

1 Experimental changes in brood size alter several levels of phenotypic variance in offspring and
2 parent pied flycatchers

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17 **Abstract**

18 The behavior of parents provisioning dependent offspring should reflect selection on important
19 life-history aspects of parental investment as well as on foraging behavior. Life history and
20 foraging theory generally make predictions about mean behavior, but some circumstances might
21 favor parents to engage in more variable parental behavior. We examined a uniquely detailed
22 dataset on free-living pied flycatchers (*Ficedula hypoleuca*) experiencing a brood size
23 manipulation. We used double-hierarchical generalized linear models to simultaneously
24 investigate patterns in means and variances of different aspects of provisioning, parental mass
25 and brood begging. As predicted by life-history theory, parents with enlarged broods that begged
26 more intensely fed their nestlings at higher rates and delivered larger loads. At the same time,
27 they delivered food at a more consistent rate, mediated by both the brood size manipulation itself
28 and the increased begging of larger broods. This contradicts the prediction from variance-
29 sensitive foraging that parents facing increased brood demand should seek out more variable
30 foraging options. Indirect evidence suggests that the reduced variance in trip time might have
31 been a byproduct of shifts in parental time budgets, because hard-working parents favored
32 provisioning over other activities. Exploratory analyses further revealed patterns in residual
33 variance of both nestling begging and parental mass changes, with enlarged broods begging less
34 consistently and female body mass changes being more variable after longer foraging trips. We
35 show that parent pied flycatchers simultaneously adjust means and variances in multiple aspects
36 of their provisioning effort to changes in brood demand and that these responses might be linked
37 with nestling begging and changes in parental body mass. Our study highlights both the
38 importance of adopting more sophisticated statistical approaches and the potential intersection of

39 two bodies of theory that may affect aspects of strategic adjustments and trade-offs individuals
40 make when engaging in central-place provisioning.

41

42 **Introduction**

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

61 reflect factors affecting either the life history elements of parenting, the foraging elements, or
62 both (e.g., Martins and Wright 1993; Wright et al. 1998).

63 These two bodies of theory usually explain variation in mean provisioning effort through
64 deterministic effects. For example, life history theory predicts that higher visit rates (i.e., shorter
65 inter-visit-intervals, or IVIs) should be associated with larger brood sizes (Royama 1966; Nur
66 1984; Wright and Cuthill 1990a; Wright and Cuthill 1990b). This arises because having more
67 offspring increases the benefits of provisioning, and so parents are predicted to shift time or
68 energy away from other activities, or take more risks, in favor of increasing food delivery rates to
69 the nest (Winkler 1987). Similarly, offspring that are hungry typically signal with greater than
70 average begging behavior, and usually parents respond immediately by increasing the mean
71 delivery of food (Kilner and Johnstone 1997; Budden and Wright 2001; Wright and Leonard
72 2002; Smiseth et al. 2008), possibly via shorter inter-visit-intervals or larger loads, or both
73 (Wright and Cuthill 1990a; Wright and Cuthill 1990b; Wright 1998; Wright et al. 1998). Some
74 evidence also suggests that offspring begging behavior, perhaps combined with other cues, can
75 affect parent decision-making also on medium (e.g., hours, Wright et al. 2010) or longer-term
76 (e.g., days, Price et al. 1996; Wright et al. 2002) time scales.

77 This array of deterministic factors generates variation in average provisioning behaviors,
78 potentially both among individuals within populations and within individuals depending on the
79 timing of changes in the underlying factors (e.g., Westneat et al. 2011). However, the expression
80 of parental behavior in any one event often deviates from these average values in the form of
81 residual variance driven by non-deterministic processes. For example, both the length of time it
82 takes for a parent to leave the nest on one visit and return (the inter-visit-interval, or IVI) and the
83 amount of food carried back to be fed to offspring (the load size) varies from trip to trip in part

84 due to the unpredictable nature of encounters with different types of prey (e.g., Frey-Roos et al.
85 1995; Weimerskirch et al. 2005). Such unpredictable variance could produce complex patterns in
86 provisioning behavior within and among individuals (e.g., Westneat et al. 2013).

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

96 Foraging theory, while also usually focused on deterministic effects on behavior, has proffered
97 some predictions about how individuals might manage unpredictable variance. For example, the
98 variance-sensitive foraging hypothesis (so-called risk-sensitivity; Caraco 1980; Stephens 1981;
99 Stephens and Charnov 1982) predicts that if foragers experience a shift from an accelerating
100 fitness gain curve when they are hungry and in a negative energy budget to a decelerating gain
101 curve when their reserves are high and they are in positive energy budget, then they should alter
102 their behavior from favoring highly variable prey distributions (being variance-prone) when in
103 poor condition to less variable prey distributions when in good condition (variance-averse).
104 Ydenberg (1994) extended this idea to parents caring for broods in poor or good condition and
105 predicted that if offspring are in a decelerating part of their utility function then parents should
106 favor lower variance options. Tests of this idea have been rare. Moore (2002; see also in

107 Ydenberg 2007) experimentally manipulated brood size in common terns (*Sterna hirundo*) and
108 found that subjects with enlarged broods, which presumably placed sufficient new demands on
109 the parents that they were in the accelerating part of an offspring fitness curve, switched from
110 foraging in a patch with moderate variance in prey to one with high variance in prey. Mathot et
111 al. (submitted) assessed the impact of brood manipulations in great tits (*Parus major*) and found
112 contrasting results in two years. In a good year when most offspring survived, parents
113 experiencing greater brood demand reduced the variance in provisioning behavior. One
114 explanation offered was that the increased demand caused a shift towards time spent on parental
115 provisioning and away from less important non-parental behaviors in ways that coincidentally
116 reduced variance in provisioning. In a poor year, however, when nestling mortality was higher
117 and growth rates lower, the increased demand increased the variance in IVI, suggesting that
118 parents were being adaptively variance-prone in seeking out more variable foraging options.
119 Two studies from red-winged blackbirds (*Agelaius phoeniceus*) have also suggested that
120 variance in the delivery of food changes in ways that are consistent with the variance-sensitivity
121 hypothesis (Whittingham and Robertson 1993; as reanalyzed by Moore 2002; Ydenberg 2007;
122 Westneat et al. 2013). Although suggestive of a role for variance sensitivity in parental
123 provisioning strategies, it is unclear how general these sorts of results really are, and whether
124 additional details about variances in parent and offspring behaviors could provide alternative
125 explanations.

126 Here we investigate patterns of variance in provisioning behavior in a woodland-dwelling
127 insectivorous bird, the pied flycatcher (*Ficedula hypoleuca*), with the goal of understanding how
128 changes in benefits of current reproduction may drive variance in phenotypes associated with
129 parenting. Our focal hypothesis was that parents with increased brood demand should seek out

130 more variable foraging options. In secondary analyses, we also investigate patterns of variance in
131 nestling begging and change in parental body mass with the idea that these are linked phenotypes
132 and may provide a richer understanding of both deterministic and unpredictable variance in
133 provisioning behaviors. We studied the pied flycatcher because it is a small (12-14g) migratory
134 passerine common across Europe and western Asia (Lundberg and Alatalo 1992) that typically
135 nests in cavities and generally exhibits considerable provisioning of nestlings. Males are
136 territorial, most pairs are socially monogamous, and both parents typically help with the
137 provisioning of 5-7 nestlings, which are fed entirely on invertebrate prey. Previous studies have
138 shown that both parents respond to brood size manipulations by increasing visit rates to the nest
139 (Moreno et al. 1995; Sanz 1997; Wright et al. 2002). Experimental manipulations of nestling
140 begging also suggest that parents are sensitive to the magnitude of begging vocalizations
141 (Ottoosson et al. 1997).

142 We analyzed a dataset collected from a population of pied flycatchers in which brood size was
143 manipulated for the whole nestling period and measures of individual visits were taken over 24 h
144 in the middle of that period. Our main goal for this analysis was to test the idea that increasing
145 offspring demand on parents would cause both deterministic shifts in parental behavior as well as
146 effects on the residual variance in delivery as predicted by variance sensitivity theory. We used a
147 statistical approach (e.g., Westneat et al. 2013) that models pattern in both the mean and residual
148 variance of a response variable simultaneously. This approach emphasizes the idea that residual
149 variance may contain considerable hidden biology that may be revealed by exploring cryptic
150 patterning in the residual variance (Westneat et al. 2015). This statistical method, combined with
151 the methods used in the field, provided us the opportunity to explore heretofore unstudied
152 patterns of variation in the components of food delivery (IVI and load), brood begging intensity,

153 and parental mass, as well as potential differences between the sexes and the two different years
154 of the study. Thus, besides reporting on tests of predictions from variance sensitivity theory, we
155 also present exploratory analyses using these new statistical techniques. The combination reveals
156 an array of previously unrecorded patterns in the variance of each of these traits, some of which
157 fit with previous studies of deterministic factors, but also others which suggest new questions
158 that need to be asked.

159 **Methods**

160 Study species and site

161 Data on provisioning behavior was collected in 1998 and 1999 on a population of pied
162 flycatchers located in Abergwyngregyn National Nature Reserve, North Wales, UK
163 (53°13'16"N3°59'59"W). This reserve is a 169 hectare area of mixed deciduous and plantation
164 coniferous woodland in a steep sided valley with acidic soils. Pied flycatchers arrive at
165 Abergwyngregyn in mid-to-late April from west Africa, the first eggs of their single reproductive
166 attempt are laid at the end of April, and the first nestlings hatch by late May. As in other studies
167 (Lundberg and Alatalo 1992), levels of polygamy at Abergwyngregyn are estimated to be around
168 10%.

169 Experimental procedure

170 In each year, 100 nest boxes were available. Pairs that nested in these boxes were randomly
171 assigned to the two brood size treatment groups within hatch dates, with 21 nests being used in
172 1998 and 16 nests in 1999. At 2-3 days of age, nestlings were moved between nests in order to
173 create 18 experimentally ‘small’ broods (mean = 3.9 nestlings, range 3-4 nestlings) and 19
174 experimentally ‘large’ broods (mean = 8.2 nestlings, range 8-9 nestlings), each being roughly

175 two nestlings either side of the mean brood size and within the natural range for this population
176 (mean = 6.6, SE \pm 0.2, range 1-9). Seven broods (five in 1998 and two in 1999) were attended by
177 a single parents and so were excluded from analysis.

178 The manipulations were carried out using normal broods from first nesting attempts hatching
179 between 20th May and 7th June. Hatch dates did not differ significantly between years ($F_{1,26} =$
180 2.7, $P = 0.12$) or between manipulated brood sizes ($F_{1,26} = 0.11$, $P = 0.74$), with no significant
181 interaction ($F_{1,26} = 2.4$, $P = 0.14$). Natural broods tended to be larger in 1999 than in 1998 ($F_{1,26} =$
182 3.23, $P = 0.08$), but there was no bias by year and brood size treatment on natural brood size
183 ($F_{1,26} = 0.41$, $P = 0.51$). Nestlings added to enlarged broods were within 1 day of age and 30% of
184 body weight of their broodmates. Natural brood sizes did not differ between the two brood size
185 treatments ($F_{1,26} = 0.31$, $P = 0.57$). Thus, natural variation in the timing and quality of pairs or
186 nestlings was unlikely to have influenced comparisons between the two brood size groups.

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

191 Data collection

192 Data on experimental pairs were obtained using video cameras (Sony Hi8 CCD-TRIIIOOE)
193 mounted in specifically designed nest boxes. These larger video nest boxes replaced the smaller
194 normal nest boxes approximately 24 hours before filming to allow parents to become
195 accustomed to them. Each video nest box contained an electronic balance (either Mettler
196 SM3000 or PB3001, powered by a 12V car battery, and accurate to 0.1 g) positioned under the

217 nest. The camera was set up to video the nest at 45°, also capturing the inside of the entrance
218 hole and the balance display. Calculation of nest mass before, during and after visits thereby
219 allowed measurement of parental mass, as well as load mass delivered (for those parental visits
220 when faecal sacs were not also removed by parents). Additional variables measured included the
221 timing of individual parent visit arrivals and departures, from which we computed inter-visit
222 intervals (IVI, the time between visits of a focal parent) and time spent in nest, as well as any
223 faecal sac removal. The latter affected which visits could be scored for load size, since if a parent
224 removed a fecal sac, the visit included both a weight gain (food brought) and weight lost (fecal
225 sac removed) and so could not be used to estimate load. In 1999, brood demand per visit was
226 also assessed via the visual assessment of each individual nestling's begging height in the nest
227 (where 0 = no begging, 0.5 = gaping with head up, and 1 = gaping with neck extension and body
228 raised).

229 For each nest, six video recordings were made lasting approximately 1.5hrs each. Recordings
230 started in the early afternoon of day one and finished at the same time on day two (approximate
231 times: 15:00-16:30, 17.30-19.00, 20:00-21:30, 05:00-06:30, 08:00-09:30, 11:00-12:30 h). The
232 mean age of nestlings during the period of taping was 9.1 days (range 7-12), and did not differ
233 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 $F_{1,23} = 0.48$, $P = 0.50$).

234 Statistical analyses

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

220 The data set is composed of a hierarchically arranged set of repeated measures with the main
 221 dependent variables measured on each visit by one of two subjects (the parents) attending one of
 222 27 nest boxes across 2 years. Some independent variables varied among boxes (e.g., brood size
 223 treatment, nestling age, and date), but most varied among visits (e.g., begging levels, behavior of
 224 nestlings or parents on previous visits). Because we were interested in deterministic (mean)
 225 effects and patterns in residual variation, we used a statistical approach called “double GLM”
 226 (Smyth 1989; Lee and Nelder 2006; Ronnegard et al. 2010). These models extend the class of
 227 generalized linear models by allowing the predictor variables to affect both the mean and
 228 variance of the response variable. The models we have fit may be more appropriately called
 229 double linear mixed effects models, because we modeled random effects at both the mean and
 230 residual variance level. In all cases we assumed that the errors were independently distributed
 231 normal random variables. The random effects were individual and box.

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

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

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

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

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

247 We fit these models in the Bayesian statistical framework. Specifically, we used Markov chain
 248 Monte Carlo (MCMC) methods implemented in the JAGS software package (Plummer 2003) to
 249 obtain samples from the joint posterior distribution of all parameters and compute posterior
 250 summary statistics. Prior distributions were chosen to be non-informative. We assigned the
 251 regression parameters for the model of the mean, β_h , and variance, φ_h , non-informative normal
 252 priors with mean 0 and variance 100^2 . We assigned the variance parameters for both the mean
 253 model, $\sigma_{\epsilon}^{box^2}$, σ_{ϵ}^{ind} , and $\sigma_{\epsilonijk}^{res}$, and variance model, σ_{ϵ}^{box} , σ_{ϵ}^{ind} , and $\sigma_{\epsilonijk}^{res}$, half-t prior
 254 distributions with 5 degrees of freedom and scale factor 5. This represents a truncated and scaled
 255 version of the t -distribution which is restricted to the positive values and has a median value
 256 1.68, 75th percentile 6.70, and 95th percentile 12.82. We ran three chains in parallel and
 257 assessed convergence via the Brooks-Gelman-Rubin Potential Scale Reduction Factor (Brooks,
 258 1998). The procedure consisted of a wrapper program in R 3.2.4 (R Development Core Team
 259 2016) that set up the model structure and priors, and then interfaced with code in the JAGS
 260 environment to conduct the MCMC simulations. The three Markov chains were run for a burn-in
 261 period of 1000 iterations plus 10000 iterations with no thinning for computing parameter

262 estimates. Significance of the effects in the models was assessed by examining the range of the
263 95% credible intervals for the regression coefficients and whether or not these included 0.

264 To address our primary hypothesis, we modeled two parental variables, inter-visit-interval (IVI)
265 and load mass. IVI was log-transformed in all models and resulted in residuals that did not
266 deviate from a Gaussian distribution, as determined from visual inspection of Q-Q plots of
267 standardized residuals. One complicating factor in the analysis of load mass was that the
268 balances only provided accurate measurements to the nearest 0.1 g. This rounding error was
269 accounted for by treating these measurements as interval censored observations known to be
270 within an interval extending 0.05 g above and below the recorded value.

271 Besides the random effects of box identity and individual subject identity, all models included
272 the fixed effect of the brood size manipulation. We also typically included the fixed effects of
273 date and nestling age, which were mean-centered among nests, and parental sex and year.
274 Nestling begging intensity was mean-centered within the individual parent and treated as a fixed
275 effect in a subset of models. For models of load size and parental mass changes, we also mean
276 centered IVI within the individual parent. We initially fitted 2-way interactions between sex and
277 year with all other fixed effects included in the respective model to investigate sex and year
278 differences. We simplified the initial models by iteratively removing all non-significant
279 interactions and present results from final models only.

280 In our secondary analyses we modeled nestling begging intensity and parental mass changes. The
281 models of begging included inter-feed interval (IFI; defined as time between feedings by either
282 parent; mean-centered within nest identity), brood size manipulation and nestling age as fixed
283 effects and nest identity as a random effect. Because begging was assessed as an average

284 intensity over all nestlings in a brood, we added a weighting variable to the analysis to control
 285 for the necessary relationship of variance in mean values with changes in brood size. To analyze
 286 changes in parental body mass we initially fitted models including the fixed effects of brood size
 287 manipulation, IVI, parental sex, year, nestling age and date and the respective 2-way interactions
 288 between sex and year with IVI and brood size manipulation treatment.

289 **Results**

290 Before reporting on these results we comment on two important aspects in the interpretation of
 291 these models. The first is that although we have considered load mass as the response variable in
 292 our models the estimated effects from these models can be interpreted equally as effects on mean
 293 delivery, with one exception. Including $\log(\text{IVI})$ as a predictor, which was found to be necessary,
 294 the model of load takes the form

$$295 \quad \log(\text{load}_{ijk}) = \beta_0 + \beta_1 \log(\text{IVI}_{ijk}) + \beta_2 x_{2,ijk} + \dots + \beta_p x_{p,ijk} + \epsilon_{ijk}$$

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

297 Equivalently

$$298 \quad \log(\text{delivery}_{ijk}) = \log\left(\frac{\text{load}_{ijk}}{\text{IVI}_{ijk}}\right)$$

$$299 \quad = \beta_0 + (\beta_1 - 1) \log(\text{IVI}_{ijk}) + \beta_2 x_{2,ijk} + \dots + \beta_p x_{p,ijk} + \epsilon_{ijk}.$$

300 It follows that a change in any of x_2 through x_p while the other predictors are held constant has
 301 the same effect on the mean of both the $\log(\text{load})$ and $\log(\text{delivery})$. In particular, the effect of
 302 the brood size manipulation on the $\log(\text{load})$ can also be interpreted as an effect of brood size
 303 manipulation on $\log(\text{delivery})$ while the remaining predictors stay fixed. The one exception to

304 this equivalence is the effect of logIVI itself which differs by 1 depending on whether the
 305 response is log(load) or log(delivery). This change is simply a function of the difference between
 306 modelling the provisioning per trip (i.e., load) versus the rate of provisioning per trip (i.e.,
 307 delivery). Moreover, if we further model the variance of the residual errors as a function of
 308 covariates, e.g.

$$309 \quad \log(\sigma_{ijk}^2) = \phi_0 + \phi_1 x_{1,ijk} + \dots + \phi_p x_{p,ijk}$$

310 then the coefficients ϕ_1 through ϕ_p can be interpreted equally as effects on both the variance of
 311 log(load) and the variance of log(delivery) while the remaining predictors remain fixed.

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

$$318 \quad Var(y) = (e^{\phi_0 + \phi_1 x} - 1) e^{(\phi_0 + 2\beta_0) + (\phi_1 + 2\beta_1)x}.$$

319 The implication is that the effect of x on $Var(y)$ cannot be determined by looking at ϕ_1 alone.
 320 We can conclude immediately that $Var(y)$ will increase as x increases if both ϕ_1 and β_1 are
 321 positive and decrease as x increases if both are negative. However, $Var(y)$ may either increase
 322 or decrease with x if ϕ_1 is positive and β_1 is negative, or vice versa, depending on their relative
 323 values.

324

325

326 Effects on mean parental behavior

327 We assessed the impact of the brood manipulation and any covariates on both the mean and
328 variance in the two main parental response variables, logIVI and load mass per trip. We first
329 investigated the relationships between the two response variables. Mean load mass increased
330 with logIVI, with this effect being stronger in 1999 (1998: $\beta = 0.06$, 95% CI: 0.02, 0.10; 1999: β
331 = 0.14, 95%CI: 0.11, 0.18; difference between 1998 and 1999: $\beta = 0.08$, 95% CI: 0.03, 0.13).
332 Residual variation in load mass also increased with logIVI ($\varphi = 0.04$, 95% CI: 0.01, 0.07). In
333 addition, we found that load masses were generally smaller in 1999 compared to 1998
334 (difference between 1999 and 1998: $\beta = -0.45$, 95% CI: -0.73, -0.17).

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

343 We included in our analyses of logIVI and load mass the covariates of nestling age, date in
344 season and year. We found some evidence for an effect of nestling age on parental logIVI that
345 differed across sexes. Nestling age negatively affected male, but not female logIVI, with males
346 with older broods tending to make shorter trips ($\beta = -0.04$, 95% CI: -0.09, 0.01; Table 1a, Table

347 S1) and therefore likely provisioning at higher rates. In contrast, there was no evidence for an
348 effect of nestling age on male or female load mass per unit of time (Table 1a). In females, date
349 negatively affected logIVI, with females recorded later in season visiting the nest more quickly.
350 In males, there was no effect of date on IVI ($\beta = 0.00$, 95% CI: -0.02, 0.03, Table S1), but males
351 of later broods also delivered less food ($\beta = -0.05$, 95% CI: -0.09, -0.01, Table S1). Yet, this
352 decrease in food delivery later in the season was less pronounced compared to females (Table 1a,
353 Table S1).

354 We assessed the potential impact of nestling begging intensity and its interaction with the brood
355 manipulation using the data from 1999, the only year when begging intensity was also measured.
356 In both sexes, we found support for a negative effect of the average begging parents experienced
357 during their previous (t-1) visit to the nest on IVI (summarized in Table 2, full model results in
358 Table S2; Fig. 1a). Begging levels at visit t-2 also negatively affected IVI, and the effect of t-1 is
359 reduced slightly and the credible interval reached 0 (Table 2, Table S3). Begging at t-3 did not
360 predict IVI nor did it alter the effects of begging at t-1 and t-2 compared to the model when t-3
361 was not included (Table 2, Table S3). The effect of begging during the previous visit did not
362 differ between brood size manipulation groups (interaction BSM \times begging t-1: $\beta = 0.04$, 95%
363 CI: -0.06, 0.13); all parents decreased their IVIs at the same rate with increasing nestling begging
364 intensity. In females, there was no evidence for an effect of nestling begging on load size
365 controlling for IVI, whereas there was a positive effect of begging at visit t-1 on load mass in
366 males ($\beta = 0.28$, 95% CI: 0.09, 0.46) (Table 2; Table S2; Fig. 1a). This resulted in males, but not
367 females, delivering food at higher rates in response to increases in nestling begging at t-1. There
368 was no additional effect of begging at visit t-2 on load size per unit time (Table 2, Table S3).

369 Patterns in residual variance in parental behavior

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

382 The main cue parents are expected to use to assess the condition of their nestlings is the intensity
383 of their begging. We assessed the potential impact of nestling begging intensity and its
384 interaction with the brood manipulation using the data from 1999, the year when begging
385 intensity was measured. Contrary to predictions, residual variance in IVIs decreased with
386 increased begging in reduced ($\varphi = -0.22$, 95% CI: -0.35, -0.08), but not in enlarged broods ($\varphi = -$
387 0.02 , 95% CI: -0.13, 0.10; difference: $\varphi = -0.20$, 95% CI: -0.38, -0.02; Table S2, Fig. 1b; Fig. 3).
388 We did not detect any effects of begging on residual variance in load size ($\varphi = -0.03$, 95% CI: -
389 0.18 , 0.13; Table S2; Fig. 1b).

390 Effects on nestling begging

391 *Mean effects on nestling begging*

392 We also explored the factors that affected nestling begging behavior. Mean nestling begging
393 intensity during different parental visits to the same brood was strongly affected by the time
394 between feedings (by either parent), called the “inter-feed interval” or IFI. Mean begging became
395 more intense when the IFI was longer (Table 3a). There were no additional effects of the IFIs of
396 even earlier visits over and above the strong effects of the most recent IFI (e.g. t-1: $\beta = 0.01$,
397 95% CI: -0.01, 0.02).

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

402 *Patterns in residual variance in begging*

403 We also modeled the residual variance in mean begging intensity (i.e. within broods over
404 repeated trips) and we used brood size as a weighting variable to control for effects of sample
405 sizes on variance in averages. We found that mean begging intensity decreased with increasing
406 parental IFIs (Table 3b). Parental IFIs of previous visits did not affect residual variances in
407 average nestling begging over and above effects of IFIs of the present visit (e.g. t-1: $\varphi = -0.03$,
408 95% CI: -0.08, 0.02). Residual variances in average begging intensity were higher in
409 experimentally enlarged compared to reduced broods (Table 3b).

410 Parental body mass changes

411 *Mean effects on parental body mass*

412 Life history theory predicts mean effects on parental condition of increased work associated with
413 provisioning. We analyzed absolute mass as a repeatedly measured trait on those visits when it
414 could be measured, but the models failed to converge. Instead, we analyzed two other mass-
415 related variables. First, we explored possible influences on mean mass of the parent during the
416 parental care observation. We found no support for the idea that parents feeding enlarged broods
417 differed in body mass compared to parents feeding reduced broods ($\beta = -0.09$, 95% CI: -0.39,
418 0.19).

419 Next, we analyzed the mass change that occurred between the focal visit and the previous one by
420 that individual. We found that parents lost more mass after longer trips (Table 4, Fig. 1a). Date in
421 the season ($\beta = -0.02$, 95% CI: -0.09, 0.08), nestling age ($\beta = -0.06$, 95% CI: 0.21, 0.18) and year
422 ($\beta = -0.05$, 95% CI: 0.42, 0.24) had no apparent effect on changes in body mass between visits.

423 *Patterns in residual variance in parental body mass*

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

432 1998: $\beta = 0.13$, 95% CI: 0.04, 0.22; Table 4). In contrast, there was no such effect of IVI in
433 males in 1998 ($\beta = 0.03$, 95% CI: -0.06, 0.12) and a tendency for a negative effect in 1999 ($\beta = -$
434 0.09, 95% CI: -0.19, 0.01; interaction IVI \times year: $\beta = -0.12$, 95% CI: -0.23, -0.01; Fig. 1b).

435 **Discussion**

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

445 Variance sensitivity theory (Caraco 1980; Stephens 1981) as applied to parental care (Ydenberg
446 1994; Ydenberg 2007) predicts that residual variance in provisioning should increase with a
447 sufficient increase in nestling demand, which itself would be driven by the experimental
448 manipulation of brood size. We thus expected that when faced with increased demand, parent
449 pied flycatchers might shift to foraging in patches of habitat or microhabitat that had either more
450 variable encounter rates with prey or more variable loads sizes due to differences in the prey
451 types encountered. Such shifts should produce an increase in the residual variation in IVI and/or
452 load size. Our analyses support the implicit assumption that the brood manipulation increased
453 demand on parents. Offspring in enlarged broods begged more intensely (Fig. 1a). Both this
454 increased begging within nests and the brood manipulation across nests led to a decrease in

455 parental mean inter-visit intervals, and increased begging within nests also resulted in an increase
456 in load size and hence in delivery in males. Thus both parents and offspring behaved as if the
457 increase in brood size made provisioning nestlings more difficult.

458 Despite the fact that the brood manipulation had the expected effects on average behavior of
459 parents and nestling, it did not produce the predicted effects on the residual variance in
460 provisioning. Increases in brood size led to reduced variance in IVI (Fig. 1b), which is opposite
461 to our prediction from variance sensitivity theory. The increased mean begging due to the brood
462 size manipulation also had its own, independent negative effect on residual variance in parental
463 IVI (Fig. 1b). Given that parents were working harder to feed larger broods that begged more,
464 this result raises several questions about the role of variance sensitivity on provisioning behavior.
465 Two prior studies that manipulated brood size to change demand on parents produced evidence
466 that parents shifted to more variable foraging options, as predicted. In common terns, Moore
467 (2002; see also in Ydenberg 2007) found that parents attending enlarged broods shifted to
468 seeking food in a patch with more variable prey types. Mathot et al. (submitted) found that great
469 tit parents attending enlarged broods provisioned more variably in one of two years. Our results
470 from pied flycatchers thus seem to contradict the predictions of variance sensitivity in this
471 regard.

472 Mathot et al. (submitted) may provide a post-hoc explanation for our results. The one year in
473 their study when parents behaved as if they were variance sensitive was a particularly bad year
474 with cooler temperatures, low levels of preferred prey, and relatively high offspring mortality
475 even in the broods that had been reduced in size. In the other year, when increased brood demand
476 led to reduced residual variance, the food supply was greater and most pairs successfully reared
477 all young even in enlarged broods. Moore (2002) similarly found greater variance sensitivity in

478 common terms in a poorer year. The pied flycatchers in our population appeared to have
479 experienced very good conditions in both years of our study. Although nestling survival to 12
480 days old for the whole population was lower in 1999 compared to 1998, it was high overall
481 (1998 = 87% ± 4%; 1999 = 70% ± 7%) and there was no effect of the brood size manipulation on
482 nestling survival or fledging dates across all 55 manipulated nests (i.e. parental provisioning was
483 not monitored in the additional 18 nests) (all p-values>0.3). In agreement with this, nestling body
484 mass at 12 days was only a little lower in enlarged broods overall ($F_{1,54}=6.2$; $P=0.017$), with
485 almost all of this differences being due to just the smallest nestlings being lighter in the enlarged
486 broods – i.e. most nestlings in enlarged broods were of comparable pre-fledging mass to those in
487 reduced brood sizes. This information leads us to the conclusion that parents in this system had
488 more than enough food available to them and had no problems almost fully compensating for the
489 experimental differences in brood size we imposed upon them. Although we enlarged brood
490 sizes to at or near the maximum observed brood size for this population, presumably increasing
491 brood demand substantially, the large amounts of natural food available to parents meant that it
492 may still not have been sufficient to place our subjects in the accelerating part of the utility curve
493 relating offspring fitness to delivery where these offspring would have been especially stressed
494 and variance-prone parental provisioning would have been adaptive.

495 An inadequate manipulation, however, cannot explain why parents of enlarged broods
496 significantly reduced the variance in provisioning behavior. There are two potential effects of the
497 increased brood demand on mean parental behavior that might have trickle-down effects on the
498 residual variance (Mathot et al. submitted). First, parents of enlarged broods may have shifted
499 how they allocated their time. Life history theory predicts that increased demand may indicate
500 increased benefits of care (Drent and Daan 1980; Nur 1984), thereby favoring shifts of parental

501 effort away from other activities and towards provisioning (e.g., Wright and Cuthill 1990b). If
502 other activities, such as interacting with distant social neighbors or searching for new foraging
503 patches, were accomplished only during a minority of trips away from the nest, possibly the
504 longer ones, then reducing time spent on those activities would reduce the variance in trip time.
505 Conversely, parents with reduced broods might have increased time spent on these other non-
506 provisioning activities. Hence, if they did not allocate that time equally on all trips, this would
507 increase the variance in provisioning for parents working less hard. Such effects on mean
508 behavior arising from life history selection, under the relatively benign conditions experienced
509 by the subjects in this study, could therefore mask any subtle shifts in patch or prey choice that
510 would have fit predictions from foraging theory.

511 Another explanation is that parents attending enlarged broods relaxed their preference for
512 particular high quality prey items. Shifts in prey preferences have been found in several other
513 studies that manipulated demand on parents (e.g., Royama 1966; Tinbergen 1981; Wright and
514 Cuthill 1990a; Wright and Cuthill 1990b; Wright et al. 1998) (Mathot et al. submitted). A
515 relaxed prey preference could have had two effects on residual variance in provisioning
516 behavior. First, it would reduce the variance in IVI, as we observed. When expressing a relaxed
517 preference, parents end up averaging the time to first encounter across several prey distributions
518 as opposed to a single, preferred prey's distribution. An average of encounter times on multiple
519 unselected prey would show less variation than that from a single selected prey distribution.
520 However, a relaxed preference should also increase load size variation in species that bring only
521 one or very few prey items back per trip, as in pied flycatchers. We found that increased brood
522 sizes had no apparent effect on the variance in load size (Fig. 1b), and a breakdown of prey types
523 for the two treatment groups revealed nearly identical distributions (Figure S1). Our results are

524 therefore most consistent with the hypothesis that the reduced variance in inter-visit intervals
525 arises from a shift in time budgets away from non-provisioning behaviors, as opposed to any
526 shift in prey preferences or variance-aversion *per se*.

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

547 We also found an effect of the brood size manipulation on residual variation in begging, with
548 enlarged broods having more residual variance in begging intensity per nestling from visit to
549 visit than small broods. If begging reflects hunger, as most studies seem to indicate (e.g.,
550 Leonard and Horn 2006), then one possibility is that residual variance in begging is being
551 affected by the opposing effects of increased hunger in larger broods but more frequent and less
552 variable visits by parents such that there are sequences of visits in which more of the nestlings
553 have recently been fed and so begging is less compared to sequences in which all nestlings are
554 hungrier and so begging is greater. In smaller broods, despite more variable trip times by
555 individual parents, individual nestlings are being fed more often and more regularly, leading to
556 lower variance in begging intensity.

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

569 Intriguingly, these same three processes (i. foraging effort reducing mass, ii. foraging for self
570 thereby increasing mass, and iii. excretion causing sudden but infrequent drops in mass), should
571 act to increase the residual variance in parental mass change with IVI. Our models produce a
572 mixed result. IVI had no effect on residual variance in males, but a significant positive effect in
573 females (Fig. 1b). A sex difference in the variance in mass change from trip-to-trip with respect
574 to the length of the trip implies a different mix of the three processes in males and females or
575 some additional processes unique to one sex. One possibility is that mass change is also linked
576 with load sizes. Males tended to have higher residual variance in these two variables than did
577 females, so perhaps males were behaving in ways that kept their mass constant and allowed other
578 elements of provisioning behavior to vary, whereas females were holding provisioning more
579 constant and allowing their own mass to vary more. Why the sexes would differ in that way is
580 not clear, but it might reflect slightly different roles, with males continuing to attend to territory
581 boundaries or interacting with neighbors during at least some trips away from the nest may
582 contribute indirectly to these sex-specific patterns (see Markman et al. 1995). Our results cannot
583 provide an answer, but suggest that more attention to sex-specific processes away from the nest
584 may influence in subtle ways the provision of care in biparental species (e.g., Markman et al.
585 2004).

586 In summary, hierarchical analysis of variance in which patterns can be detected in the residual
587 variance can provide new insights into behavioral strategies (Westneat et al. 2015). We took
588 advantage of a brood size manipulation in pied flycatchers to assess the impact of increased
589 brood demand on both the mean and variance of the length of foraging trips and load sizes
590 delivered. The results did not fit predictions of variance-sensitive foraging theory concerning
591 how parents should exploit foraging options that differ in variance. Indirect evidence instead

592 suggested that parents with larger broods adjusted their time budgets as predicted under life
593 history theory to prioritize provisioning, but this had unexpected effects in reducing residual
594 variances in provisioning behaviors. Hierarchical analyses of variance also revealed patterns in
595 the residual variance of both begging and parental mass changes. These more exploratory
596 analyses stimulate some new ideas and reaffirm the value of thoroughly exploring pattern in
597 repeatedly expressed traits such as provisioning behavior.

598

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607

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717

718 **Table 1.** Sources of variation in two different aspects of parental provisioning behavior in 1998 and
719 1999: inter-visit intervals (IVI) and load size in two brood size manipulation groups. Estimates were
720 derived from a Bayesian double GLM with random intercepts for nest identity ($N = 27$) and individual (N
721 $= 54$). BSM (brood size manipulation, factor with 2 levels: reduced, increased), mean-centered brood age
722 (days), date (mean-centered), year (factor with 2 levels: 1998, 1999), and log-transformed IVI (centered
723 within individuals) were fitted as fixed effects. Point estimates are given with their 95% credible
724 intervals (CI). Effects that were strongly supported by the model (95% CI not overlapping zero) are
725 indicated in bold. (a) Effects on means (b) Effects on residual variances.

(a)	Log(IVI)	Load size
<i>Means</i>	β (95% CI)	β (95% CI)
Intercept ¹	2.05 (1.99, 2.12)	-2.54 (-2.68, -2.39)
BSM (I-R)	-0.08 (-0.15, 0.01)	0.11 (-0.03, 0.25)
Log(IVI)	-	0.24 (0.18, 0.30)
Nestling age	0.03 (-0.02, 0.08)	0.04 (-0.05, 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, 0.03)
Year(1999-1998)	-0.05 (-0.11, 0.01)	-0.11 (-0.26, 0.04)
Sex × date	0.04 (0.01, 0.09)	0.03 (-0.01, 0.08)
Sex × nestling age	-0.07 (-0.13, -0.01)	-
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, 0.27)
Box	0.03 (0.00, 0.07)	0.08 (0.00, 0.17)
(b)		
<i>Residual variances</i>	φ (95% CI)	φ (95% CI)
Intercept ¹	-0.98 (-1.05, -0.90)	-0.45 (-0.56, -0.34)
BSM(I-R)	-0.08 (-0.15, -0.01)	0.02 (-0.10, 0.15)
Log(IVI)	-	0.11 (0.03, 0.18)
Nestling age	-0.00 (-0.05, 0.04)	-0.03 (-0.11, 0.04)
Date	0.02 (0.00, 0.04)	0.03 (-0.01, 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, 0.19)
	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)
<i>N</i> observations	8740	4693

726 ¹ Reference category is BSM ‘reduced’, sex ‘female’, and year ‘1998’

727

728 **Table 2.** Effects of begging in previous visits on parental IVI and load size. Estimates were derived from
 729 double GLMs including the same fixed and random effects as described for Table 1 with model 1
 730 additionally including begging at t-1, model 2 including begging at t-1 and t-2, and model 3 begging at t-
 731 1, t-2 and t-3. The effects of begging on load differed across sexes and are therefore given separately for
 732 male and females. Effects that were strongly supported by the model (95% CI not overlapping zero) are
 733 indicated in bold. For complete results see Tables S1 and S2.

	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	-0.05 (-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			
Model 1			
Female	-0.10 (-0.27, 0.07)	-	-
Male	0.28 (0.09, 0.46)	-	-
Model 2			
Female	-0.10 (-0.28, 0.09)	-0.03 (-0.21, 0.16)	-
Male	0.28 (0.08, 0.48)	-0.01 (-0.20, 0.18)	-

734

735 **Table 3.** Sources of variation in average nestling begging intensity in two brood size manipulation groups
736 for (a) effects on the means, and (b) effects on the residual variances. Estimates were derived from a
737 Bayesian double GLM with random intercepts for nest identity ($N = 13$). BSM (brood size manipulation
738 factor with 2 levels: reduced, increased), mean-centered brood age (days), and log-transformed IFI
739 (mean-centered within nest) were fitted as fixed effects. Point estimates are given with their 95%
740 credible intervals (CI). Effects that were strongly supported by the model (95% CI not overlapping zero)
741 are indicated in bold.

(a)	
<i>Means</i>	β (95% CI)
Intercept ¹	0.35 (0.29, 0.41)
BSM(I-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	0.16 (0.00, 0.68)
(b)	
<i>Residual variances</i>	φ (95% CI)
Intercept ¹	-0.56 (-0.72, -0.40)
BSM(I-R)	0.17 (0.11, 0.23)
Nestling age	-0.06 (-0.12, -0.01)
Log(IFI)	-0.12 (-0.16, -0.07)
	σ^2 (95% CI)
Box	0.65(0.00, 3.13)
<i>N observations</i>	4289

742 ¹ Reference category is BSM 'reduced'

743 **Table 4.** Sources of variation in mass changes between successive visits for parent pied flycatchers in
744 two brood size manipulation groups. Estimates were derived from a Bayesian double GLM with random
745 intercepts for individual ($N = 58$). Brood size manipulation (BSM factor with 2 levels: reduced, enlarged),
746 mean-centered nestling age (days), year (factor with 2 levels), mean-centered date, parental IVI (mean-
747 centered within-individual) and parental sex were fitted as fixed effects. Point estimates are given with
748 their 95% credible intervals (CI). Effects that were strongly supported by the model (95% CI not
749 overlapping zero) are indicated in bold.

	Mean	Residual variance
<i>Fixed effects</i>	β (95% CI)	φ (95% CI)
Intercept ¹	0.004 (-0.006, 0.014)	-1.998 (-2.270, -1.739)
BSM(I-R)	-0.001 (-0.012, 0.009)	0.027 (-0.222, 0.289)
Log(IVI)	-0.024 (-0.037, -0.012)	0.251 (0.147, 0.355)
Nestling age	0.000 (-0.02, 0.003)	-0.093 (-0.262, 0.075)
Date	0.000 (-0.002, 0.03)	0.023 (-0.047, 0.097)
Sex (male-female)	-0.002 (-0.012, 0.007)	0.044 (-0.192, 0.290)
Year (1999-1998)	0.007 (-0.005, 0.020)	0.640 (0.364, 0.929)
Log(IVI) \times year	-	-0.120 (-0.233, -0.010)
Log(IVI) \times sex	-	-0.220 (-0.332, -0.110)
<i>Random effects</i>	σ^2 (95% CI)	σ^2 (95% CI)
Individual	0.0026 (0.0001, 0.0077)	0.42 (0.33, 0.53)
Box	0.0029 (0.0001, 0.0089)	0.14 (0.01, 0.33)

750 ¹ Reference category is BSM 'reduced', sex 'female', and year '1998'

751

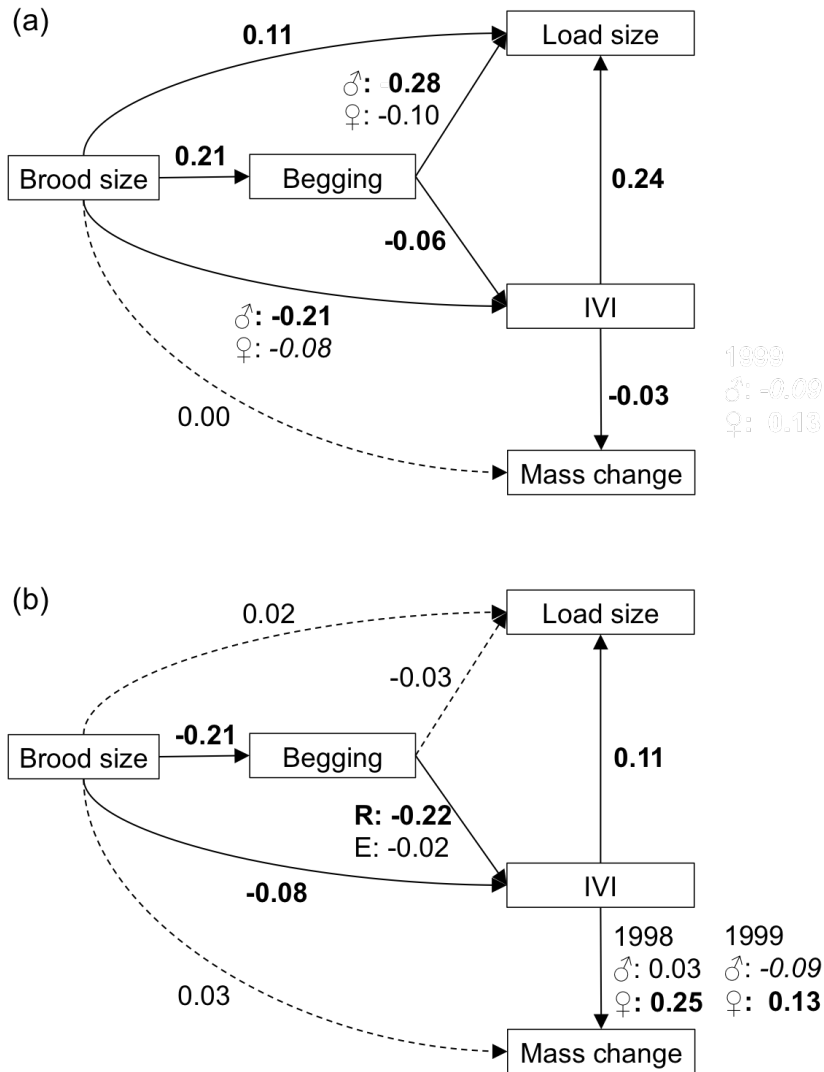
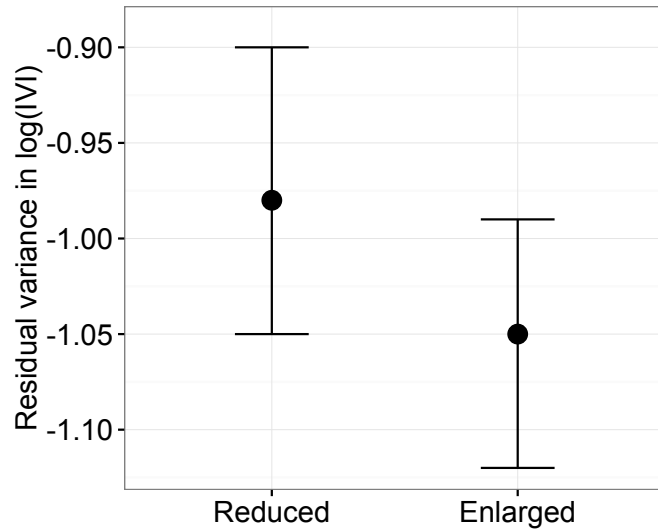


Figure 1. Summary of results from separate analyses of the impact of experimentally enlarged brood size on two aspects of parental provisioning behavior (IVI and load mass), average nestling begging at the previous visit (begging) and changes in parental body mass (mass change) across two consecutive 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.



753

754 **Figure 2.** Residual variances in log-transformed IVI for reduced and enlarged broods across both seasons

755 of the study. Estimates are retrieved from the double hierarchical generalized linear model described

756 under Table 1. Dots show mean values and whiskers indicate 95%CI on the estimate of the parameter.

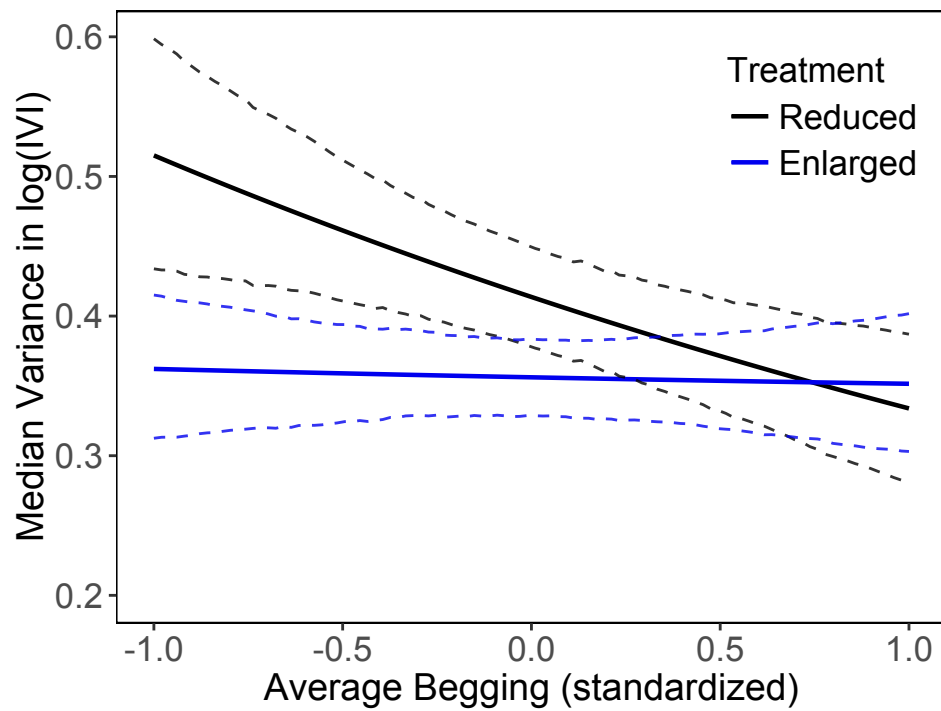


Figure 3. Effects of average begging intensity on residual variances in log-transformed IVI for reduced and enlarged broods. Thick lines indicate the posterior means, thin dashed lines indicate the 95% credible intervals.

759 **Table S1.** Effects on means in two different aspects of parental provisioning behavior in 1998 and 1999:
 760 inter-visit intervals (IVI) and load size in two brood size manipulation groups for females and males,
 761 respectively. Point estimates and their 95% credible intervals (CI) are retrieved from the full model
 762 described under Table 1 by retrieving and summing up the posterior samples from the respective
 763 estimates. Effects that were strongly supported by the model (95% CI not overlapping zero) are
 764 indicated in bold.

	Log(IVI)		Load size	
	Females	Males	Females	Males
	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)
Intercept ¹	2.05 (1.99, 2.12)	2.14 (2.08, 2.22)	-2.54 (-2.68, -2.39)	-2.62 (-2.76, -2.48)
BSM (I-R)	-0.08 (-0.15, 0.01)	-0.21 (-0.30, -0.13)	0.11 (-0.03, 0.25)	0.11 (-0.03, 0.25)
Log(IVI)	-	-	0.24 (0.18, 0.30)	0.24 (0.18, 0.30)
Nestling age	0.03 (-0.02, 0.08)	-0.04 (-0.10, 0.01)	0.04 (-0.05, 0.13)	0.04 (-0.05, 0.13)
Date	-0.04 (-0.06, -0.01)	0.00 (-0.02, 0.03)	-0.08 (-0.12, -0.04)	-0.05 (-0.09, -0.01)
Year(1999-1998)	-0.05 (-0.11, 0.01)	-0.05 (-0.11, 0.01)	-0.11 (-0.26, 0.04)	-0.11 (-0.26, 0.04)

765 ¹ Reference category is BSM 'reduced' and year '1998'

766

767 **Table S2.** Sources of variation in two different aspects of parental provisioning behavior in 1999: inter-
768 visit intervals (IVI) and load size in two brood size manipulation groups on (a) effects on the means, and
769 (b) effects on the residual variances. Estimates were derived from a Bayesian double hierarchical
770 generalized linear model with random intercepts for nest identity ($N = 13$) and individual ($N = 26$). BSM
771 (brood size manipulation, factor with 2 levels: reduced, increased), mean-centered brood age (days),
772 average nestling begging at t-1 (mean-centered within-individual), date (mean-centered), log-
773 transformed IVI (mean-centered within individual) and the interaction between BSM and begging were
774 fitted as fixed effects. Point estimates are given with their 95% credible intervals (CI). Effects that were
775 strongly supported by the model (95% CI not overlapping zero) are indicated in bold.

(a)	Log(IVI)	Load
<i>Means</i>	β (95% CI)	β (95% CI)
Intercept ¹	2.05 (1.94, 2.15)	-2.59 (-2.78, -2.39)
BSM(I-R)	-0.15 (-0.29, -0.02)	0.04 (-0.19, 0.28)
Log(IVI)	-	0.32 (0.24, 0.41)
Nestling age	-0.04 (-0.16, 0.09)	-0.01 (-0.21, 0.19)
Date	-0.05 (-0.08, -0.01)	-0.13 (-0.20, -0.06)
Sex (male-female)	0.03 (-0.07, 0.12)	-0.02 (-0.20, 0.16)
Begging t-1	-0.06 (-0.10, -0.01)	-0.10 (-0.28, 0.06)
Sex × date	0.05 (0.00, 0.09)	0.11 (0.02, 0.20)
Sex × nestling age	-	-
Sex × BSM	-	-
BSM × begging t-1	-	-
Sex × begging t-1	-	0.37 (0.12, 0.62)
	σ^2 (95% CI)	σ^2 (95% CI)
Individual	0.11 (0.07, 0.16)	0.21 (0.13, 0.30)
Box	0.06 (0.00, 0.13)	0.08 (0.00, 0.20)
(b)		
<i>Residual variances</i>	φ (95% CI)	φ (95% CI)
Intercept ¹	-0.88 (-0.97, -0.80)	-0.45 (-0.59, -0.31)
BSM(I-R)	-0.15 (-0.26, -0.04)	0.11 (-0.07, 0.29)
Log(IVI)	-	0.09 (-0.02, 0.19)
Nestling age	-0.06 (-0.16, 0.04)	0.00 (-0.14, 0.13)
Date	0.04 (0.02, 0.07)	0.02 (-0.02, 0.06)
Sex (male-female)	-0.01 (-0.07, 0.09)	0.05 (-0.04, 0.14)
Begging t-1	-0.22 (-0.35, -0.08)	-0.03 (-0.18, 0.13)
BSM × begging t-1	0.20 (0.02, 0.38)	-
	σ^2 (95% CI)	σ^2 (95% CI)
Individual	0.07 (0.03, 0.13)	0.05 (0.00, 0.12)
Box	0.04 (0.00, 0.11)	0.11(0.00, 0.21)
<i>N observations</i>	4291	2451

776 ¹ Reference category BSM 'reduced' and sex 'female'.

777 **Table S3.** Same model as in Table 1a but with average begging at t-2 and t-3 subsequently added to the
 778 mean part of the model (any interactions with BSM were not included). Adding begging t-2 to the
 779 variance part did not explain any additional variation on top of begging t-1 (results not shown).

(a)	Log(IVI)	Log(IVI)
<i>Means</i>	β (95% CI)	β (95% CI)
Intercept ¹	2.05 (1.95, 2.16)	2.04 (1.93, 2.15)
BSM(I-R)	-0.15 (-0.29, -0.03)	-0.15 (-0.29, -0.02)
Nestling age	0.03 (-0.16, 0.09)	0.04 (-0.16, 0.08)
Date	-0.04 (-0.08, -0.00)	-0.04 (-0.08, -0.00)
Begging t-1	-0.05 (-0.09, 0.00)	-0.05 (-0.10, 0.00)
Begging t-2	-0.07 (-0.12, -0.03)	-0.08 (-0.13, -0.03)
Begging t-3	-	-0.01 (-0.06, 0.04)
Sex (male-female)	0.03 (-0.07, 0.12)	0.03 (-0.07, 0.12)
Sex × date	0.04 (-0.00, 0.09)	0.05 (-0.00, 0.09)
	σ^2 (95% CI)	σ^2 (95% CI)
Individual	0.12 (0.07, 0.16)	0.12 (0.07, 0.16)
Box	0.06 (0.00, 0.13)	0.06 (0.00, 0.13)
(b)		
<i>Residual variances</i>	ϕ (95% CI)	ϕ (95% CI)
Intercept ¹	-0.89 (-0.97, -0.79)	-0.88 (-0.98, -0.78)
BSM(I-R)	-0.16 (-0.27, -0.05)	-0.15 (-0.27, -0.04)
Nestling age	-0.05 (-0.16, 0.05)	-0.06 (-0.17, 0.04)
Date	0.04 (0.02, 0.07)	0.04 (0.02, 0.07)
Begging t-1	-0.22 (-0.36, -0.08)	-0.23 (-0.37, -0.08)
Sex (male-female)	0.01 (-0.07, 0.09)	0.01 (-0.0780.09)
BSM × begging	0.22 (0.04, 0.40)	0.25 (0.06, 0.42)
	σ^2 (95% CI)	σ^2 (95% CI)
Individual	0.08 (0.03, 0.13)	0.08 (0.04, 0.14)
Box	0.05 (0.00, 0.12)	0.05 (0.00, 0.13)
<i>N observations</i>	4149	4010

780 ¹ Reference category is BSM 'reduced' and sex 'female'.

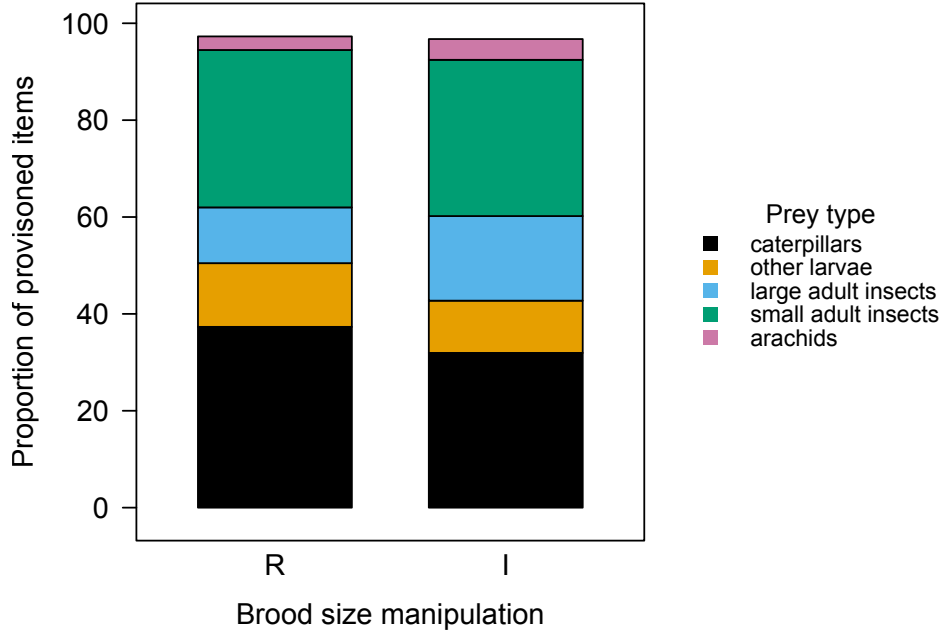


Figure S1. Proportion of different prey types delivered to nestlings in relation to brood size manipulation. R = Reduced, I = Enlarged. Caterpillars consist of small green winter moth larvae while other larvae prey items comprise other colored larvae and pupae. Large adult insects are mostly flies and midges and small insects contain ants, weevils, etc.

781

782