Behavioral Ecology and Sociobiology (2019) 73: 130
https://doi.org/10.1007/s00265-019-2747-z

ORIGINAL ARTICLE

Variable parental responses to changes in offspring demand have implications for life history theory

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Received: 20 May 2019 / Revised: 13 August 2019 / Accepted: 21 August 2019 / Published online: 27 August 2019

Abstract

Parental care, a component of reproductive effort, should evolve in response to its impact on both offspring and parent fitness. If so, manipulations in brood value should shift levels of care in predictable ways, provided that appropriate cues about the change in offspring value are altered. Prior brood size manipulations in birds have produced considerable variation in responses that have not been fully investigated. We conducted paired, short-term (2 h) reductions and enlargements in brood size (± 2 nestlings) of house sparrows in each of 4 years. Parents at reduced broods shifted parental care downward in all four seasons. Parents experiencing increased broods responded significantly variably across years; in some, they increased care, but in others, they decreased care compared with control periods. Nestlings in both treatments gained less mass than during control sessions, with year producing variable effects. We found evidence that parents experiencing reduced broods behave as if recurring predation is a risk, but we found no evidence that parents with enlarged broods were responding to inappropriate cues. Instead, parent sparrows may be behaving prudently and avoid costs of reproduction when faced with either broods that are too small or too large. We modified a published model of optimal care, mimicked our empirical manipulation, and found that the model replicated our results provided cost and benefit curves were of a particular shape. Variation in ecology among years might affect the exact nature of the relationship between care and either current or residual reproductive value. Other data from the study population support this conclusion.

Significance statement

Parent animals often adjust their levels of care in response to manipulations of offspring value, but considerable variation in these responses exists. This suggests either a mismatch between manipulation and natural cues or undetected subtleties in the fitness consequences of care. Over 4 years, we conducted manipulations of offspring number in the biparental house sparrow (*Passer domesticus*). We found little evidence that parents misinterpreted cues regarding the change in number, but they behaved differently depending on the year of the manipulation. A model recovered the observed patterns if a parameter influencing the curve relating offspring fitness to levels of care was altered. This parameter should vary with food supply, and our data suggested that this varied in the years of our study. Our results emphasize that predictions about patterns of parental care are risky without attending to the shapes of fitness curves and that some organisms may be particularly sensitive to food supply.

Keywords Parental care · Phenotypic plasticity · Residual reproductive value · Brood value · House sparrow

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Communicated by M. Leonard

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-019-2747-z) contains supplementary material, which is available to authorized users.

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Introduction

Parental care, the aid given by an adult to offspring, varies among taxa, among individuals within a population, and among contexts within individuals (Clutton-Brock 1991; Royle et al. 2012). The dominant adaptive explanation for this variation is that differences in ecological circumstances influence the magnitude of the benefits of care to offspring (Lack 1947, 1954) and/or the costs of that care to the caregiver's future fitness (residual reproductive value (RRV); e.g., Williams 1966; Trivers 1972; Winkler 1987; Kvarnemo 2010). Considerable evidence exists to support this idea. In birds alone, manipulations of brood size, the number of offspring simultaneously needing care, presumably change the value to parents of the current group of offspring. These have typically produced the predicted changes in parental effort, with parents making more trips to the nest in response to larger brood sizes and fewer to smaller broods (e.g., Kluijver 1933; Klomp 1970; Nur 1984; García-Navas and Sanz 2010). Some of these studies have demonstrated a cost of altered parenting to the caregiver, including higher weight loss during the period of parental care (e.g., Askenmo 1977; Nur 1984; Martins and Wright 1993), reduced probability of renesting in the same season (Tinbergen and Daan 1990), reduced clutch size in subsequent breeding attempts (Hegner and Wingfield 1987; Gustafsson and Sutherland 1988), or lowered parental survival (e.g., Askenmo 1977; Dijkstra et al. 1990).

Despite the considerable effort undertaken to test elements of life history theory pertaining to parental care, some important puzzles remain. For example, many of the avian studies that have searched for costs of care have failed to find them (Santos and Nakagawa 2012). There are several hypotheses for why. One is that parents may respond in ways that protect their residual reproductive value (RRV) at the expense of the current brood, but it is then not clear when this should happen as opposed to parents sacrificing RRV for current reproduction. A second possibility is that changes in brood size do not change brood value in the ways that one might expect. For example, increases in brood size may actually reduce brood value if parents are unable to provide food for all the extra mouths. Both these possibilities could be sensitive to varying ecology. Högstedt (1980) manipulated the clutch size of black-billed magpies (*Pica pica*) and found optimal clutch size corresponded to territory quality. Ardia (2007) manipulated brood size in tree swallows (*Tachycineta bicolor*) in two locations and uncovered some site and sex differences in responses. Three studies have found effects of year on the response to brood manipulations in great tits (*Parus major*). In one, year influenced the symmetry in the change in parental response to increased versus reduced brood sizes (Smith et al. 1988). In the other two studies on the same population in the same years, year influenced the asymmetry in nestling mass changes from before to after the manipulation (Nicolaus et al. 2015) and affected the magnitude but not the direction of the asymmetry of reduced versus increased brood size compared with controls (Mathot et al. 2017). A study in willow tits (*Poecile montanus*; Orell and Koivula 1988) also found that year modulated the impact of the manipulation on nestling mass. These results suggest that variable ecology might have a major effect on how parents respond to brood size, possibly in adaptive ways.

A third, rarely tested possibility is that the variation in response to brood manipulations could be due to how a brood manipulation affects the cues parents use to adjust their care. The general assumption that care is plastic has strong support because most brood manipulations conducted to date have had some effect on parental care. Active plasticity requires appropriate cues to generate shifts in behavior. Begging intensity by nestlings clearly provides parents information about offspring state (e.g., Budden and Wright 2001; Leonard and Horn 2006), but do parents interpret the summed begging of a manipulated brood in the correct way? Two potential problems may exist. First, brood reductions are natural, but the reasons for them occurring naturally may alter care directly. Partial brood loss in birds could arise from brood reduction, partial predation, and disease. Each of these could engender a potentially different response by parents. Brood reduction might cause parents to increase care to a reduced brood because the value of the remaining nestlings is now higher than before. Alternatively, nestling loss could indicate partial predation, which may reduce provisioning because either the predator could be dangerous to parents, the nest needs protecting, or provisioning might alert the predator that some nestlings remain (Martin et al. 2000). Conversely, natural increases in number after clutch completion are exceedingly rare, and so manipulations increasing brood size might create unusual responses, including repeated inspection of the nest and behavior that suggests confusion about the change. In general, these effects seem likely to be short-lived, but because few studies have investigated them, their potential to impact life history trade-offs is unknown.

If manipulations of brood size create deviant cues from those that parents use naturally to regulate feeding effort, then this should be most evident immediately after the manipulation. Although several studies have employed temporary brood manipulations (e.g., Magrath et al. 2007; García-Navas and Sanz 2010), none has specifically examined behavior in visits immediately following the manipulation. Short-term manipulations thus provide the opportunity to assess parental responses in the necessary detail to uncover if parents misinterpret the manipulated change in their broods. Short-term manipulations are unlikely to induce reproductive costs, but the changes induced in the short-term provide clues as to how parents might react over the longer term and may be relevant to understanding selection acting on traits like parental care.

Here, we report on a series of short-term manipulations of brood size in house sparrows (*Passer domesticus*) to investigate plasticity in parental behavior. House sparrows are a socially monogamous bird, native to Europe yet widely established in several other parts of the world including North America (Anderson 2006). House sparrows of both sexes exhibit multiple forms of parental care including nest defense and incubation of eggs (Anderson 2006), but the most conspicuous is the provisioning of dependent offspring, which lasts for 16–18-days of nestlings in the nest plus some 7–10 days after they fledge. Both parents provision a wide diversity of insects although sex differences in the timing of provisioning exist (Anderson 2006; Ringsby et al. 2009; Westneat et al. 2011). Both brood size and nestling age, among other factors, have strong deterministic effects on provisioning rate (Westneat et al. 2011). Parent sparrows adjust immediately (within 1 visit) to experimental shifts in brood demand when nestling age is manipulated (Pelletier et al. 2016) but show few changes to manipulations of partner effort (Schwagmeyer et al. 2002) or nestling hunger (Mock et al. 2005). Hegner and Wingfield (1987) manipulated brood size equally in both directions just after hatching and found effects of brood size on both parental behavior and nestling mass at fledging. The statistical test used (regression against brood size) did not assess for asymmetric effects of enlargement versus reduction, although the relationship between brood size and provisioning appeared linear, suggesting a symmetric response.

We report data that arose from a larger study of plasticity and variance sensitivity that is currently unpublished. In the present analysis, we investigate a subset of trials performed when nestlings were between 6 and 8 days of age (see below). Thus, the results presented here are a consequence of exploiting data collected for other reasons and they address some ideas that, while previously present in the literature in some form, only emerged as potentially important as we began to scrutinize our data. We investigated two major ideas. First, because we conducted trials over multiple years, we included year in our analysis and so we asked if the parental response to a short-term change in the number of offspring was sensitive to year-to-year differences. To aid in interpreting those results, we subsequently examined nestling performance in broods within the same year that were not manipulated at the time. Second, we assessed if parental responses to the manipulation might be a byproduct of altering the cues parents use normally to regulate parental behavior. We predicted that if this was correct, then sudden brood reduction might lead parents to behave abnormally, especially early in the manipulation. For example, if they interpreted a reduction in brood size as partial predation, they would either avoid the nest more or sit on or in the nest more early on in the manipulation than in the control session or late in the manipulation session. Because brood enlargements are so unnatural, specific predictions were not possible, but we expected that if parents were confused, they would inspect the nest more frequently (visit without bringing food) early on during the manipulation phase.

Methods

Population

We collected data on provisioning behavior and nestling mass changes and conducted short-term manipulations of brood size on pairs of house sparrows located on the University of Kentucky's North Farm, approximately 5 km north of downtown Lexington, KY, USA. The population has been monitored since 1992, and details of the study site and field procedures are described in Westneat et al. (2002, 2009, 2011). During the years described here (2011–2014), we monitored 116 artificial nest boxes, 78 mounted on 6 barns and 38 solitary boxes on poles. Mean brood size during this time was 4.0 and ranged from one to six. Members of the field team inspected nest boxes every other day for nest building, appearance of new eggs, and hatching, starting in mid-March and continuing until mid-August. Once eggs had hatched and we could determine an initial brood size for two nests with the same hatch date (date when half or more of eggs had hatched), we assigned them to a dyad, randomly if there were more than two nests with the same hatch date. If one brood failed, it was either replaced with another brood with the same hatch date, or the surviving nest was removed from the experiment.

Brood manipulations

Before the day of manipulation, we randomly assigned the two nests in a dyad to a treatment. These were either "reduced," in which brood size was to be decreased by two nestlings, or "enlarged," in which the nest would receive the two nestlings from the reduced nest within the dyad. Some exceptions occurred for a small number ($n = 7$) of cases in which one brood in the dyad had fewer than 3 nestlings and thus could not be reduced by a further two nestlings. This biased pre-manipulation brood size slightly in 2 years (2011 and 2012) but appears to have had little effect on the results. In a few cases ($n = 5$ dyads of 45 total), only 1 nestling was swapped, usually because of an unexpected event such as nestling mortality on the day of the experiment.

In 2011, we manipulated 10 dyads when nestlings were 6–8 days post-hatch. In 2012–2014, we similarly manipulated brood size at days 6–8, but these pairs also experienced the same manipulation at nestling age 2; here, we report data from only the manipulation done on days 6–8.

On the day of the manipulation, each box in a dyad was visited; the brood was weighed (except for most nests in 2011) and replaced in the nest. We then turned on a digital camcorder, installed in a camera box permanently mounted nearby on the barn or on a tripod for the solitary nest boxes, and focused it on the entrance to the nest box. The camcorder recorded for 2 h parent arrivals and departures and in most cases also the food items they carried. We call this the "pre" stage, which serves as a control for the disturbance effect of handling nestlings and setting up the camera. At the end of 2 h, we revisited the box assigned as "reduced" and arbitrarily selected 2 nestlings for removal. In most cases, we separately weighed the 2 transfers and the remaining nestlings that were placed back in the focal nest box. We then immediately restarted the camcorder to record parental visits during this "manipulation" stage. We marked the 2 removed nestlings either with an indelible marker on the leg or with a plastic colored leg band and quickly transferred them to the nest box targeted as "enlarged." There, we removed the host brood, weighed them, and returned them in the nest with the two transfers. The camcorder at this box was also restarted and recorded parental visits for another 2 h under experimental conditions. The two nests within a dyad typically differed by less than 10 min in the timing of the start of the manipulation. After 2 h, we then revisited the box with the increased brood, collected the camera, obtained the mass of all nestlings and also that of the two fostered nestlings separately, and returned the natural brood to the nest. The two fostered nestlings were returned to their home nest, where we also obtained the mass of their siblings that had remained with their natural parents.

We note that the repeated measures design does not control for the appearance of potentially unfamiliar nestlings in enlarged broods, but there is little evidence that parent sparrows recognize offspring at this age (Pelletier et al. 2016). The control-then-manipulation order of observations also does not control for timing effects. However, dyads differed in their timing, with some days having two sets back-to-back, and all nests had been disturbed via nest checks many times before the experiment. Time of day has minor effects in a separate dataset (Westneat et al. 2011) and variance in timing had no effect on behavior or mass changes in the present one (Electronic Supplementary Material, Tables S1, S10).

Scoring of videotapes

The authors and a team of assistants scored the camcorder files blindly with respect to whether the nest was enlarged or reduced (since video could only view the outside entrance to the box), but we knew when we scored the pre-manipulation control files versus the manipulation period. We collected the time of arrival, time of entry into the box, time of emergence, and time leaving the camera view and the sex of the parent for each visit. We also scored the size of the load, if any, for each visit using bill size as the referent (as in Pelletier et al. 2016). Load size scores are repeatable across scorers (Pelletier et al. 2016), but do exhibit some observer differences, so scorer identity was included in any models of load size. We could not score load sizes for some visits if the bird entered the box too quickly, was blocked from view by another bird, or if the load was entirely inside their bill and so could not be seen at all. We labeled as non-feeding any visit in which the bird did not enter the box, opened its bill or wiped it before entering the box, or emerged from the box without visible food and then returned inside without leaving the camera view.

Population-wide analysis of nestling growth

To assess if the results we obtained from the experiment reflected population-wide conditions, we collected data on nestling mass and change in mass of unmanipulated broods throughout 2012–2014. As with the experiments described here, the procedure was to weigh the whole brood, videotape parental behavior for approximately 2 h, and then weigh the brood again. These sessions occurred approximately every other day from day 1 through day 11. We assessed if year differences were evident in the per hour mass change of nestlings in these broods.

Analysis

Some problems with video cameras or disturbances near the nest during the trial caused us to omit some data from the brood manipulation before analysis. The final dataset consisted of 8620 total visits and 7120 individual feeding visits from 45 dyads, involving 82 breeding attempts and 148 unique adults. These visits were scored for time elapsed from when a specific individual left the nest previously after bringing food and returned with food, subtracting any time at the box when the subject returned without food (trip time, calculated for all trips except the first one). We also scored the duration the bird was at the nest box and the load size it brought converted to cubic mm assuming a standard bill volume of 218 mm^3 (Pelletier et al. 2016). Visits clustered hierarchically into the stage in the experiment (pre-manipulation control period or manipulation period), bird identity, and dyad identity.

We created two datasets on provisioning. One contained summary variables of the total number of trips by the pair, the rate of trips to the nest per pair per hour, the cumulative load size per pair per hour, and the change in brood mass per hour for each breeding attempt. Both visit rate and load size rates were analyzed using the untransformed values with linear mixed models. We also reanalyzed the total number of visits using a generalized linear model with a log link function under a Poisson distribution. We included the duration of the observation as an offset covariate. For clarity and ease of interpretation, we present the parametric analysis here and the GLMM in the supplementary material (Electronic

Supplementary Material, Table S3). For the pair level dataset, we included dyad identity (Dyad) and breeding attempt identity (BreedID) as random effects. In early models, we included the mated pair's identity as a random effect since a few pairs were part of more than one trial, but there were too few of these ($n = 4$) to analyze separately from the other random effects, so we dropped that term. For fixed effects, we included the year and date in season as potential confounds, and for models of cumulative load per hour, we included scorer and number of trips that load could be scored (grand mean-centered). All models also included stage (pre and manipulated), treatment (reduced vs enlarged), the interaction between them, and all interactions with year. Our main prediction was first that a stage by treatment interaction would influence parental care, but we included a year by stage by treatment interaction given that we suspected year would have mitigating effects. Residuals were checked visually for any major deviations from those expected under assumptions of normal distributions. In most cases there were deviations at both the extremes of the distribution, but the majority of residuals fit a normal distribution.

The second dataset was composed of each visit to the nest by each individual parent over both phases of the experiment. In this dataset, we conducted fine-grained analysis of shifts in behavior to assess in what way changes in parenting occurred and if behavior might indicate that manipulations produced abnormal cues. We investigated patterns in trip time ($\log_{10}$ transformed), load size, and time spent at the nest site on each visit ($\log_{10}$ transformed). For each of these, we employed a linear mixed model with Dyad, BreedID, and two new random effects, individual identity (Individual), and an identifier for the 2-h observation session (Observation). In early analyses of this and the other dependent variables, we also tested if location (box identity) explained significant variance or if it mattered whether we nested Individual ID within BreedID or not, since some individuals participated in more than one trial of the experiment. Box identity did not explain much variation in any variable, and we opted for keeping Individual ID unnested. We included the year, date in season, time of day, and scorer identity (for load size only) in the fixed effects portion to control for any confounding effects. All analyses also included stage, treatment, their interaction, and all interactions with year. As above, we also included a priori contrasts to assess if the absolute value of any change from the pre to manipulation period differed between the treatment groups.

We analyzed known non-feeding visits at the observation level using a generalized linear mixed model with Poisson distribution and log link and observation duration as a covariate. We also analyzed the probability any visit was a non-feeding visit with elapsed time in the observation as a predictor variable using a GLMM with binomial distribution and logit link. These were conducted with the same random effects structure as described above.

We analyzed brood mass changes per hour during non-experimental video trials using linear mixed models with breeding attempt identity as a random effect and time of year, brood size, nestling age, and year in the study as fixed effects. We included an interaction between brood size and nestling age, and interactions between year and all other variables.

All analyses were conducted in both SAS 9.4 (SAS, Inc.) and lme4 in R (version 3.4.2) environment (R Development Core 2017) for comparison (the code for both is provided in Electronic Supplementary Material), but they provide nearly the same results and those from SAS are presented here.

Model of optimal parental effort

Our empirical results suggested an unexpected but possibly strategic response by parent sparrows. We assessed if the nature of that response was plausible given existing theory on parental effort. We modified the models of Winkler and Wallin (1987) and Tammaru and Horak (1999) to assess the predicted behavior of parents in response to brood manipulation. We use somewhat different nomenclature. Offspring survival, J_s, as a function of PE (the summed parental effort by the two parents) followed the equation:

$$J_s = 1/\left[1 + e^{-k(E/B-c)}\right].$$

Here, k is a parameter affecting the rate of increase in survival with increasing summed parental effort (E) and c is the level of care where the curve inflects from accelerating to decelerating. Current reproductive success, R, for a given level of PE was modeled as $B \times J_s$, where B is the brood size.

Parent residual reproductive value was affected by its own parental effort via its impact on parental survival and expected reproductive success in the future. Parental survival, S, is

$$S = S_m\left(1 - \left(\frac{E}{2}\right)^d\right)$$

where S_m is maximal parental survival when no care is expressed, and d is a parameter affecting the change in slope of the effect of care on survival. When $d = 1$, the effect of care is linear, when $d > 1$, then increasing PE has an accelerating, negative effect on parent survival. Residual reproductive value was calculated by the product of $S \times F$, where F is the expected future reproductive success.

Net fitness was the sum of $R + F$. We examined this to adjust parameter values that gave an optimal brood size of approximately 4, close to the average number of hatchlings produced by house sparrows in Lexington, KY (Westneat et al. 2009, 2014). We considered these to be the default parameters. For each set of parameters, we ran the model and found the optimal level of care and the offspring survival given that level of care. The main parameter of interest was the brood size, and we simulated brood manipulations producing brood sizes of 2, 4, and 6 offspring. We then adjusted other parameters to assess patterns in both the parental response and the offspring survival. Table S11 shows the three main models we explored.

Results

Pair behavior

House sparrow parents altered several aspects of their provisioning behavior in response to the short-term manipulation of brood size (Fig. 1), but they did so differently between years (feeding rate: stage × treatment × year interaction: $F_{3,77} = 7.9$, $P = 0.0001$; Table S1). While visual inspection of Fig. 1 would suggest that the experimental groups differed before the manipulation, analysis of just the control period revealed no difference in visit rates between treatments ($F_{1,41.6} = 0.4$, $P = 0.53$) nor did this depend on year (treatment by year interaction; $F_{3,40.8} = 1.9$, $P = 0.14$). Delivery appears more extreme, but after controlling for scorer and loads scored, treatments were not different ($F_{1,37.9} = 3.6$, $P = 0.06$) nor was the interaction with year ($F_{3,35.2} = 2.7$, $P = 0.06$). Pairs experiencing enlarged broods increased their rate of feeding visits per hour in 2011 and 2014, but reduced feeding rate in response to more nestlings in 2012 and 2013, compared with those in the control session (Fig. 1a). Parents of reduced broods decreased their feeding rate during the experiment, but this ranged in magnitude between 5.7 and 13.6 total feeds/hour less than during control periods, and the year by stage interaction for reduced broods was significant ($F_{3,39} = 4.0$, $P = 0.01$). Total food delivered per hour exhibited similar patterns (Fig. 1b, Table S2). Redoing the analysis using a generalized linear model assuming a Poisson distribution (Table S3) or modeling relative changes in brood size (Table S4) did not alter the main results. Neither date in season nor time of day affected parental behavior (see Electronic Supplementary Material).

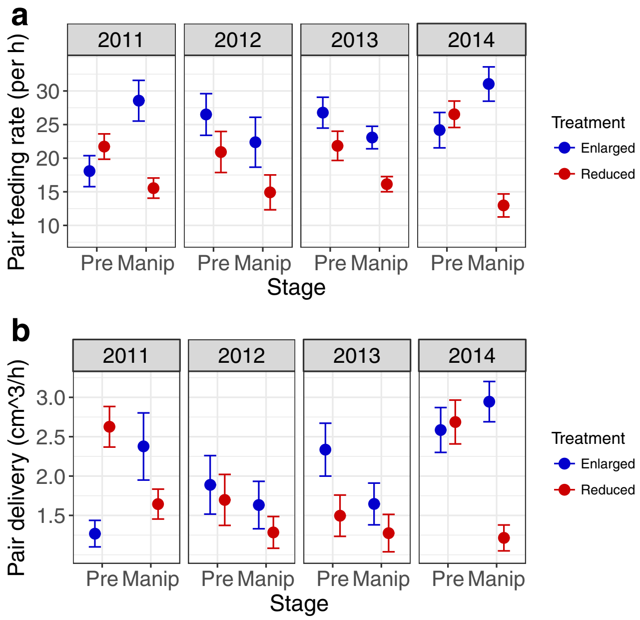


Fig. 1 Mean feeding rate (**a**) of house sparrow pairs per hour and cumulative food delivery (**b**) by the pair per hour ± SE, as measured during the control period (Pre) or the manipulation period (Manip) for breeding attempts in the enlarged (indicated in blue) and reduced (indicated in red) treatments over 4 years of study. Values of food delivery are uncorrected for feeding visits that could not be scored, whereas this was accounted for in the statistical analysis (see text and Table S2). Tests of significance using both parametric linear mixed models and generalized linear mixed models (visits only) are presented in Tables S1-S3

Changes in visit-level behavior

The experimental change in brood size impacted how parents allocated time on each visit to the nest (Table 1). We found a significant effect of year on the stage by treatment interaction for time spent away from the nest before each feeding visit (Table 1). In each year, parents of reduced broods increased their trip times during the experimental stage. In 2 of the 4 years, parents of enlarged broods decreased trip time, but in the other 2 years (2012 and 2013), parents increased trip times when confronted with a larger brood (Table 1, S5). In all 4 years, the absolute value of the change in behavior was greater for parents of reduced broods. There thus was a strong overall interaction between stage and treatment (Table 1, S5), with parents of reduced broods shifting an average of 0.17 ± 0.03 (SE) log seconds longer per trip (~ 1.5 s longer), and parents of enlarged broods shifting only 0.001 ± 0.03 log seconds shorter, with a significant asymmetry between those (difference in absolute value = 0.17 ± 0.04, $t_{131} = 4.7$, $P < 0.0001$). We found no differences between the sexes in overall trip time (M-F = 0.009 ± 0.03 log seconds, $F_{1,103} = 0.0$, $P = 0.87$).

The treatments also affected the time during each visit that parents spent at the box, either inside with the nestlings or sitting on the outside (for the full model, see Table S5). Females spent significantly longer at the box (1.7 ± 0.03 log seconds) on each trip than did males (1.5 ± 0.03 log seconds; $F_{1,77} = 54.4$, $P < 0.0001$), or a difference of 1.6 s/trip. There were, however, no significant interactions with sex, so we retained only the main effect in the model. As with other behaviors, year had a significant modulating effect on the effect of the experiment (Table 1). In all years, parents of reduced broods increased the time they spent at the box, averaging 0.19 ± 0.03 log seconds (~ 2 s) more ($t_{157} = 6.6$, $P < 0.0001$). In three of the years, parents of enlarged broods decreased time at box when the brood was increased, but in 2012, they slightly increased time at box. The overall average was − 0.09 ± 0.03 log seconds ($t_{138} = 3.4$, $P = 0.0009$). In all 4 years, parents of reduced broods changed behavior more

Table 1 Estimates and significance tests of variables included in linear mixed models of the time spent at the box and trip time (both log-transformed) for each visit by individual parent house sparrows measured during both a control and brood manipulation phase (stage) in which some broods were increased and others reduced (treatment)

	Foraging trip time (log s)			Time at box (log s)		
Effect	Estimate ± SE	LRT[1]	*P* value	Estimate ± SE	LRT[1]	*P* value
Random						
Dyad	0.007 ± 0.004	433.7	< 0.0001	0.006 ± 0.004	308.7	< 0.0001
BreedID	0 ± 0	201.2	< 0.0001	0	177.2	< 0.0001
Individual	0.027 ± 0.006	440.9	< 0.0001	0.020 ± 0.005	409.5	< 0.0001
Observation	0.013 ± 0.003	71.3	< 0.0001	0.020 ± 0.003	194.1	< 0.0001
Residual	0.173 ± 0.003	–	–	0.192 ± 0.003	–	–
Fixed		*F*(df)			*F*(df)	
Sex	–	0.0 (1, 108)	0.98		50.5 (1, 115)	< 0.0001
Year	–	0.7 (3, 39.1)	0.55	–	2.6 (3, 42.1)	0.06
Treatment	–	12.0 (1, 124)	0.0007	–	0.1 (1, 131)	0.72
Stage	–	16.9 (1, 130)	< 0.0001	–	3.7 (1, 151)	0.06
Year × treatment	–	0.8 (3, 122)	0.47	–	3.8 (3, 129)	0.01
Year × stage	–	3.3 (3, 129)	0.02	–	1.9 (3, 149)	0.13
Stage × treatment	–	27.9 (1, 130)	< 0.0001	–	33.2 (1, 151)	< 0.0001
Year × stage × treatment	–	5.1 (3, 129)	0.002	–	5.2 (3, 149)	0.002

[1] Random effects tested sequentially by dropping nested terms in order; variance estimates are from full model

than parents of enlarged broods, and overall, this asymmetry was significant (0.09 ± 0.04 log seconds, $t_{147} = 2.3$, $P = 0.02$).

We found weak evidence the treatments affected the amount of food brought on each visit. Load size (log cubic mm) was significantly different among scorers ($F_{9,104} = 3.4$, $P = 0.001$), and males brought slightly smaller loads (1.86 ± 0.03 log mm^3) than did females (1.91 ± 0.04 log mm^3; $F_{1,78.8} = 7.4$, $P = 0.009$), although the difference is small in the observed scale (1.1 mm^3). Load size also varied significantly among years ($F_{3,69.2} = 3.5$, $P = 0.02$). The overall stage by treatment interaction had little impact on load size ($F_{1,144} = 0.2$, $P = 0.69$), but there was a weak effect of year on this relationship ($F_{3,142} = 3.0$, $P = 0.03$), with variable and slight effects in opposite directions for both treatments (Table S6).

Did manipulations alter cues artificially?

We assessed if parents showed responses suggesting they were interpreting brood size manipulations differently than we intended. We had predicted that if cues were inappropriate, we might see elevated non-feeding nest inspections during manipulations, especially early in the trial. Overall, we found that the number of non-feeding visits was no different in the manipulated stage than in control (GLMM [Poisson], $F_{1,159} = 0.17$, $P = 0.69$; Table S7). There was a significant interaction between stage and treatment on non-feeding visits ($F_{1,159} = 14.1$, $P = 0.0002$), but the direction of effects was counter to our initial predictions. Parents of reduced broods inspected the nest more during the manipulation than control (0.18 ± 0.08 ln-visits, $t_{1,159} = 2.4$, $P = 0.02$) whereas parents of enlarged broods inspected less frequently (− 0.22 ± 0.08 ln-visits, $t_{1,159} = -2.8$, $P = 0.005$; Table S7). The probability a given visit was non-feeding was 0.15 at the start of the control period for parents of reduced broods and significantly declined with elapsed time (GLMM [binary]; effect of elapsed time, − 0.0002 ± 0.00004 logits/s, $F_{1,3978} = 34.6$, $P < 0.0001$; Table S8; i.e., the probability a visit was non-feeding would be about 0.08 an hour into the observation). Non-feeding visits were somewhat more likely at the start of the reduction in brood size (0.22) and declined significantly less than controls (interaction between elapsed time and stage, $F_{1,3920} = 5.4$, $P = 0.02$; Table S8; estimated probability at 1 h was 0.17). But we found that while time spent at the box on each trip declined with elapsed time in control sessions (− 0.0003 ± 0.5E-5 log seconds/s, $F_{1,3843} = 40.2$, $P < 0.0001$), there was no significant difference in that pattern between control and experimental sessions for reduced broods (stage × time interaction, $F_{1,3842} = 2.8$, $P = 0.09$). These results suggest parents may be interpreting nestling removal as partial predation and are checking the nest more frequently after brood reduction.

By contrast, the sudden appearance of new nestlings in the nest did not produce unusual behavior by parents. As with the reduced treatment, the probability a visit was non-feeding started at ~ 0.19 and declined through the control period (to 0.11 an hour later; $F_{1,4634} = 79.0$, $P < 0.0001$; Table S9) but there was no effect of the manipulation on either the starting probability ($F_{1,445.5} = 0.01$, $P = 0.99$; estimated probability 0.18) or the effect of time elapsed ($F_{1,4634} = 1.5$, $P = 0.21$; estimated probability 1 h later = 0.09; Table S9). Similarly, the time a parent spent at the box on each visit declined with elapsed time during the control period (− 0.0004 ± 0.4E-5 log sec/s, $F_{1,4671} = 153.5$, $P < 0.0001$) and was no different during the experimental phase (stage by time interaction, $F_{1,4670} = 0.4$, $P = 0.54$). This suggests that these parents were influenced more by our disturbance before each observational stage than by the appearance of two new nestlings and that repeated disturbance had no additional effect.

Changes in brood mass during experiment

Parent provisioning behavior during the control session increased nestling growth rates. Per nestling mass change during the control period was positively correlated with both the number of pair feeding trips (Fig. 2a) and the rate of food delivery by the pair (Fig. 2b). A LMM of brood mass change with brood size as a covariate and dyad ID as a random effect revealed that the number of feeding visits explained more variation in per nestling mass change than did our estimate of delivery per hour (visit rate, 0.037 ± 0.01; $F_{1,58.8} = 3.3$, $P = 0.002$; delivery rate in cm^3/h, 0.15 ± 0.09; $F_{1,58.6} = 3.0$, $P = 0.09$).

The manipulation of brood size had a significant but unexpected effect on nestling mass change in the 3 years that we measured it. The effect of the experiment on per nestling mass change was significantly different by year (stage by treatment by year, $F_{2,109} = 4.9$, $P = 0.009$; Fig. 3, Table S10). While per nestling mass gains of enlarged broods were near 0 during the treatment stage in all 3 years (Fig. 3), nestlings in reduced broods showed mass gains but these were less during the experimental compared with those during the control period in 2 of 3 years with a significant year by stage interaction ($F_{2,27.1} = 5.2$, $P = 0.01$; Fig. 3, Table S10).

There was no evidence that date in the season (− 0.0002 ± 0.003; $F_{1,109} = 0$, $P = 0.99$), time of day (− 0.003 ± 0.002, $F_{1,109} = 1.9$, $P = 0.17$), or starting brood size (0.17 ± 0.09; $F_{1,109} = 3.8$, $P = 0.054$) strongly influenced nestling mass change in experimental broods.

Population-wide changes in brood mass

Analysis of per nestling mass changes in unmanipulated broods in three of the years of this study (2012–2014) revealed evidence of year effects and interactions between other variables and year (Table 2). First, nestlings averaged significantly different growth during the 2-h video sessions across the 3 years ($F_{2,\ 794} = 8.1$, $P = 0.0003$), with 2012 the lowest and 2014 the highest. Mass changes declined as nestlings grew older and this decline accelerated as nestlings aged (Table 2), but both the linear and, marginally, the quadratic were variable among years (nestling age by year, $F_{2,720} = 4.8$, $P = 0.009$; nestling age^2 by year, $F_{2,720} = 2.8$, $P = 0.06$), with 2012 showing the most negative and 2014 the least negative relationship. Finally, nestling mass changes during the 2-h video sessions declined with date in the season (Table 2) but did so variably among years ($F_{2,272} = 3.7$, $P = 0.03$), with 2012 and 2013 having similar declines but 2014 having a flat relationship. All of these results suggest that 2014 was a better year than 2012, with 2013 intermediate.

Model results

We did not engage in an exhaustive analysis of the model since we made minor extensions of already published analyses. As illustrated in Fig. 4, parental care affected offspring fitness depending on the survival curve of a single offspring and the fact that total care was divided among all offspring. Care also reduced parent residual reproductive value. In Fig. 4a–c, a conventional pattern is illustrated. If we assumed the starting brood size was 4 (in the population we studied, natural

Fig. 2 Mass change per nestling house sparrow per hour during the 2-h control period as a function of the pair feeding visit rate per hour (**a**) and the estimated volume of food in cubic mm delivered by the pair per hour (**b**). The red line is the univariate least squares regression of mass gain on feed rate or delivery, which was tested formally in a linear mixed model (Table S10)

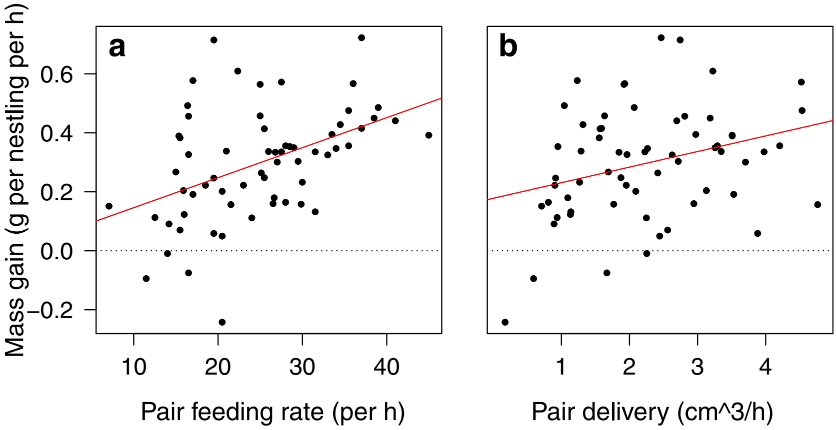
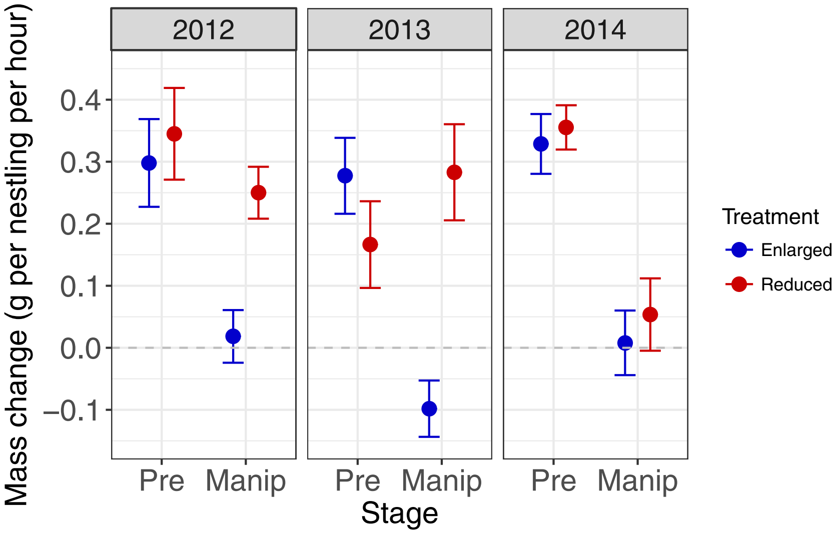


Fig. 3 Mean ± SE of mass changes (g per nestling house sparrow per h) during the two stages ("Pre," control, and "Manip," manipulation) for enlarged (in blue) and reduced (in red) broods over 3 years



brood size at 7 days of age in 2011–2014 averaged 3.4–4.0 nestlings), then a reduction to 2 decreased optimal parental effort and increased offspring survival (*Y*-value at intersection between orange line and gray line, divided by brood size). An increase in brood size increased care and decreased parent survival. In Fig. 4d–f, the same brood size manipulation had a dramatically different effect on enlarged broods. In this case, the optimal response to more offspring was to reduce care, and offspring survival dramatically declined, but parent RRV increased. The difference between these two sets of results was due to a difference of 0.03 in the proportion of summed parental effort that is required for an individual nestling to reach the inflection point in its survival curve (parameter *c*).

The modified model had more difficulty producing the apparent over-response we observed when brood size was reduced, with its apparent cost to offspring growth. Variation in the inflection point did not duplicate that result. Instead, we found that if the effect of care on parent RRV was close to linear, then some combinations of parameters produced net fitness curves with two local optima, one at no care (Fig. S1). This outcome was more likely when broods were reduced.

Discussion

Parent house sparrows adjusted food delivery to the nest following changes in the number of nestlings they provisioned, as has been found in many other species. We found little evidence that these changes arose from altering the load per trip, in contrast to findings in some other species (e.g., Wright and Cuthill 1990; Mathot et al. 2017). Instead, parents shifted time budgets, with those experiencing reduced broods taking longer trips away from the nest and spending more time at the nest. While the effects were quite small in magnitude on each trip, over a 2-h period they sum up in ways that influence the number of visits, the best predictor of nestling mass increases. Parent sparrows at enlarged broods tended to alter their behavior in the opposite direction but did so only slightly, an asymmetry found in some studies (e.g., Moreno et al. 1995; Vitousek et al. 2017) but not others (e.g., Smith et al. 1988; Sanz and Tinbergen 1999). House sparrows show two more rarely documented responses. One is that the magnitude of the behavioral shift, and the impact of it on offspring, varied among years, a result reported previously only in willow tits (Orell and Koivula 1988) and two experiments on great tits (Smith et al. 1988; Nicolaus et al. 2015; Mathot et al. 2017). The most surprising result in our study given the history of brood manipulations in birds was that in some years, parents experiencing reduced brood sizes decreased their provisioning to the remaining nestlings so much that nestling mass gain rates were less than in control periods when food deliveries by the same parents were shared among more offspring. The effect of year and the unusual over-response to reduced broods thus provide cause to reexamine how manipulating brood size may alter the cues of brood value and the presumed selective forces shaping parental care and family size.

Manipulations of cues

Our short-term manipulations allowed detailed inspection of the behavioral responses of parents to the two types of brood manipulations. There is no question that brood size manipulations change parent behavior in this and many other studies, usually qualitatively in a direction predicted if it were adaptive. This means the manipulation creates cues that at least correlate with the cues or signals that parents attend to naturally. But might such changes arise for other reasons besides

Table 2 Results from a linear mixed effects model of change in brood mass per hour, in which attempt identity was a random effect and all fixed effects were centered (nestling age at 10 days, brood size at the mode of 4 nestlings, and date at the mean of 158 (Julian date))

Variable	Effect (g/h) ± SE	Statistic (X^2 or F)	df	P value
Attempt ID	0.04 ± 0.02	6.2		0.02
Residual	0.57 ± 0.03	–		–
Year		8.1	794	0.0003
Intercept (2012)	0.03 ± 0.10	0.13	673	0.73
2013	0.26 ± 0.18	2.1	789	0.14
2014	0.72 ± 0.18	16.1	799	< 0.0001
Brood size	0.13 ± 0.03	23.4	351	< 0.0001
Nestling age (2012)	− 0.39 ± 0.05	63.6	771	< 0.0001
(Nestling age)^2 (2012)	− 0.04 ± 0.006	67.2	765	< 0.0001
Date in season (2012)	− 0.005 ± 0.002	12.6	287	0.0004
Nestling age by year		719	4.8	0.009
Nestling age, 2013	0.09 ± 0.08	1.2	734	0.27
Nestling age, 2014	0.25 ± 0.08	9.6	722	0.002
(Nestling age)^2 by year		2.8	720	0.06
(Nestling age)^2, 2013	0.01 ± 0.009	1.6	734	0.21
(Nestling age)^2, 2014	0.02 ± 0.009	5.6	727	0.02
Date by year		3.7	272	0.03
Date in season, 2013	− 0.0004 ± 0.002	0.02	260	0.88
Date in season, 2014	0.004 ± 0.002	4.7	307	0.03

the intended one of creating changes in brood value? Decreases in brood size are a common, natural event in most birds, including in house sparrows where partial predation or natural brood reduction can affect over half of nests (Anderson 2006; Mock et al. 2009). Parents might interpret the sudden reduction in brood size as a recent predation event. The details of the behavior of parents experiencing reduced broods were not consistent with them shifting from provisioning to either defense or avoidance of the nest after the manipulation. They did inspect the nest more frequently and this persisted longer during the manipulation than during control sessions, suggesting that parents may be checking the nest for possible return visits by predators. A possibility we cannot eliminate is that if parents interpreted brood reduction as predation, they may have devalued the brood more than expected from just the reduction of two nestlings because once one predation event occurs, more may be likely. The sparrows in our population experience three main types of predators: raccoons (*Procyon lotor*), which take the whole brood at once; other house sparrows, which can be defended against; and American kestrels (*Falco sparverius*), which can return to take nestlings successively and are dangerous to the parents. The presence of kestrel predation in our population might mean that parents check for repeat predation and devalue reduced broods more than their proportion of the original brood size.

By contrast, increases in brood size rarely occur in most birds that nest in separated locations such as nest boxes or on territories. The asymmetry in parental response we observed (Fig. 1) could be explained by this difference in how manipulations interface with the normal cues parents use to assess brood value. A well-studied cue is the intensity of begging (Redondo and Castro 1992; Leonard and Horn 1996; Wright et al. 2002); adding more nestlings presumably increased both the aural and visual stimuli associated with begging (Wright et al. 2002). We did not measure begging in this study. However, parents did not respond proportionately to the addition of nestlings. While this could result from the fact that increases in the number of nestlings are not natural and the period we gave them to adjust was too short, this lack of a response is particularly odd given three other bits of knowledge we have. Firstly, we found no evidence that parent sparrows found the addition of two nestlings unusual, as their time in the box declined rather than increased and they did not exhibit more non-feeding visits, a response expected if they were checking on unusual nestlings in their nest. Secondly, the impact of brood size enlargements was variable among years, which seems unlikely to occur if the response was solely about mismatches between manipulations and natural cues of brood value. Finally, in a separate study, parent sparrows shifted behavior symmetrically to swaps of nestlings that differed in age (Pelletier et al. 2016), despite the fact that nestlings never get younger in nature. They thus treat cues of age differently than they do cues of number. This difference is provocative in two ways. First, it argues against the idea that parents use a single cue dimension such as begging intensity. Other cues of age or number seem necessary to explain these results, which means responses to begging intensity may be conditional on other types of information. That begging is multivariate has

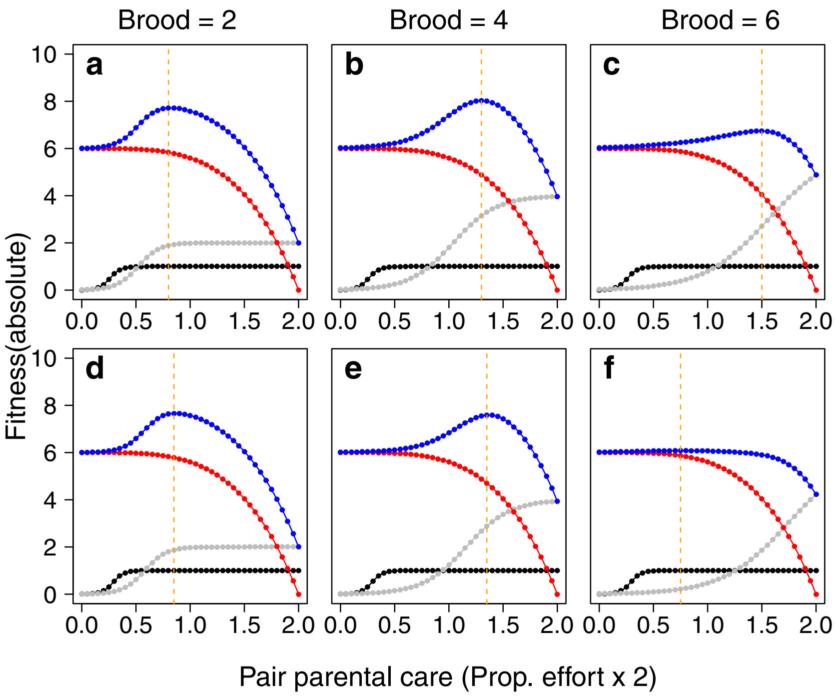


Fig. 4 Results of model modified from Tammaru and Horak (1999) showing the impact of parental care on various fitness components under varying conditions. Black lines indicate the effect of total care (by the pair, E) on the survival of a single offspring ($1/(1+e^{(-20(E/B-c))})$), with gray lines showing the impact of PE on the number of offspring surviving in a brood (B) of the specified size ($B/(1+e^{(-20(E/B-c))})$). Red lines indicate the parent's residual reproductive value, the number of offspring produced in the future, as a function of the level of individual care provided ($6(1-(E/2)^{3.9})$). Blue lines indicate the net fitness, present plus residual. In each panel, the vertical orange dashed line indicates the level of care that maximizes net fitness. Brood size is indicated at the top of the graph. Parameters and their values are presented in the Electronic Supplementary Material, but in panels **a**–**c**, the parameter c that determines the value of care at which the survival curve for an individual offspring inflects from accelerating to decelerating was equal to 0.26. In panels **d**–**f**, all other parameters are the same except $c = 0.29$. This gives a different effect of brood size on optimal care, with care declining for both $B = 2$ and 6 compared with the "control" size of 4

been appreciated (Kilner et al. 1999), but whether components of begging or status of the brood interact non-additively to affect provisioning is not known. Second, any manipulation may alter the natural cues used by parents in unexpected ways, and so any response may be due to its effect on any of several possible types of cues (e.g., number of mouths, total begging loudness, gape area, posture; Budden and Wright 2001; Glassey and Forbes 2002). Nevertheless, the differences between the two types of manipulations on sparrows suggest different use of natural cues. Finally, the conspicuous differences between years argue against misaligned cues being the driving force behind our results. It seems unlikely that the same manipulation would misalign cues in one season but have a different effect on another.

The strategic hypothesis and variation in response

Assuming that misaligned cues are unlikely to explain our results, could the patterns of behavior reflect strategic responses? To explore this idea, we slightly modified the model of Tammaru and Horak (1999), based on a previous model presented by Winkler and Wallin (1987). Our model results suggest the empirical results are possibly strategic under some apparently realistic sets of parameters. Fluctuation in a parameter that reflects the parental effort required to reach a given level of offspring survival qualitatively duplicated the variation in results we observed for enlarged broods. That parameter may be especially sensitive to environmental variation. Even slight changes in the abundance of prey or how cryptic they are could cause the effort required to obtain a given unit of food to change. The pattern of nestling mass changes across the whole population suggests that 2012 and 2013 were poorer years than 2014 and implies that year-to-year differences may be driving differences in how parental effort translates to offspring fitness. Our results suggest that parent sparrows are sensitive to this. Our data from 2011 would fit with it being a better year, but we have no other data to confirm that.

We had less success in finding combinations of model parameters to produce the surprising decline in offspring mass gains in reduced broods. We did find some cases in which total fitness exhibited a bimodal distribution, with one mode at zero parental effort (Fig. S1). If the current brood has low value or parents are struggling, it may make sense for a parent to preserve RRV instead of providing any care. It is not clear how this explains the over-response of house sparrows, because no subject in our study dropped their care to 0. Moreover, this apparent over-response occurred in the 2 years with opposite patterns in nestling mass changes in the population at large (i.e., in both a bad and good year for nestlings). Sparrows are multi-brooded, making the impact on RRV of caring for the current brood potentially high. However, it is difficult to understand how year-to-year variation would drive an accelerating cost curve to become almost linear, for parents to be able to assess this change and produce an adaptive over-response to brood reductions. We need to know more about the nature of this over-response, which occurs only some of the time and may instead be a response to the risk of recurring predation.

Conclusions

Manipulations of the number of offspring receiving care have provided a major experimental approach to assessing the central idea of life history theory that there is a trade-off between current and future reproduction. The results of this effort have been mixed (e.g., Reznick et al. 2000), especially in birds (Santos and Nakagawa 2012). The core assumption of the experimental approach is that parents should be plastic and alter their parental effort upward if brood size is increased and downward if it is decreased. The parent house sparrows in our study were plastic in both visit level behavior, as well as the emergent property of the rate of visits by the pair to the nest. However, they were not necessarily plastic in the ways one might expect, and they showed considerable variation across years in their response to the manipulation. We cannot eliminate completely the possibility that brood size manipulations introduced unusual stimuli that cause parents to behave inappropriately. How experiments alter the cues parents use to monitor brood value is a neglected part of testing life history theory. But our results suggest this is unlikely to be the dominant explanation in the case of house sparrows. We show, using an idea originally presented by Tammaru and Horak (1999), that life history theory itself could explain at least some of the responses we observed, due to conditions that would make critical tests of the theory in this case difficult if approached only superficially. The combination of our results, the modified theory and the variation in responses across the many prior studies manipulating brood size, means that quantitative test of this aspect of life history theory will require more information about the array of cues that parents might use to adjust care. We will also need to know more about the underlying functions that translate such care into effects on both offspring fitness and parental residual reproductive value. That the sparrows in the present study exhibit substantial year-to-year differences despite routinely switching among prey types serves to emphasize that it matters exactly how care influences fitness components and that general conclusions from experimental approaches will unfortunately not emerge until such details are known.

Acknowledgments We thank the managers and staff at Maine Chance and Coldstream Farms for accommodating us in the midst of their daily routine. We are deeply indebted to the many people who helped in the field (Jonathan Brown, Stephanie Cervino, David Moldoff, Kat Sasser, Dan Wetzel, Chelsey Oedewaldt, Kate Pelletier, and Becky Fox) and with the scoring of video files (Jonathan Brown, Annie Griggs, Laura Westneat, Jamile Naciemento, and Stephanie Cervino). We also appreciate many useful suggestions on the manuscript from Allyssa Kilanowski, Allison McLaughlin, Tim Salzman, Eduardo Santos, Kat Sasser, Jonathan Wright, and several anonymous reviewers.

Funding This project was supported by the U.S. National Science Foundation (IOS1257718) and the University of Kentucky.

Data availability The data files associated with results in this paper have been archived with Dryad under the DOI: https://doi.org/10.5061/dryad.cs673qg.

Compliance with ethical standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All basic activities and the manipulation described were approved by the Institutional Animal Care and Use Committee of the University of Kentucky (protocols 2007-0227 and 2012-0948).

Conflict of interest The authors declare that they have no conflicts of interest.

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