



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



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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.

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The care that parents provide to offspring often exhibits fundamental properties with general implications. An example is that most forms of care are part of a life-history trade-off between the impact of care on offspring and the costs of providing care to the parent's ability to produce more offspring (Clutton-Brock, 1991; Klug & Bonsall, 2010; Trivers, 1972; Winkler & Wilkinson, 1988). Because both the benefits to offspring and the costs to parents depend on the environmental context, selection on parental care is tightly tied to ecology. Many of the ecological factors that could influence selection on parental care are spatially and temporally variable, usually on a scale that favours the

evolution of phenotypic plasticity (Pigliucci, 2001; Scheiner, 1993). Indeed, flexibility in expression of care is another general property exhibited by parents in most species that have evolved parental care. Across a wide array of organisms, individual parents adjust their care to a variety of conditions, such as the number of offspring (e.g. Gow & Wiebe, 2014), the availability of new mates (Muldal, Moffatt, & Robertson, 1986), the value of resources needed for offspring (Trumbo, 1991) and the potential risks of care to either the parents (Ghalambor, Peluc, & Martin, 2013) or the offspring (Eggers, Griesser, & Ekman, 2005). Such flexibility is predicted by both life-history theory about parental care (e.g. Clutton-Brock, 1991; Winkler, 1987) and theory on phenotypic plasticity (e.g. Moran, 1992; Scheiner, 1993).

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

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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. [Charmantier et al., 2008](#); [Lack, 1968](#); [Nussey, Postma, Gienapp, & Visser, 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, Schwander, & Faoro, 2003](#)), or the posture of the nestlings ([Redondo & Castro, 1992](#)) or aural sounds such as begging calls ([Kilner, Noble, & Davies, 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 timescales 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 timescale (a day or two rather than either minutes or a week). The unidirectional nature of the change in demand plus the timescale 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 and postfledging 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, Leanza, and King \(1993\)](#) 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 whether parents would adjust to sudden changes in cues to offspring age and, if so, how quickly. House sparrows are nonmigratory 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, Berge, Saether, & Jensen, 2009](#); [Westneat, Hatch, Wetzel, & Ensminger, 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 whether they show 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 whether 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 whether 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., 2011](#); [Westneat, Stewart, & Hatch, 2009](#)). We performed temporary cross-foster experiments with birds breeding in nestboxes 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 young in both nests were between 2 and 8 days of age.

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