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Experimental manipulation of brood size affects several levels of phenotypic variance in offspring and parent pied flycatchers

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Abstract

Parental provisioning of offspring should reflect selection on life history aspects of parenting and on foraging behavior. Life history and foraging theory generally make predictions about mean behavior, but some circumstances might favor changes in the variance of parent and offspring behaviors. We analyzed data on free-living pied flycatchers (*Ficedula hypoleuca*) experiencing a brood size manipulation. We used double hierarchical generalized linear models to investigate patterns in means and variances of provisioning, brood begging, and parental mass. As predicted by life history theory, parents with enlarged broods of intensely begging nestlings fed at higher rates and delivered more food per unit of time. They also delivered food at a more consistent rate. This contradicts the prediction from variance-sensitive foraging theory that parents facing higher brood demand should choose more variable foraging options. Indirect evidence suggests that reduced variance in trip time arose from shifts in parental time budgets. Exploratory analyses revealed patterns in residual variance of both nestling begging and parental mass changes, with enlarged broods begging less consistently and female body mass changes being more variable after longer foraging trips. We show that parent pied flycatchers simultaneously adjust means and variances in multiple aspects of their provisioning effort to changes in brood demand and that these responses might be linked with nestling begging and changes in parental body mass. Our study highlights both the importance of adopting sophisticated statistical approaches and the potential intersection of two bodies of theory that may affect strategic adjustments of individuals engaged in central place provisioning.

Communicated by B. Voelkl

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Significance statement

Central place foragers, such as many parent birds provisioning offspring, are subject to selective forces from both life history and foraging ecology. Most effects of selection are expected on mean behaviors, but adaptive life histories or foraging decisions can also influence variances. We analyzed both means and variances in parent pied flycatchers experiencing either increases or decreases in brood size. Parents with enhanced broods had shorter foraging trips and offspring that begged more, matching predictions from life history theory. They also exhibited less variation in trip time, contrary to predictions from variance sensitive foraging theory. However, patterns in the residual variance in offspring begging and parental mass are less easily explained and raise new questions. Statistical models of means and variances illuminate the intersection between two bodies of theory and reveal new processes affecting provisioning behavior.

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Introduction

Systems in which parents forage to find food for dependent offspring provide a model for understanding the intersection between two usually separate bodies of theory. Firstly, parental care behavior fits well into life history theory (Stearns 1977; Roff 2002), which postulates that current reproductive effort (e.g., parental provisioning effort) will (1) increase with factors that increase the benefits of producing current offspring and (2) decrease with the potential negative impact of this reproductive effort on the parent's residual reproductive value (Trivers 1972; Winkler 1987; Clutton-Brock 1991; Martins and Wright 1993; Royle et al. 2012). Secondly, provisioning, as occurs in many birds, also requires parents to forage for food and deliver it to offspring in a nest or "central place". Such behavior therefore also falls under the purview of optimal foraging theory as applied to such central place foraging (e.g., Orians and Pearson 1979; Kacelnik 1984; Houston 1985; Houston and McNamara 1985; Stephens et al. 2007). The costs to parents of travel to suitable patches, capturing, loading, and then delivering that food to their offspring from different locations and distances from the nest should also influence elements of parent foraging behavior. Therefore, the density and distribution of different prey types in time and space, the nutritional demands of the brood and the parent themselves, and the behavior of any partners provisioning at the same nest will combine to shape the central place foraging strategies of parents (Wright et al. 1998). The behavior exhibited by provisioning parents is thus expected to reflect factors affecting either the life history elements of parenting, the foraging elements, or both (e.g., Martins and Wright 1993; Wright et al. 1998).

These two bodies of theory usually explain variation in mean provisioning effort through deterministic effects. For example, life history theory predicts that higher visit rates (i.e., shorter inter-visit intervals, or IVIs) should be associated with larger brood sizes (Royama 1966; Nur 1984; Wright and Cuthill 1990a, b). This arises because having more offspring increases the benefits of provisioning, and so parents are predicted to shift time or energy away from other activities, or take more risks, in favor of increasing food delivery rates to the nest (Winkler 1987). Similarly, offspring that are hungry typically signal with greater than average begging behavior, and usually, parents respond quickly by increasing the mean delivery of food (Kilner and Johnstone 1997; Budden and Wright 2001; Wright and Leonard 2002; Smiseth et al. 2008), possibly via shorter inter-visit intervals or larger loads, or both (Wright and Cuthill 1990a, b; Wright 1998; Wright et al. 1998). Some evidence also suggests that offspring begging behavior, perhaps combined with other

cues, can affect parent decision-making also on medium (Wright et al. 2010) or longer term (Price et al. 1996; Wright et al. 2002) time scales.

This array of deterministic factors generates variation in average provisioning behaviors, potentially both among individuals within populations and within individuals depending on the timing of changes in the underlying factors (e.g., Westneat et al. 2011). However, the expression of parental behavior in any one event often deviates from these average values in the form of residual variance driven by non-deterministic processes. For example, both the inter-visit interval and the amount of food carried back to be fed to offspring (the load size) vary from trip to trip in part due to the unpredictable nature of encounters with different types of prey (e.g., Frey-Roos et al. 1995; Weimerskirch et al. 2005). Such unpredictable variance could produce complex patterns in provisioning behavior within and among individuals (e.g., Westneat et al. 2013).

Both life history theory and optimal foraging theory have been relatively silent about the variance associated with these distributions and under what conditions we might expect it to vary within and among individuals (but see Ydenberg 1994, 2007). Some extensions of life history theory suggest that there may be environmental conditions that lead to a change in the variance in the phenotype *per se* (e.g., Real and Ellner 1992). However, when applied to parental care, it is not clear how unpredictable variance in nestling signals of demand or the costs of provisioning might influence mean behavior, what factors would affect residual variance in parental care, or how residual variance in parental care *per se* might influence current reproduction or residual reproductive value.

Foraging theory, while also usually focused on deterministic effects on behavior, has proffered some predictions about how individuals might manage unpredictable variance. For example, suppose foragers experience a shift from an accelerating fitness gain curve when in a negative energy budget to a decelerating gain curve when in a positive energy budget. The variance-sensitive foraging hypothesis (so-called risk sensitivity; Caraco 1980; Stephens 1981; Stephens and Charnov 1982) proposes that such foragers should correspondingly shift their behavior from favoring highly variable prey distributions (being variance-prone) to less variable prey distributions (being variance averse). Ydenberg (1994) extended this idea to parents caring for broods in poor or good condition and predicted that if offspring are in a decelerating part of their utility function, then parents should favor lower variance options. Tests of this idea have been rare. Moore (2002; see also in Ydenberg (2007)) experimentally manipulated brood size in common terns (*Sterna hirundo*) and found that subjects with enlarged broods, which presumably placed sufficient new demands on the parents that they were in the accelerating part of an

offspring fitness curve, switched from foraging in a patch with moderate variance in prey to one with high variance in prey. Mathot et al. (2017) assessed the impact of brood manipulations in great tits (*Parus major*) and found contrasting results in 2 years. In a good year when most offspring survived, parents experiencing greater brood demand reduced the variance in provisioning behavior. One explanation offered was that the increased demand caused a shift towards time spent on parental provisioning and away from less important non-parental behaviors in ways that coincidentally reduced variance in provisioning. In a poor year, however, when nestling mortality was higher and growth rates lower, the increased demand increased the variance in IVI, suggesting that parents were being adaptively variance prone in seeking out more variable foraging options. Two studies from red-winged blackbirds (*Agelaius phoeniceus*) have also suggested that variance in the delivery of food changes in ways that are consistent with the variance-sensitivity hypothesis (Whittingham and Robertson 1993; as reanalyzed by Moore 2002; Ydenberg 2007; Westneat et al. 2013). Although suggestive of a role for variance sensitivity in parental provisioning strategies, it is unclear how general these results are, and whether additional details about variances in parent and offspring behaviors could provide alternative explanations.

Here, we report on patterns of variance in provisioning behavior in a woodland-dwelling insectivorous bird, the pied flycatcher (*Ficedula hypoleuca*), with the goal of understanding how changes in benefits of current reproduction may drive variance in phenotypes associated with parenting. Our focal hypothesis was that parents with increased brood demand should seek more variable foraging options, and so the delivery of food (load per unit of time) to the nest would be more variable across trips. In secondary analyses, we also investigated patterns of variance in nestling begging and change in parental body mass with the idea that these are linked phenotypes and may provide a richer understanding of both deterministic and unpredictable variance in provisioning behaviors. We studied the pied flycatcher, because it is a small (12–14 g) migratory passerine common across Europe and western Asia (Lundberg and Alatalo 1992) that typically nests in cavities and generally exhibits considerable provisioning of nestlings. Males are territorial, most pairs are socially monogamous, and both parents typically help with the provisioning of of 5–7 nestlings, which are fed entirely on invertebrate prey. Previous studies have shown that both parents respond to brood size manipulations by increasing visit rates to the nest (Moreno et al. 1995; Sanz 1997; Wright et al. 2002). Experimental manipulations of nestling begging also suggest that parents are sensitive to the magnitude of begging vocalizations (Ottosson et al. 1997).

Methods

Study species and site

Data on provisioning behavior were collected in 1998 and 1999 on a population of pied flycatchers located in Abergwyngregyn National Nature Reserve, North Wales, UK (53° 13′ 16″ N 3° 59′ 59″ W). This reserve is a 169-ha area of mixed deciduous and plantation coniferous woodland in a steep-sided valley with acidic soils. Pied flycatchers arrive at Abergwyngregyn in mid-to-late April from West Africa, the first eggs of their single reproductive attempt are laid at the end of April, and the first nestlings hatch by late May. As in other studies (Lundberg and Alatalo 1992), levels of polygamy at Abergwyngregyn are estimated to be around 10%.

Experimental procedure

In each year, 100 nest boxes were available. Pairs that nested in these boxes were randomly assigned to the 2 brood size treatment groups within hatch dates, with 21 nests being used in 1998 and 16 nests in 1999. At 2–3 days of age, nestlings were moved between nests in order to create 18 experimentally "small" broods (mean = 3.9 nestlings, range 3–4 nestlings) and 19 experimentally "large" broods (mean = 8.2 nestlings, range 8–9 nestlings), each being roughly 2 nestlings either side of the mean brood size and within the natural range for this population (mean = 6.6, SE ± 0.2, range 1–9). Seven broods (5 in 1998 and 2 in 1999) were attended by a single parents and so were excluded from analysis.

The manipulations were carried out using normal broods from first nesting attempts hatching between 20th May and 7th June. Hatch dates did not differ significantly between years ($F_{1, 26} = 2.7$, $P = 0.12$) or between manipulated brood sizes ($F_{1, 26} = 0.11$, $P = 0.74$), with no significant interaction ($F_{1,26} = 2.4$, $P = 0.14$). Natural broods tended to be larger in 1999 than in 1998 ($F_{1,26} = 3.23$, $P = 0.08$), but there was no bias by year and brood size treatment on natural brood size ($F_{1,26} = 0.41$, $P = 0.51$). Nestlings added to enlarged broods were within 1 day of age and 30% of the body weight of their broodmates. Natural brood sizes did not differ between the two brood size treatments ($F_{1,26} = 0.31$, $P = 0.57$). Thus, natural variation in the timing and quality of pairs or nestlings was unlikely to have influenced comparisons between the 2 brood size groups.

One brood in 1999 was partially preyed upon during the 24-h video recording period, and for 2 nests, there were problems with extracting valid time scores of visits from the video. We omitted these 3 cases to end up with a final sample size of 14 biparental nests in 1998 (6 reduced, 8 increased) and 13 (6 reduced, 7 increased) in 1999.

Data collection

Data on experimental pairs were obtained using video cameras (Sony Hi8 CCD-TRIIOOE) mounted in specifically designed nest boxes. These larger video nest boxes replaced the smaller normal nest boxes approximately 24 h before filming to allow parents to become accustomed to them. Each video nest box contained an electronic balance (either Mettler SM3000 or PB3001, powered by a 12-V car battery, and accurate to 0.1 g) positioned under the nest. The camera was set up to video the nest at a 45° angle, also capturing the inside of the entrance hole and the balance display. Calculation of nest mass before, during, and after visits thereby allowed measurement of parental mass, as well as load mass delivered (for those parental visits when fecal sacs were not also removed by parents). Additional variables measured included the timing of arrivals and departures of individual parents, from which we computed inter-visit intervals (IVI, the time between visits of a focal parent) and time spent in the nest, as well as any fecal sac removal. The latter affected which visits could be scored for load size, since if a parent removed a fecal sac, the visit included both a weight gain (food brought) and weight lost (fecal sac removed) and so could not be used to estimate load. In 1999, brood demand per visit was also assessed via the visual assessment of each individual nestling's begging height in the nest (where 0 = no begging, 0.5 = gaping with head up, and 1 = gaping with neck extended and body raised). Scoring could not be made blindly with respect to the experimental conditions, because brood size was evident in the videos.

For each nest, 6 video recordings were made lasting approximately 1.5 h each. In pied flycatchers, the brief disturbance caused by human activity near the nest has no discernable effect on subsequent provisioning behavior (Tilgar et al. 2011) and we detected little impact beyond the first two visits. Recordings started in the early afternoon of day one and finished at the same time on day two (approximate times: 15:00–16:30, 17:30–19:00, 20:00–21:30, 05:00–06:30, 08:00–09:30, and 11:00–12:30 h). The mean age of nestlings during the period of taping was 9.1 days (range 7–12), and did not differ significantly between experimental brood sizes or year (brood size $F_{1,23} = 0.01$, $P = 0.93$; year $F_{1,23} = 0.19$, $P = 0.67$, interaction $F_{1,23} = 0.48$, $P = 0.50$).

Statistical analyses

The core dataset we analyzed included information on parents of both sexes from 27 nest boxes, but sample sizes were reduced slightly in some tests because data from specific parents were not available. Data on begging was collected only in the 1999 season, so sample sizes regarding brood demand were reduced to 13 nests.

The dataset is composed of a hierarchically arranged set of repeated measures with the main dependent variables measured on each visit by 1 of 2 subjects (the parents) attending 1 of 27 nest boxes across 2 years. Some independent variables varied among boxes (e.g., brood size treatment, nestling age, and date), but most varied among visits (e.g., begging levels, behavior of nestlings or parents on previous visits). Because we were interested in deterministic (mean) effects and patterns in residual variation, we used a statistical approach called "double GLM" (Smyth 1989; Lee and Nelder 2006; Rönnegård et al. 2010). These models extend the class of generalized linear models by allowing the predictor variables to affect both the mean and the variance of the response variable. The models we have fit may be more appropriately called double linear mixed effects models, because we modeled random and fixed effects at both the mean and the residual variance level. In all cases, we assumed that the errors were independently distributed normal random variables. The random effects were individual and box.

Mathematically, let Y_{ijk} denote the value of one of the dependent variables (either load, IVI, begging intensity, or change in parental mass) measured on the kth visit by adult j to box i. Our models followed the general structure:

$$Y_{ijk} = \beta_0 + \sum_{h=1}^{n} \beta_h x_{\text{hijk}} + \epsilon_i + \epsilon_{ij} + \epsilon_{ijk}$$

In this equation, x_{hijk} represents the value of the hth fixed effect and β_h the corresponding regression coefficient. The terms ϵ_i and ϵ_{ij} represent the random effects for box i and individual j within box i, respectively, and ϵ_{ijk} is the residual deviation. These 3 terms were assumed to be independent and normally distributed random variables with mean 0 and standard deviations $\sigma_\epsilon^{\text{box}}$, $\sigma_\epsilon^{\text{ind}}$, and $\sigma_{\epsilon,i,j,k}^{\text{res}}$, respectively. Further to this, our models allowed the standard deviation of residuals to vary between observations such that

$$\log(\sigma_{ijk}) = \varphi_0 + \sum_{h=1}^{n} \varphi_h x_{\text{hijk}} + \xi_i + \xi_{ij}$$

The term φ_0 denotes the population mean log standard deviation, and φ_h is the change in log standard deviation with the hth covariate. Quantities ξ_i and ξ_{ij} represent random effects that influence the variance instead of the mean. Again, we assumed that these variables are independent and normally distributed with mean 0 and standard deviations σ_ξ^{box} and σ_ξ^{ind}. Similar models were used to study the provisioning behavior of red-winged blackbirds according to Westneat et al. (2013).

We fit these models in the Bayesian statistical framework. Specifically, we used Markov chain Monte Carlo (MCMC) methods implemented in the "Just Another Gibbs Sampler" (JAGS) software package (Plummer 2003) to obtain samples

from the joint posterior distribution of all parameters and compute posterior summary statistics. Prior distributions were chosen to be non-informative. We assigned the regression parameters for the model of the mean, β_h, and variance, φ_h, non-informative normal priors with mean 0 and variance 100^2. We assigned the variance parameters for both the mean model, $\sigma_\epsilon^{\text{box}2}$, $\sigma_\epsilon^{\text{ind}}$, and $\sigma_{\epsilon ijk}^{\text{res}}$, and variance model, $\sigma_\epsilon^{\text{box}}$, $\sigma_\epsilon^{\text{ind}}$, and $\sigma_{\epsilon ijk}^{\text{res}}$, half t prior distributions with 5 df and scale factor 5. This represents a truncated and scaled version of the t distribution which is restricted to the positive values and has a median value of 1.68, 75th percentile of 6.70, and 95th percentile of 12.82. We ran 3 chains in parallel and assessed convergence via the Brooks-Gelman-Rubin potential scale reduction factor (Brooks 1998). The procedure consisted of a wrapper program in R 3.2.4 (R Development Core Team 2016) that set up the model structure and priors, and then interfaced with code in the JAGS environment to conduct the MCMC simulations. The 3 Markov chains were run for a burn-in period of 10,000 iterations plus 100,000 iterations with no thinning for computing parameter estimates. Significance of the effects in the models was assessed by examining the range of the 95% credible intervals for the regression coefficients and whether or not these included 0.

To address our primary hypothesis, we modeled two parental variables, IVI and load mass. Both were log transformed because of highly skewed distributions (Fig. S1), which resulted in residuals that did not deviate from a Gaussian distribution, as determined from visual inspection of Q-Q plots of standardized residuals. One complicating factor in the analysis of load mass was that the balances only provided accurate measurements to the nearest 0.1 g. This rounding error was accounted for by treating these measurements as interval censored observations known to be within an interval extending 0.05 g above and below the recorded value.

Besides the random effects of box identity and individual subject identity, all models included the fixed effect of the brood size manipulation. We also typically included the fixed effects of date and nestling age, which were mean centered among nests, and parental sex and year. Nestling begging intensity was mean centered within the individual parent and treated as a fixed effect in a subset of models. For models of load size and parental mass changes, we also mean centered IVI within the individual parent. We initially fitted the two-way interactions between sex and year ($N = 6$) with all other fixed effects included in the respective model to investigate sex and year differences. We simplified the initial models by removing all minimally influential interactions and present results from final models only.

We also point out two important aspects in the interpretation of these models. The first is that although we have considered load mass as the response variable, the estimated effects from these models can be interpreted as effects on delivery when log(IVI) is included as a predictor, which was found to be necessary (see Results). The model of load takes the form

$$\log\left(\text{load}_{ijk}\right) = \beta_0 + \beta_1 \log\left(\text{IVI}_{ijk}\right) + \beta_2 x_{2,ijk} + \ldots + \beta_p x_{p,ijk}$$
$$+ \epsilon_{ijk}$$

where the terms $\beta_2 x_{2,ijk}$ to $\beta_p x_{p,ijk}$ represent the effects of other predictors in the model. This is equivalent to

$$\log\left(\text{delivery}_{ijk}\right) = \log\left(\frac{\text{load}_{ijk}}{\text{IVI}_{ijk}}\right)$$
$$= \beta_0 + (\beta_1 - 1)\log\left(\text{IVI}_{ijk}\right) + \beta_2 x_{2,ijk} + \ldots + \beta_p x_{p,ijk}$$
$$+ \epsilon_{ijk}.$$

It follows that a change in any of x_2 through x_p while the other predictors are held constant has the same effect on the mean of both the log(load) and log(delivery), including the effect of the brood size manipulation. The effect of log(IVI) itself differs by 1 depending on whether the response is log(load) or log(delivery). This change is simply a function of the difference between modeling the provisioning per trip (i.e., load) versus the rate of provisioning per trip (i.e., delivery). Hence, we will refer to all effects in the model of log(load) except for the effect of log(IVI) as effects on delivery. Similarly, in the equation, for the variance of the residual errors as a function of covariates, e.g.,

$$\log\left(\sigma_{ijk}^2\right) = \phi_0 + \phi_1 x_{1,ijk} + \ldots + \phi_p x_{p,ijk}$$

the coefficients ϕ_1 through ϕ_p can be interpreted as effects on either the variance of log(load) or the variance of log(delivery) while the remaining predictors remain fixed.

The second interpretation of note is that if the response is modeled on the log scale, as we have done with both load and IVI, then the variance on the natural scale will depend on the coefficient from both the mean and the variance portions of the model. Suppose, for example, that we have a single predictor x used to model both the mean and the variance of log(y) such that $\log(y_i) = \beta_0 + \beta_1 x_i + \epsilon_i$ and $\log\left(\sigma_i^2\right) = \phi_0 + \phi_1 x_1$. We can interpret ϕ_1 to mean that the variance of log(y) increases by ϕ_1 when x_1 increases by one unit. However, the variance of y on the natural scale is

$$Var(y) = \left(e^{\phi_0 + \phi_1 x} - 1\right) e^{(\phi_0 + 2\beta_0) + (\phi_1 + 2\beta_1)x}.$$

The implication is that the effect of x on $Var(y)$ cannot be determined by looking at ϕ_1 alone. We can conclude immediately that $Var(y)$ will increase as x increases if both ϕ_1 and β_1 are positive and decrease as x increases if both are negative. As it turns out, this was the case in all of our main results.

In our secondary analyses, we modeled nestling begging intensity and parental mass changes. The models of begging

included log-transformed inter-feed interval (IFI; defined as time between successive feedings of the brood by either parent; mean centered within nest identity), brood size manipulation, and nestling age as fixed effects and nest identity as a random effect. Because begging was assessed as an average intensity over all nestlings in a brood, we added a weighting variable to the analysis to control for the necessary relationship of variance in mean values with changes in brood size. To analyze changes in parental body mass, we initially fitted models including the fixed effects of brood size manipulation, individual mean-centered log(IVI), parental sex, year, nestling age and date, and the respective two-way interactions between sex and year with log(IVI) and brood size manipulation treatment.

Results

Effects on mean parental behavior

We assessed the impact of the brood manipulation and any covariates on both the mean and the variance in the two main parental response variables, log(IVI), and log(load mass) per trip. We first investigated the relationships between the two response variables. Mean load mass increased with log(IVI), with this effect being stronger in 1999 (1998: $\beta = 0.06$, 95% CI: 0.02, 0.10; 1999: $\beta = 0.14$, 95% CI: 0.11, 0.18; difference between 1998 and 1999: $\beta = 0.08$, 95% CI: 0.03, 0.13). Residual variation in load mass also increased with log(IVI) ($\varphi = 0.04$, 95% CI: 0.01, 0.07). In addition, we found that load masses were generally smaller in 1999 compared to 1998 (difference between 1999 and 1998: $\beta = -0.45$, 95% CI: -0.73, -0.17). For these reasons, we included log(IVI) in all models of log(load mass), and we interpret all other effects in these models as effects on delivery.

As expected from life history theory and many previous studies on both pied flycatchers and other birds, parents feeding enlarged broods tended to have shorter IVIs and higher delivery, on average, compared to those feeding reduced broods in both sexes (Table 1a, Fig. 1a, Table S1). At the same time, males provisioning reduced broods had longer IVIs, on average, compared to females, but increasing the brood size produced a much larger difference in males than in females (Table 1a, Fig. 1a, Table S1). Even though the analysis is based on different individuals, because treatments were assigned without regard to baseline provisioning behavior, this implies that male responses to changes in brood size were more plastic.

We included in our analyses of log(IVI) and log(load mass) the covariates of nestling age, date in season and year. We found some evidence for an effect of nestling age on parental log(IVI) that differed across sexes. Nestling age negatively affected male, but not female IVI, with males with older

Table 1 Sources of variation in two different aspects of parental provisioning behavior in 1998 and 1999: inter-visit intervals (IVI) and load mass in two brood size manipulation groups

(a)	log(IVI)	log(load mass)
Means	β (95% CI)	β (95% CI)
Intercept[a]	2.05 (1.98, 2.12)	−2.53 (−2.67, −2.39)
BSM (E-R)	−0.07 (−0.15, 0.01)	0.11 (−0.03, 0.26)
log(IVI)	–	*0.24 (0.18, 0.30)*
Nestling age	0.03 (−0.02, 0.08)	0.04 (−0.04, 0.13)
Date	*−0.04 (−0.06, −0.01)*	*−0.08 (−0.12, −0.04)*
Sex(male-female)	*0.09 (0.01, 0.18)*	−0.09 (−0.21, 0.04)
Year(1999–1998)	−0.05 (−0.11, 0.01)	−0.11 (−0.26, 0.04)
Sex × date	*0.04 (0.01, 0.07)*	0.03 (−0.01, 0.07)
Sex × nestling age	−0.07 (−0.13, 0.00)	–
Sex × BSM	*−0.14 (−0.25, −0.03)*	–
	σ^2 (95% CI)	σ^2 (95% CI)
Individual	*0.10 (0.07, 0.12)*	*0.20 (0.14, 0.26)*
Box	0.03 (0.00, 0.07)	0.08 (0.00, 0.17)
(b)		
Residual variances	φ (95% CI)	φ (95% CI)
Intercept[a]	−0.97 (−1.04, −0.90)	−0.45 (−0.56, −0.34)
BSM(E-R)	*−0.08 (−0.15, −0.01)*	0.02 (−0.10, 0.14)
log(IVI)	–	*0.11 (0.03, 0.18)*
Nestling age	−0.01 (−0.05, 0.04)	−0.04 (−0.11, 0.04)
Date	0.02 (0.00, 0.04)	0.03 (0.00, 0.06)
Sex (male-female)	−0.03 (−0.03, 0.09)	0.06 (0.00, 0.12)
Year (1999–1998)	0.05 (−0.02, 0.13)	0.07 (−0.05, 0.20)
	σ^2 (95% CI)	σ^2 (95% CI)
Individual	*0.10 (0.07, 0.13)*	0.03 (0.00, 0.08)
Box	0.04 (0.00, 0.09)	*0.13 (0.06, 0.20)*
N observations	8740	4693

Because log(IVI) is included in the log(load mass) analysis, all other effects are interpreted as effects on delivery (food per unit of time). Estimates were derived from a Bayesian double GLM with random intercepts for nest identity ($N = 27$) and individual ($N = 54$). BSM (brood size manipulation, factor with two levels: reduced (R), enlarged (E)), mean-centered brood age (days), date (mean-centered), year (factor with two levels: 1998, 1999), and log-transformed IVI (centered within individuals) were fitted as fixed effects. Point estimates are given with their 95% credible intervals (CI). Effects that were strongly supported by the model (95% CI not overlapping zero) are indicated in italic. Effects on (a) means and (b) on the residual variance

[a] Reference category is BSM "reduced," sex '"female," and year "1998"

broods tending to make shorter trips ($\beta = -0.04$, 95% CI: -0.10, 0.01; Table 1a, Table S1) and therefore likely provisioning at higher rates. In contrast, there was no evidence for an effect of nestling age on male or female delivery (Table 1a). In females, date negatively affected IVI, with females recorded later in the season taking less time per trip, but delivering less food per unit of time (Table 1a). In males, there was no effect of date on IVI ($\beta = 0.00$, 95% CI: -0.02, 0.03; Table S1), but males of later broods also delivered less food
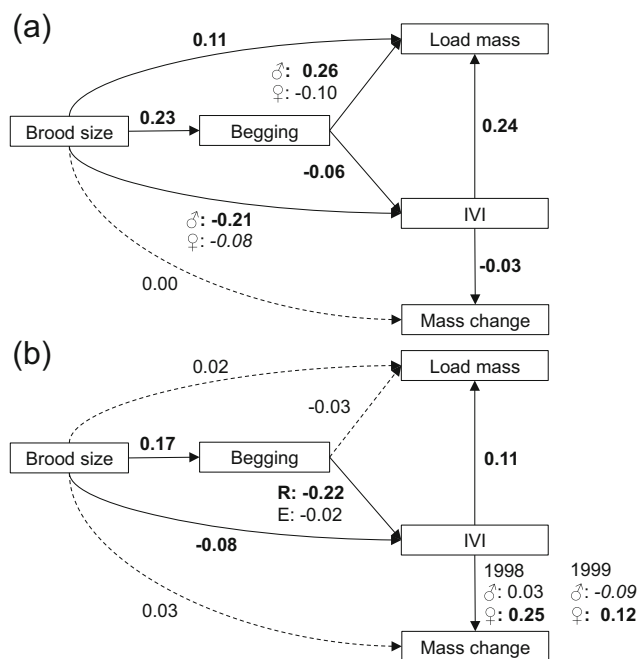
Fig. 1 Summary of results from separate analyses of the impact of experimentally enlarged brood size on two aspects of parental provisioning behavior (IVI and load mass), average nestling begging at the previous visit (begging), and changes in parental body mass (mass change) across two consecutive visits on (**a**) means and (**b**) residual variances in pied flycatchers. *Arrow direction* indicates independent to dependent variable; *arrows with bold numbers* indicate strong support (credible intervals not overlapping zero), *arrows with italic numbers* indicate some support (credible intervals slightly overlapping zero), and *dashed black lines* indicate little support for a non-zero relationship. Sex, brood size (reduced vs enlarged), and year differences are indicated when they existed

($\beta = -0.05$, 95% CI: -0.09, -0.01, Table S1). Yet, this decrease in food delivery later in the season was less pronounced compared to females (Table 1a, Table S1).

We assessed the potential impact of nestling begging intensity and its interaction with the brood manipulation using the data from 1999, the only year when begging intensity was also measured. In both sexes, we found support for a negative effect of the average begging parents experienced during their previous (t-1) visit to the nest on IVI (summarized in Table 2, full model results in Table S2; Fig. 1a). Begging levels at visit t-2 also negatively affected IVI, and the effect of t-1 was reduced slightly and the credible interval reached 0 (Table 2, Table S3). Begging at t-3 did not predict IVI nor did it alter the effects of begging at t-1 and t-2 compared to the model when t-3 was not included (Table 2, Table S3). The effect of begging during the previous visit did not differ between brood size manipulation groups (interaction BSM × begging t-1: $\beta = 0.04$, 95% CI: -0.06, 0.13); all parents decreased their IVIs at the same rate with increasing nestling begging intensity. In females, there was no evidence for an effect of nestling begging on delivery, whereas there was a positive effect of begging at visit t-1 on delivery in males ($\beta = 0.26$, 95% CI:

0.08, 0.45) (Table 2; Table S2; Fig. 1a). This resulted in males, but not females, having higher delivery in response to increases in nestling begging at t-1. There was no additional effect of begging at visit t-2 on delivery (Table 2, Table S3).

Patterns in residual variance in parental behavior

Our main goal in analyzing this dataset was to assess predictions from variance sensitivity theory as applied to parental behavior. If increased offspring demand due to the manipulation of brood size indicates to parents that the average delivery of food is not sufficient for their needs, then the theory predicts they should shift to a more variable patch and this would affect the realized variance in delivery. Contrary to these predictions, we found no evidence that variance in delivery was influenced by the brood size manipulation (Table 1b, Fig. 1b) and strong evidence for lower residual variance in parental IVIs in enlarged compared to reduced broods (Table 1b, Figs. 1b and 2). Older nestlings might demand more than younger nestlings, but we found no support for residual variance in IVI or delivery differing for parents feeding older compared to younger nestlings (Table 1b). There was some evidence for residual variance in delivery being higher in males compared to females, but residual variance in IVI did not differ between the sexes (Table 1b).

The main cue parents are expected to use to assess the condition of their nestlings is the intensity of their begging. We assessed the potential impact of nestling begging intensity and its interaction with the brood manipulation using the data from 1999, the year when begging intensity was measured. Contrary to predictions, residual variance (measured as log standard deviations) in IVIs decreased with increased begging in reduced ($\varphi = -0.22$, 95% CI: -0.35, -0.08), but not in enlarged broods ($\varphi = -0.02$, 95% CI: -0.13, 0.10; difference: $\varphi = -0.20$, 95% CI: -0.38, -0.02; Table S2, Figs. 1b and 3). We did not detect any effects of begging on residual variance in delivery ($\varphi = -0.03$, 95% CI: -0.18, 0.13; Table S2; Fig. 1b).

Effects on nestling begging

Mean effects on nestling begging

We also explored the factors that affected nestling begging behavior. Mean nestling begging intensity during different parental visits to the same brood was strongly affected by the time between feedings (by either parent), called the "inter-feed interval" or IFI. Mean begging became more intense when the IFI was longer (Table 3a). There were no additional effects of the IFIs of even earlier visits over and above the strong effects of the most recent IFI (e.g., t-1: $\beta = 0.01$, 95% CI: -0.01, 0.03).

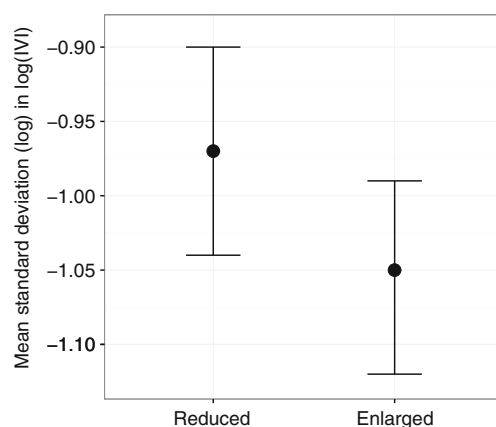**Table 2** Effects of begging in previous visits on parental IVI and load mass

	Beg(t-1) β (95% CI)	Beg(t-2) β (95% CI)	Beg(t-3) β (95% CI)
IVI			
Model 1	*−0.06 (−0.10, −0.01)*	–	–
Model 2	−0.04 (−0.09, 0.00)	*−0.07 (−0.12, −0.03)*	–
Model 3	−0.05 (−0.10, 0.00)	*−0.08 (−0.13, −0.03)*	−0.01 (−0.06, 0.04)
Load mass			
Model 1			
Female	−0.10 (−0.27, 0.06)	–	–
Male	*0.26 (0.08, 0.45)*	–	–
Model 2			
Female	−0.10 (−0.28, 0.09)	−0.03 (−0.21, 0.16)	–
Male	*0.26 (0.08, 0.45)*	−0.01 (−0.20, 0.18)	–

Estimates were derived from double GLMs including the same fixed and random effects as described for Table 1 with model 1 additionally including begging at t-1, model 2 including begging at t-1 and t-2, and model 3 begging at t-1, t-2, and t-3. The effects of begging on load differed across sexes and are therefore given separately for male and females. Effects that were strongly supported by the model (95% CI not overlapping zero) are indicated in italic. For complete results, see Tables S1 and S2

The experimental brood size manipulation had a strong and independent effect on mean begging intensity, with the average nestling in enlarged broods begging at higher levels than the average nestling in reduced broods (Table 3a). We also found that older nestlings begged more intensely than younger ones (Table 3a).

Patterns in residual variance in begging

We also modeled the residual variance in mean begging intensity (i.e., within broods over repeated trips), and we used brood size as a weighting variable to control for effects of sample sizes on variance in averages. We found that mean begging intensity decreased with increasing parental IFIs

(Table 3b). Parental IFIs of previous visits did not affect residual variances in average nestling begging over and above effects of IFIs of the present visit (e.g., t-1: $\varphi = -0.03$, 95% CI: −0.08, 0.02). Residual variances in average begging intensity were higher in experimentally enlarged compared to reduced broods (Table 3b).

Parental body mass changes

Mean effects on parental body mass

Life history theory predicts mean effects on parental condition of increased work associated with provisioning. We analyzed the absolute mass as a repeatedly measured trait on those visits when it could be measured, but the models failed to converge. Instead, we analyzed two other mass-related variables. First, we explored possible influences on mean mass of the parent
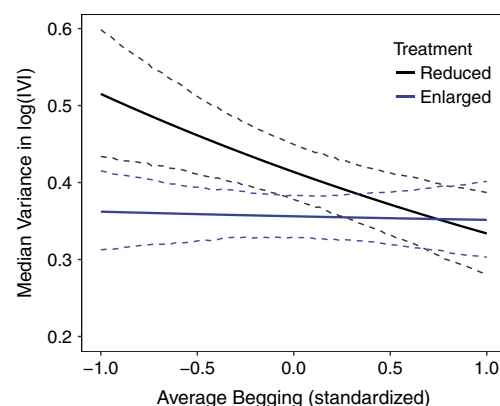

Fig. 2 Residual variances of log-transformed IVI, measured in log standard deviations, for reduced and enlarged broods across both seasons of the study. Estimates were retrieved from the double hierarchical generalized linear model described under Table 1. *Dots* show mean values, and *whiskers* indicate 95% CI on the estimate of the parameter

Fig. 3 Effects of average begging intensity on residual variances in log-transformed IVI for reduced and enlarged broods. *Thick lines* indicate the posterior means; *thin dashed lines* indicate the 95% credible intervals

Table 3 Sources of variation in average nestling begging intensity in two brood size manipulation groups

(a)

Means	β (95% CI)
Intercept[a]	0.35 (0.29, 0.41)
BSM(E-R)	*0.23 (0.21, 0.25)*
Nestling age	*0.24 (0.22, 0.26)*
log(IFI)	*0.15 (0.13, 0.17)*
	σ^2 (95% CI)
Box	0.71 (0.00, 3.35)

(b)

Residual variances	φ (95% CI)
Intercept[a]	*−0.55 (−0.71, −0.38)*
BSM(E-R)	*0.17 (0.11, 0.23)*
Nestling age	*−0.07 (−0.12, −0.01)*
log(IFI)	*−0.12 (−0.17, −0.07)*
	σ^2 (95% CI)
Box	0.57 (0.00, 3.13)
N observations	4289

Estimates were derived from a Bayesian double GLM with random intercepts for nest identity ($N = 13$). BSM (brood size manipulation factor with two levels: reduced, enlarged), mean-centered brood age (days), and log-transformed inter-feed interval (IFI, mean centered within nest) were fitted as fixed effects. Point estimates are given with their 95% credible intervals (CI). Effects that were strongly supported by the model (95% CI not overlapping zero) are indicated in italic. Effects on (a) means and (b) on the residual variance

[a] Reference category is BSM "reduced"

Table 4 Sources of variation in mass changes between successive visits for parent pied flycatchers in two brood size manipulation groups

	Mean	Residual variance
Fixed effects	β (95% CI)	φ (95% CI)
Intercept[a]	0.00 (−0.01, 0.01)	*−1.99 (−2.25, −1.74)*
BSM(E-R)	0.00 (−0.01, 0.01)	0.02 (−0.24, 0.28)
log(IVI)[b]	*−0.03 (−0.04, −0.01)*	*0.25 (0.15, 0.35)*
Sex (male-female)	0.00 (−0.01, 0.01)	0.04 (−0.19, 0.27)
Year (1999–1998)	0.01 (0.00, 0.02)	*0.64 (0.38, 0.90)*
log(IVI) × year	–	*−0.12 (−0.23, −0.01)*
log(IVI) × sex	–	*−0.22 (−0.33, −0.11)*
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
Individual	0.00 (0.00, 0.01)	0.42 (0.32, 0.52)
Box	0.00 (0.00, 0.01)	0.12 (0.00, 0.28)

Estimates were derived from a Bayesian double GLM with random intercepts for individual ($N = 58$). Brood size manipulation (BSM factor with two levels: reduced, enlarged), year (factor with two levels), parental IVI (mean-centered within individual), and parental sex were fitted as fixed effects. Point estimates are given with their 95% credible intervals (CI). Effects strongly supported by the model (95% CI not overlapping zero) are indicated in italic

[a] Reference category is BSM "reduced," sex "female," and year "1998"

[b] Reference category for residual variance part is sex "female" and year "1998"

was present in both years, but stronger in 1998 compared to 1999 (difference between 1999 and 1998: $\varphi = 0.12$, 95% CI: 0.01, 0.23; Table 4). In contrast, there was no such effect of log(IVI) in males in either year (1998: $\varphi = 0.03$, 95% CI: −0.06, 0.12; 1999: $\varphi = −0.09$, 95% CI: −0.19, 0.01; Fig. 1b).

during the parental care observation. We found no support for the idea that parents feeding enlarged broods differed in body mass compared to parents feeding reduced broods ($\beta = −0.09$, 95% CI: −0.39, 0.19).

Next, we analyzed the mass change that occurred between the focal visit and the previous one by that individual. We found that parents of both sexes lost more mass after longer trips (Table 4, Fig. 1a). The brood manipulation and year (Table 4) had no apparent effect on changes in body mass between visits.

Patterns in residual variance in parental body mass

Neither life history theory nor foraging theory make any clear predictions about residual variance in parental body mass. We found no effect of the brood size manipulation treatment or of sex on the residual variance in mass change between visits (Table 4; Fig. 1b). In 1999, residual variance in mass change was higher compared to 1998 (Table 4). We also found effects of log(IVI) on residual variance in change in mass that differed across year and sex. Females coming back from longer feeding trips varied more in how much their body mass had changed from the previous visit compared to when they came back from shorter trips (Table 4, Fig. 1b). This effect of IVI

Discussion

The hierarchical statistical analysis of the means and the variances in parental provisioning, nestling begging, and parental body mass in male and female pied flycatchers revealed a complex set of both deterministic and possibly stochastic effects (Fig. 1). Some of these match predictions from theory and are consistent with previous results on this species and others. However, our central prediction arising from variance-sensitive foraging theory, that parents attending enlarged broods would show greater variance in delivery, via either trip time or load size, was not upheld. This result, and several others occurring at both the deterministic (mean) level and at the level of residual variance, raise some new questions about the intersection between life history theory and foraging theory as applied to parental provisioning.

Variance sensitivity theory (Caraco 1980; Stephens 1981) as applied to parental care (Ydenberg 1994, 2007) predicts that residual variance in provisioning should increase with a sufficient increase in nestling demand, which itself would be driven by the experimental manipulation of brood size. We

thus expected that when faced with increased demand, parent pied flycatchers might forage more in patches of habitat or microhabitat that had either more variable encounter rates with prey or more variable loads sizes due to differences in the prey types encountered. Such decisions should have produced a difference from parents of reduced broods in the residual variation in IVI and/or load size. Our analyses support the implicit assumption that the brood manipulation increased demand on parents. Offspring in enlarged broods begged more intensely (Fig. 1a). Differences in begging within nests and the manipulated brood size across nests led to a difference in parental mean inter-visit intervals, and increased begging within nests also resulted in an increase in delivery in males. Thus, both parents and offspring behaved as if the increase in brood size made provisioning nestlings more difficult.

Despite the fact that the brood manipulation had the expected effects on average behavior of parents and nestling, it did not produce the predicted effects on the residual variance in provisioning. Enlarged brood size had no effect on residual variance in delivery and led to reduced variance in IVI (Fig. 1b) compared to reduced brood size, which is opposite to the prediction. The higher mean begging due to the brood size manipulation also had its own, independent negative effect on residual variance in parental IVI (Fig. 1b). Given that parents were working harder to feed larger broods that begged more, this result raises several questions about the role of variance sensitivity on provisioning behavior. Two prior studies that manipulated brood size to change demand on parents produced evidence that parents shifted to more variable foraging options, as predicted. In common terns, Moore (2002; see also Ydenberg (2007)) found that parents attending enlarged broods shifted to seeking food in a patch with more variable prey types. Mathot et al. (2017) found that great tit parents attending enlarged broods provisioned more variably in 1 of 2 years. Our results from pied flycatchers thus seem to contradict the predictions of variance sensitivity in this regard.

Mathot et al. (2017) provides a *post hoc* explanation for our results. The year in their study when parents behaved as if they were variance sensitive was a particularly bad year with cooler temperatures, low levels of preferred prey, and relatively high offspring mortality even in the broods that had been reduced in size. In the other year, when higher brood demand led to reduced residual variance, the food supply was greater and most pairs successfully reared all young even in enlarged broods. Moore (2002) similarly found greater variance sensitivity in common terns in a poorer year. Our pied flycatcher subjects appeared to have experienced very good conditions in both years of the study. Although nestling survival to 12 days old for the whole population was lower in 1999 compared to 1998, it was high overall (1998 = 87 ± 4%; 1999 = 70 ± 7%)

and there was no effect of the brood size manipulation on nestling survival or fledging dates (all *P* values >0.3). Although nestling body mass at 12 days was significantly lower in enlarged broods ($F_{1,54} = 6.2$; $P = 0.017$), this was due to just the smallest nestlings being lighter in the enlarged broods. We conclude that parents in this system had more than enough food available to them and had no problems almost fully compensating for the experimental differences in brood size we imposed upon them. Thus, our subjects might not have been sufficiently displaced into the accelerating part of the fitness-delivery utility curve to produce adaptive variance-prone provisioning.

An inadequate manipulation cannot explain why parents of enlarged broods significantly reduced the variance in IVI. Two potential effects of the increased brood demand on mean parental behavior might have trickle-down effects on the residual variance (Mathot et al. 2017). First, parents of enlarged broods may have differed in how they allocated their time. Life history theory predicts that increased demand may indicate increased benefits of care (Drent and Daan 1980; Nur 1984), thereby favoring shifts of parental effort away from other activities and towards provisioning (e.g., Wright and Cuthill 1990b). If other activities, such as interacting with distant social neighbors or searching for new foraging patches, are not distributed equally on all trips, then spending less time on those activities would make for lower variance in trip time compared to parents of reduced broods. Such effects on mean behavior arising from life history selection, under the relatively benign conditions experienced by the subjects in this study, could therefore mask any subtle differences in patch or prey choice that would have fit predictions from foraging theory.

Another explanation is that parents attending enlarged broods may have had a different preference for high-quality prey items. Differences in prey preferences have been found in several other studies that manipulated demand on parents (e.g., Royama 1966; Tinbergen 1981; Wright and Cuthill 1990a, b; Wright et al. 1998). A relaxed prey preference could have had two effects on residual variance in provisioning behavior. First, it would reduce the variance in IVI, as we observed. When expressing a relaxed preference, parents end up averaging the time to first encounter across several prey distributions as opposed to a single, preferred prey's distribution. An average of encounter times on multiple unselected prey would show less variation than that from a single selected prey distribution. However, a relaxed preference should also increase load size variation in species that bring only one or very few prey items back per trip, as in pied flycatchers. We found that larger brood sizes had no apparent effect on the variance in delivery (Fig. 1b), and a breakdown of prey types for the two treatment groups revealed nearly identical distributions (Fig. S2). Our results are therefore most consistent with the hypothesis that the smaller variance in inter-visit intervals arose from spending less time on non-provisioning behaviors,

as opposed to any difference in prey preferences or variance aversion *per se*.

Several other results in both the mean and variance portion of our models demand additional explanation. First, the brood size manipulation affected IVI independently of offspring begging. The prevailing view of begging is that parents are sensitive to begging intensity, which honestly reflects offspring hunger (Wright and Leonard 2002; Royle et al. 2012). A brood manipulation would seemingly impact parental perception of offspring demand via begging intensity, which presumably goes up with the number of nestlings. An independent effect of brood size on provisioning implies other mechanisms of information gathering. For example, one possibility is that parents count the number of nestlings (*sensu* Lyon 2003; Hunt et al. 2008) and adjust provisioning in response to that cue independently of begging. Alternatively, parents may assess begging over a different time scale than we incorporated in our models. To illustrate, if parents assess begging levels over, for example, the previous day, this daily value could be better correlated with brood size than the visit-by-visit assessment of begging. There is, however, relatively little evidence that any longer term assessment of nestling demand is occurring (Wright and Leonard 2002). Other combinations of cue use by parents provide another possible explanation here (e.g., additional auditory begging cues to greater brood demand in larger broods, which was not included in our postural scoring of begging), any of which could explain why both our measure of begging and brood size independently affected provisioning behavior. Non-linear relationships between either brood size versus begging, or begging versus parental behavior, could also produce the separate effects of brood size and begging in our models.

We also found that enlarged broods had more residual variance in begging intensity per nestling than small broods. Most studies seem to indicate that begging reflects hunger (e.g., Leonard and Horn 2006). If so, one possibility is that residual variance in begging is affected by the opposing effects of greater hunger in larger broods but more frequent and less variable visits by parents. This could produce sequences of visits in which more of the nestlings had recently been fed and so were begging less compared to sequences in which all nestlings were hungrier and so begging was greater. In smaller broods, despite more variable trip times by individual parents, individual nestlings may have been fed more often and more regularly, leading to lower variance in begging intensity.

A final set of results from our study is the impact of several variables on the variance in parental mass changes. Some of these are possibly deterministic. For example, longer IVIs tended to produce larger between-visit mass losses (Table 4). Life history theory is founded on the assumption that parental care is costly (Williams 1966), and while parent condition is not the only potential cost of foraging for offspring, it is often assumed to be important (see Martins and Wright 1993). The negative relationship between IVI and mass change suggests that the longer the active search for nestling food, the greater the impact on parental condition. However, longer trips might be more likely to include time that parents spend foraging for themselves, which would increase condition. Finally, body mass is a balance between food ingested and waste excreted, and since excretion occurs sporadically, it is more likely to occur during long trips. These processes likely combine in some way to affect the overall negative relationship between IVI and mass change.

Intriguingly, these same three processes (i. foraging effort reducing mass, ii. foraging for self thereby increasing mass, and iii. excretion causing sudden but infrequent drops in mass) should act to increase the residual variance in parental mass change with IVI. Our models produced a mixed result. IVI had no effect on residual variance in males, but a significant positive effect in females (Fig. 1b), and this effect differed between the 2 years. A sex difference in the variance in mass change from trip to trip with respect to the length of the trip implies a different mix of the 3 processes in males and females or some additional processes unique to one sex. One possibility is that mass change is also linked with load size. Males tended to have higher residual variance in these two variables than did females, so perhaps males were behaving in ways that kept their mass constant and allowed other elements of provisioning behavior to vary, whereas females were holding provisioning more constant and allowing their own mass to vary more, which may mean they were also more sensitive to variation between years. Why the sexes would differ in that way is not clear, but it might reflect slightly different roles, with males continuing to attend to territory boundaries or interacting with neighbors during at least some trips away from the nest may contribute indirectly to these sex-specific patterns (see Markman et al. 1995). Our results cannot provide an answer, but suggest that more attention to sex-specific processes away from the nest may influence in subtle ways the provision of care in biparental species (e.g., Markman et al. 2004).

In summary, hierarchical analyses of variance allow detection of patterns in the residual variance, which then provide new insights into behavioral strategies (Westneat et al. 2015). We took advantage of a brood size manipulation in pied flycatchers to assess the impact of increased brood demand on both the mean and variance of the length of foraging trips and load sizes delivered. The results did not fit predictions of variance-sensitive foraging theory concerning how parents should exploit foraging options that differ in variance. Indirect evidence instead suggested that parents with larger broods adjusted their time budgets as predicted under life history theory to prioritize provisioning, but this had unexpected effects in reducing residual variances in provisioning behaviors. Hierarchical analyses of variance also revealed patterns in the residual variance of both begging and parental mass

changes. These more exploratory analyses stimulate some new ideas and reaffirm the value of thoroughly exploring pattern in repeatedly expressed traits such as provisioning behavior.

Compliance with ethical standards

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

Data disposition   The data used in the analyses described here are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.8kt67.

Ethical statement   This article does not contain any studies with human participants, but it does contain data collected from studies on animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in this study were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

References

Brooks SP (1998) Quantitative convergence assessment for Markov chain Monte Carlo via cusums. Stat Comput 8:267–274

Budden AE, Wright J (2001) Begging in nestling birds. In: Val Nolan J, Thompson CF (eds) Current ornithology, vol 16. Springer US, New York, pp 83–118

Caraco T (1980) On foraging time allocation in a stochastic environment. Ecology 61:119–128

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton

Drent RH, Daan S (1980) The prudent parent—energetic adjustments in avian breeding. Ardea 68:225–252

Frey-Roos F, Brodmann PA, Reyer H-U (1995) Relaionships between food resources, foraging patterns, and reproductive success in the water pipit, *Anthus* sp. *spinoletta*. Behav Ecol 6:287–295

Houston A (1985) Central-place foraging—some aspects of prey choice for multiple-prey loaders. Am Nat 125:811–826

Houston AI, McNamara JM (1985) A general theory of central place foraging for single-prey loaders. Theor Popul Biol 28:233–262

Hunt S, Low J, Burns KC (2008) Adaptive numerical competency in a food-hoarding songbird. Proc R Soc Lond B 275:2373–2379

Kacelnik A (1984) Central place foraging in starlings (*Sturnus vulgaris*). 1. Patch residence time. J Anim Ecol 53:283–299

Kilner R, Johnstone RA (1997) Begging the question: are offspring solicitation behaviours signals of needs. Trends Ecol Evol 12:11–15

Lee Y, Nelder JA (2006) Double hierarchical generalized linear models. J Roy Stat Soc C-App 55:139–167

Leonard ML, Horn AG (2006) Age-related changes in signalling of need by nestling tree swallows (*Tachycineta bicolor*). Ethology 112:1020–1026

Lundberg A, Alatalo RV (1992) The pied flycatcher. R & AD Poyser Ltd, London

Lyon BE (2003) Egg recognition and counting reduce costs of avian conspecific brood parasitism. Nature 422:495–499

Markman S, Yom-Tov Y, Wright J (1995) Male parental care in the orange-tufted sunbird—behavioral adjustments in provisioning and nest guarding effort. Anim Behav 50:655–669

Markman S, Pinshow B, Wright J, Kotler BP (2004) Food patch use by parent birds: to gather food for themselves or for their chicks? J Anim Ecol 73:747–755

Martins TLF, Wright J (1993) Cost of reproduction and allocation of food between parents and young in the swift (*Apus apus*). Behav Ecol 4:213–223

Mathot KJ, Olsen A-L, Mutzel A, Araya-Ajoy YG, Nicolaus M, Westneat DF, Wright J, Kempenaers B, Dingemanse NJ (2017) Provisioning tactics of great tits in response to long-term brood manipulations differ across years. Behav Ecol. doi:10.5061/dryad.406fd

Moore DJ (2002) The provisioning tactics of parent common terns (*Sterna hirundo*) in relation to brood energy requirement. Dissertation, Simon Fraser University

Moreno J, Cowie RJ, Sanz JJ, Williams RSR (1995) Differential response by males and females to brood manipulations in the pied flycatcher—energy expenditure and nestling diet. J Anim Ecol 64:721–732

Nur N (1984) Feeding frequencies of nestling blue tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. Oecologia 65:125–137

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs RD (eds) Analysis of ecological systems. Ohio State University Press, Columbus, pp 154–177

Ottosson U, Backman J, Smith HG (1997) Begging affects parental effort in the pied flycatcher, *Ficedula hypoleuca*. Behav Ecol Sociobiol 41:381–384

Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Hornik K, Leisch F, Zeileis A (eds) Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003). r-Project.org. Vienna, Austria

Price K, Harvey H, Ydenberg R (1996) Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. Anim Behav 51:421–435

R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna https://www.R-project.org/

Real LA, Ellner S (1992) Life-history evolution in stochastice environments—a graphical mean-variance approach. Ecology 73:1227–1236

Roff DA (2002) Life history evolution. Sinauer Associates, Sunderland

Rönnegård L, Felleki M, Fikse F, Mulder HA, Strandberg E (2010) Genetic heterogeneity of residual variance-estimation of variance components using double hierarchical generalized linear models. Genet Sel Evol 42:8

Royama T (1966) Factors governing feeding rate food requirement and brood size of nestling great tits *Parus major*. Ibis 108:313–347

Royle NJ, Smiseth PT, Kölliker M (2012) The evolution of parental care. Oxford University Press, Oxford

Sanz JJ (1997) Clutch size manipulation in the pied flycatcher: effects on nestling growth, parental care and moult. J Avian Biol 28:157–162

Smiseth PT, Wright J, Kölliker M (2008) Parent-offspring conflict and co-adaptation: behavioural ecology meets quantitative genetics. Proc R Soc Lond B 275:1823–1830

Smyth GK (1989) Generalized linear models with varying dispersion. J R Stat Soc B Met 51:47–60

Stearns SC (1977) Evolution of life-history traits—critique of theory and a review of data. Annu Rev Ecol Syst 8:145–171

Stephens DW (1981) The logic of risk-sensitive foraging preferences. Anim Behav 29:628–629

Stephens DW, Charnov EL (1982) Optimal foraging—some simple stochastic models. Behav Ecol Sociobiol 10:251–263

Stephens DW, Brown JS, Ydenberg RC (2007) Foraging. Chicago University Press, Chicago

Tilgar V, Moks K, Saag P (2011) Predator-induced stress changes parental feeding behavior in pied flycatchers. Behav Ecol 22:23–28

Tinbergen JM (1981) Foraging decisions in starlings (*Sturnus vulgaris*). Ardea 69:1–67

Trivers RL (1972) Parental investment and sexual selection. In: Campell B (ed) Sexual selection and the descent of man, 1871–1971. Aldine-Atherton, Chicago, pp 136–179

Weimerskirch H, Gault A, Cherel Y (2005) Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. Ecology 86:2611–2622

Westneat DF, Hatch MI, Wetzel DP, Ensminger AL (2011) Individual variation in parental care reaction norms: integration of personality and plasticity. Am Nat 178:652–667

Westneat DF, Schofield M, Wright J (2013) Parental behavior exhibits among-individual variance, plasticity, and heterogeneous residual variance. Behav Ecol 24:598–604

Westneat DF, Wright J, Dingemanse NJ (2015) The biology hidden inside residual within-individual phenotypic variation. Biol Rev 90:729–743

Whittingham LA, Robertson RJ (1993) Nestling hunger and parental care in red-winged blackbirds. Auk 110:240–246

Williams GC (1966) Natural selection costs of reproduction and a refinement of Lacks principle. Am Nat 100:687–690

Winkler DW (1987) A general model for parental care. Am Nat 130:526–543

Wright J (1998) Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. Behav Ecol Sociobiol 42:423–429

Wright J, Cuthill I (1990a) Biparental care: short-term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris*. Behav Ecol 1:116–124

Wright J, Cuthill I (1990b) Manipulation of sex differences in parental care—the effect of brood size. Anim Behav 40:462–471

Wright J, Leonard ML (2002) The evolution of begging: competition, cooperation and communication. Kluwer Academic, Dordrecht

Wright J, Both C, Cotton PA, Bryant D (1998) Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. J Anim Ecol 67:620–634

Wright J, Hinde C, Fazey I, Both C (2002) Begging signals more than just short-term need: cryptic effects of brood size in the pied flycatcher (*Ficedula hypoleuca*). Behav Ecol Sociobiol 52:74–83

Wright J, McDonald PG, te Marvelde L, Kazem AJN, Bishop CM (2010) Helping effort increases with relatedness in bell miners, but 'unrelated' helpers of both sexes still provide substantial care. Proc R Soc Lond B 277:437–445

Ydenberg RC (1994) The behavioral ecology of provisioning in birds. Ecoscience 1:1–14

Ydenberg RC (2007) Provisioning. In: Stephens DW, Brown J, Ydenberg RC (eds) Foraging. University of Chicago Press, Chicago, pp 273–303