 flycatcher, *Ficedula hypoleuca*. *Behavioral Ecology and Sociobiology* 41(6), 381-384.
- 615 Palumbi, S.R. (2001). Humans as the world's greatest evolutionary force. *Science* 293(5536),
616 1786-1790.
- 617 Pigliucci, M. (2001). *Phenotypic plasticity: beyond nature and nurture*. Baltimore, MD, U.S.:
618 John Hopkins University Press
- 619 Redondo, T., & Castro, F. (1992). Signalling of nutritional need by magpie nestlings. *Ethology*,
620 92(3), 193-204.
- 621 Rehling, A., Spiller, I., Krause, E. T., Nager, R. G., Monaghan, P., & Trillmich, F. (2012).
622 Flexibility in the duration of parental care: zebra finch parents respond to offspring needs.
623 *Animal Behaviour*, 83(1), 35-39.
- 624 Ringsby, T. H., Berge, T., Saether, B. E., & Jensen, H. (2009). Reproductive success and
625 individual variation in feeding frequency of House Sparrows (*Passer domesticus*). *Journal*
626 *of Ornithology*, 150(2), 469-481.
- 627 Scheiner, S. M. (1993). Genetics and evolution of phenotypic plasticity. *Annual Review of*
628 *Ecology and Systematics*, 24, 35-68.

- 629 Schwagmeyer, P. L., Mock, D. W., & Parker, G. A. (2002). Biparental care in house sparrows:
630 negotiation or sealed bid? *Behavioral Ecology*, 13(5), 713-721.
- 631 Sih, A., Ferrari M. C. O., Harris D. J. (2011). Evolution and behavioural responses to human-
632 induced rapid environmental change. *Evolutionary Applications*, 4(2), 367-387.
- 633 Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid
634 environmental change: a conceptual overview. *Animal Behaviour*, 85(5), 1077–1088.
- 635 Summers-Smith, D. (1963). *The house sparrow*. London, U.K.: Collins.
- 636 Tanner, M., Kölliker, M., & Richner, H. (2008). Differential food allocation by male and female
637 great tit, *Parus major*, parents: are parents or offspring in control? *Animal Behaviour*, 75(4),
638 1563-1569.
- 639 Tufto, J. (2000). The evolution of plasticity and nonplastic spatial and temporal adaptations in
640 the presence of imperfect environmental cues. *The American Naturalist*, 156(2), 121-130.
- 641 Trivers, R. L. (1972). Parental investment and sexual selection In B. Campbell (Ed.), *Sexual*
642 *Selection and the Descent of Man 1871-1971* (pp. 136-179). Chicago, U.S.: Aldine.
- 643 Trumbo, S. T. (1991). Reproductive benefits and the duration of paternal care in a biparental
644 burying beetle, *Necrophorus orbicollis*. *Behaviour*, 117(1-2), 82-105.
- 645 Westneat, D. F., Stewart, I. R., & Hatch, M. I. (2009). Complex interactions among temporal
646 variables affect the plasticity of clutch size in a multi-brooded bird. *Ecology*, 90(5), 1162-
647 1174.
- 648 Westneat, D. F., Hatch, M. I., Wetzel, D. P., & Ensminger, A. L. (2011). Individual variation in
649 parental care reaction norms: integration of personality and plasticity. *The American*
650 *Naturalist*, 178(5), 652-667.

- 651 Whittingham, L. A., & Robertson, R. J. (1993). Nestling hunger and parental care in Red-winged
652 Blackbirds. *The Auk*, 110(2), 240-246
- 653 Whittingham, L. A., Dunn, P. O., and Clotfelter, E. D. (2003). Parental allocation of food to
654 nestling tree swallows: the influence of nestling behaviour, sex and paternity. *Animal*
655 *Behaviour*, 65(6), 1203-1210.
- 656 Wiebe, K. L., & Slagsvold, T. (2014). Prey size increases with nestling age: are provisioning
657 parents programmed or responding to cues from offspring? *Behavioral Ecology and*
658 *Sociobiology*, 68(5), 711-719.
- 659 Winkler, D. W. (1987). A general model for parental care. *The American Naturalist*, 130(4),
660 526-543.
- 661 Winkler, D. W., & Wilkinson, G. S. (1988). Parental effort in birds and mammals: theory and
662 measurement. *Oxford Surveys in Evolutionary Biology*, 5, 185-214.
- 663 Wright, J., & Cuthill, I. (1990). Manipulation of sex differences in parental care: the effect of
664 brood size. *Animal Behaviour*, 40(3), 462-471.
- 665 Wright, J., Hinde, C., Fazey, I., & Both, C. (2002). Begging signals more than just short-term
666 need: cryptic effects of brood size in the pied flycatcher. *Behavioral Ecology*
667 *Sociobiology*, 52(1), 74-83.
- 668 Wright, J., Karasov, W. H., Kazem, A. J. N., Gonçalves, I. B., & McSwan, E. (2010a). Begging
669 and digestive responses to differences in long-term and short-term need in nestling pied
670 flycatchers. *Animal Behaviour*, 80(3), 517-525.
- 671 Wright, J., McDonald, P. G., Marvelde, L., Kazem, A. J. N., & Bishop, C. M. (2010b). Helping
672 effort increases with relatedness in bell miners, but 'unrelated' helpers of both sexes still

- 673 provide substantial care. *Proceedings of the Royal Society of London: Biological Sciences*,
674 277(1680), 437-445.
- 675 Yasukawa, K., Leanza, F., & King, C. D. (1993). An observational and brood-exchange study of
676 paternal provisioning in the red-winged blackbird, *Agelaius phoeniceus*. *Behavioral*
677 *Ecology*, 4(1), 78-82.
- 678