

Behavioral Ecology and Sociobiology

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

--Manuscript Draft--

Manuscript Number:					
Full Title:	Experimental changes in brood size alter several levels of phenotypic variance in offspring and parent pied flycatchers				
Article Type:	Original Article				
Corresponding Author:	David F Westneat University of Kentucky Lexington, Kentucky United States				
Corresponding Author Secondary Information:					
Corresponding Author's Institution:	University of Kentucky				
Corresponding Author's Secondary Institution:					
First Author:	David F Westneat				
First Author Secondary Information:					
Order of Authors:	David F Westneat Ariane Mutzel Simon Bonner Jonathan Wright				
Order of Authors Secondary Information:					
Funding Information:	<table border="1"> <tr> <td>Directorate for Biological Sciences (IOS1257718)</td> <td>Dr. David F Westneat</td> </tr> <tr> <td>Norwegian Research Council (223257)</td> <td>Dr. Jonathan Wright</td> </tr> </table>	Directorate for Biological Sciences (IOS1257718)	Dr. David F Westneat	Norwegian Research Council (223257)	Dr. Jonathan Wright
Directorate for Biological Sciences (IOS1257718)	Dr. David F Westneat				
Norwegian Research Council (223257)	Dr. Jonathan Wright				
Abstract:	<p>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 (<i>Ficedula hypoleuca</i>) 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 increased 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.</p>				
Suggested Reviewers:	<p>Ron Ydenberg ydenberg@sfu.ca First to extend variance sensitivity theory to parental care.</p>				

	<p>Toni Laaksonen toni.laaksonen@utu.fi Knowledgeable of behavioral ecology, pied flycatchers, and statistical models of variance</p>
	<p>Anne Charmantier anne.charmantier@cefe.cnrs.fr Knowledgeable of behavioral ecology, pied flycatchers, and mixed model analyses</p>
	<p>Ian R Cleasby I.R.Cleasby@exeter.ac.uk Has done behavioral ecology on birds, well-versed in statistical methods</p>
	<p>Ellen Ketterson ketterso@indiana.edu Expert in avian parental care</p>

[Click here to view linked References](#)

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

3

4

5 David F. Westneat¹, Ariane Mutzel¹, Simon Bonner^{2,3}, and Jonathan Wright⁴

6 ¹Department of Biology, 101 Morgan Building, University of Kentucky, Lexington, KY 40506-

7 0225

8 ²Department of Statistics, Multidisciplinary Science Building, University of Kentucky,

9 Lexington, KY 40506-0082

10 ³Department of Biology/Department of Statistical and Actuarial Sciences, Western University,

11 London, Ontario, Canada N6A 5B7.

12 ⁴Centre for Biodiversity Dynamics, Department of Biology, NTNU, N-7491 Trondheim,

13 Norway

14 **Abstract**

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

34

35

36 **Introduction**

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

57 These two bodies of theory usually explain variation in mean provisioning effort through
58 deterministic effects. For example, life history theory predicts that higher visit rates (i.e., shorter

59 inter-visit-intervals, or IVIs) should be associated with larger brood sizes (Royama 1966; Nur
60 1984; Wright and Cuthill 1990a; Wright and Cuthill 1990b). This arises because having more
61 offspring increases the benefits of provisioning, and so parents are predicted to shift time or
62 energy away from other activities, or take more risks, in favor of increasing food delivery rates to
63 the nest (Winkler 1987). Similarly, offspring that are hungry typically signal with greater than
64 average begging behavior, and usually parents respond quickly by increasing the mean delivery
65 of food (Kilner and Johnstone 1997; Budden and Wright 2001; Wright and Leonard 2002;
66 Smiseth et al. 2008), possibly via shorter inter-visit-intervals or larger loads, or both (Wright and
67 Cuthill 1990a; Wright and Cuthill 1990b; Wright 1998; Wright et al. 1998). Some evidence also
68 suggests that offspring begging behavior, perhaps combined with other cues, can affect parent
69 decision-making also on medium (Wright et al. 2010) or longer-term (Price et al. 1996; Wright et
70 al. 2002) time scales.

71 This array of deterministic factors generates variation in average provisioning behaviors,
72 potentially both among individuals within populations and within individuals depending on the
73 timing of changes in the underlying factors (e.g., Westneat et al. 2011). However, the expression
74 of parental behavior in any one event often deviates from these average values in the form of
75 residual variance driven by non-deterministic processes. For example, both the inter-visit-
76 interval and the amount of food carried back to be fed to offspring (the load size) varies from trip
77 to trip in part due to the unpredictable nature of encounters with different types of prey (e.g.,
78 Frey-Roos et al. 1995; Weimerskirch et al. 2005). Such unpredictable variance could produce
79 complex patterns in provisioning behavior within and among individuals (e.g., Westneat et al.
80 2013).

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

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

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

118 Here we report on patterns of variance in provisioning behavior in a woodland-dwelling
119 insectivorous bird, the pied flycatcher (*Ficedula hypoleuca*), with the goal of understanding how
120 changes in benefits of current reproduction may drive variance in phenotypes associated with
121 parenting. Our focal hypothesis was that parents with increased brood demand should seek out
122 more variable foraging options and so the delivery of food (load per unit of time) to the nest
123 would be more variable across trips. In secondary analyses, we also investigated patterns of
124 variance in nestling begging and change in parental body mass with the idea that these are linked
125 phenotypes and may provide a richer understanding of both deterministic and unpredictable
126 variance in provisioning behaviors. We studied the pied flycatcher because it is a small (12-14g)

127 migratory passerine common across Europe and western Asia (Lundberg and Alatalo 1992) that
128 typically nests in cavities and generally exhibits considerable provisioning of nestlings. Males
129 are territorial, most pairs are socially monogamous, and both parents typically help with the
130 provisioning of 5-7 nestlings, which are fed entirely on invertebrate prey. Previous studies have
131 shown that both parents respond to brood size manipulations by increasing visit rates to the nest
132 (Moreno et al. 1995; Sanz 1997; Wright et al. 2002). Experimental manipulations of nestling
133 begging also suggest that parents are sensitive to the magnitude of begging vocalizations
134 (Ottoosson et al. 1997).

135 **Methods**

136 Study species and site

137 Data on provisioning behavior was collected in 1998 and 1999 on a population of pied
138 flycatchers located in Abergwyngregyn National Nature Reserve, North Wales, UK
139 ($53^{\circ}13'16''N3^{\circ}59'59''W$). This reserve is a 169 hectare area of mixed deciduous and plantation
140 coniferous woodland in a steep sided valley with acidic soils. Pied flycatchers arrive at
141 Abergwyngregyn in mid-to-late April from west Africa, the first eggs of their single reproductive
142 attempt are laid at the end of April, and the first nestlings hatch by late May. As in other studies
143 (Lundberg and Alatalo 1992), levels of polygamy at Abergwyngregyn are estimated to be around
144 10%.

145 Experimental procedure

146 In each year, 100 nest boxes were available. Pairs that nested in these boxes were randomly
147 assigned to the two brood size treatment groups within hatch dates, with 21 nests being used in
148 1998 and 16 nests in 1999. At 2-3 days of age, nestlings were moved between nests in order to

149 create 18 experimentally ‘small’ broods (mean = 3.9 nestlings, range 3-4 nestlings) and 19
150 experimentally ‘large’ broods (mean = 8.2 nestlings, range 8-9 nestlings), each being roughly
151 two nestlings either side of the mean brood size and within the natural range for this population
152 (mean = 6.6, SE \pm 0.2, range 1-9). Seven broods (five in 1998 and two in 1999) were attended by
153 a single parents and so were excluded from analysis.

154 The manipulations were carried out using normal broods from first nesting attempts hatching
155 between 20th May and 7th June. Hatch dates did not differ significantly between years ($F_{1,26} =$
156 2.7, $P = 0.12$) or between manipulated brood sizes ($F_{1,26} = 0.11$, $P = 0.74$), with no significant
157 interaction ($F_{1,26} = 2.4$, $P = 0.14$). Natural broods tended to be larger in 1999 than in 1998 ($F_{1,26} =$
158 3.23, $P = 0.08$), but there was no bias by year and brood size treatment on natural brood size
159 ($F_{1,26} = 0.41$, $P = 0.51$). Nestlings added to enlarged broods were within 1 day of age and 30% of
160 body weight of their broodmates. Natural brood sizes did not differ between the two brood size
161 treatments ($F_{1,26} = 0.31$, $P = 0.57$). Thus, natural variation in the timing and quality of pairs or
162 nestlings was unlikely to have influenced comparisons between the two brood size groups.

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

167 Data collection

168 Data on experimental pairs were obtained using video cameras (Sony Hi8 CCD-TRIIIOOE)
169 mounted in specifically designed nest boxes. These larger video nest boxes replaced the smaller
170 normal nest boxes approximately 24 hours before filming to allow parents to become

171 accustomed to them. Each video nest box contained an electronic balance (either Mettler
172 SM3000 or PB3001, powered by a 12V car battery, and accurate to 0.1 g) positioned under the
173 nest. The camera was set up to video the nest at 45°, also capturing the inside of the entrance
174 hole and the balance display. Calculation of nest mass before, during and after visits thereby
175 allowed measurement of parental mass, as well as load mass delivered (for those parental visits
176 when faecal sacs were not also removed by parents). Additional variables measured included the
177 timing of arrivals and departures of individual parents, from which we computed inter-visit
178 intervals (IVI, the time between visits of a focal parent) and time spent in nest, as well as any
179 faecal sac removal. The latter affected which visits could be scored for load size, since if a parent
180 removed a faecal sac, the visit included both a weight gain (food brought) and weight lost (faecal
181 sac removed) and so could not be used to estimate load. In 1999, brood demand per visit was
182 also assessed via the visual assessment of each individual nestling's begging height in the nest
183 (where 0 = no begging, 0.5 = gaping with head up, and 1 = gaping with neck extension and body
184 raised).

185 For each nest, six video recordings were made lasting approximately 1.5hrs each. Recordings
186 started in the early afternoon of day one and finished at the same time on day two (approximate
187 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
188 mean age of nestlings during the period of taping was 9.1 days (range 7-12), and did not differ
189 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 $F_{1,23} = 0.48$, $P = 0.50$).

191 Statistical analyses

192 The core dataset we analyzed included information on parents of both sexes from 27 nest boxes,
193 but sample sizes were reduced slightly in some tests because data from specific parents was not

194 available. Data on begging was collected only in the 1999 season, so sample sizes regarding
195 brood demand were reduced to 13 nests.

196 The data set is composed of a hierarchically arranged set of repeated measures with the main
197 dependent variables measured on each visit by one of two subjects (the parents) attending one of
198 27 nest boxes across 2 years. Some independent variables varied among boxes (e.g., brood size
199 treatment, nestling age, and date), but most varied among visits (e.g., begging levels, behavior of
200 nestlings or parents on previous visits). Because we were interested in deterministic (mean)
201 effects and patterns in residual variation, we used a statistical approach called “double GLM”
202 (Smyth 1989; Lee and Nelder 2006; Ronnegard et al. 2010). These models extend the class of
203 generalized linear models by allowing the predictor variables to affect both the mean and
204 variance of the response variable. The models we have fit may be more appropriately called
205 double linear mixed effects models, because we modeled random effects at both the mean and
206 residual variance level. In all cases we assumed that the errors were independently distributed
207 normal random variables. The random effects were individual and box.

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

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

211 In this equation, x_{hijk} represents the value of the h^{th} fixed effect and β_h the corresponding
212 regression coefficient. The terms ϵ_i and ϵ_{ij} represent the random effects for box i and individual
213 j within box i respectively, and ϵ_{ijk} is the residual deviation. These three terms were assumed to
214 be independent and normally distributed random variables with mean 0 and standard deviations

215 σ_{ϵ}^{box} , σ_{ϵ}^{ind} , and $\sigma_{\epsilon,i,j,k}^{res}$ respectively. Further to this, our models allowed the standard deviation of
 216 residuals to vary between observations such that

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

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

223 We fit these models in the Bayesian statistical framework. Specifically, we used Markov chain
 224 Monte Carlo (MCMC) methods implemented in the JAGS software package (Plummer 2003) to
 225 obtain samples from the joint posterior distribution of all parameters and compute posterior
 226 summary statistics. Prior distributions were chosen to be non-informative. We assigned the
 227 regression parameters for the model of the mean, β_h , and variance, φ_h , non-informative normal
 228 priors with mean 0 and variance 100^2 . We assigned the variance parameters for both the mean
 229 model, $\sigma_{\epsilon}^{box^2}$, σ_{ϵ}^{ind} , and $\sigma_{\epsilon,ijk}^{res}$, and variance model, σ_{ϵ}^{box} , σ_{ϵ}^{ind} , and $\sigma_{\epsilon,ijk}^{res}$, half-t prior
 230 distributions with 5 degrees of freedom and scale factor 5. This represents a truncated and scaled
 231 version of the t -distribution which is restricted to the positive values and has a median value
 232 1.68, 75th percentile 6.70, and 95th percentile 12.82. We ran three chains in parallel and
 233 assessed convergence via the Brooks-Gelman-Rubin Potential Scale Reduction Factor (Brooks,
 234 1998). The procedure consisted of a wrapper program in R 3.2.4 (R Development Core Team
 235 2016) that set up the model structure and priors, and then interfaced with code in the JAGS

236 environment to conduct the MCMC simulations. The three Markov chains were run for a burn-in
237 period of 1000 iterations plus 10000 iterations with no thinning for computing parameter
238 estimates. Significance of the effects in the models was assessed by examining the range of the
239 95% credible intervals for the regression coefficients and whether or not these included 0.

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

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

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

$$261 \quad \log(\text{load}_{ijk}) = \beta_0 + \beta_1 \log(\text{IVI}_{ijk}) + \beta_2 x_{2,ijk} + \cdots + \beta_p x_{p,ijk} + \epsilon_{ijk}$$

262 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
 263 equivalent to

$$264 \quad \log(\text{delivery}_{ijk}) = \log\left(\frac{\text{load}_{ijk}}{\text{IVI}_{ijk}}\right)$$

$$265 \quad = \beta_0 + (\beta_1 - 1) \log(\text{IVI}_{ijk}) + \beta_2 x_{2,ijk} + \cdots + \beta_p x_{p,ijk} + \epsilon_{ijk}.$$

266 It follows that a change in any of x_2 through x_p while the other predictors are held constant has
 267 the same effect on the mean of both the $\log(\text{load})$ and $\log(\text{delivery})$, including the effect of the
 268 brood size manipulation. The effect of $\log(\text{IVI})$ itself differs by 1 depending on whether the
 269 response is $\log(\text{load})$ or $\log(\text{delivery})$. This change is simply a function of the difference between
 270 modeling the provisioning per trip (i.e., load) versus the rate of provisioning per trip (i.e.,
 271 delivery). Hence we will refer to all effects in the model of $\log(\text{load})$ except for the effect of
 272 $\log(\text{IVI})$ as effects on delivery. Similarly, in the equation for the variance of the residual errors as
 273 a function of covariates, e.g.

$$274 \quad \log(\sigma_{ijk}^2) = \phi_0 + \phi_1 x_{1,ijk} + \cdots + \phi_p x_{p,ijk}$$

275 the coefficients ϕ_1 through ϕ_p can be interpreted as effects on either the variance of $\log(\text{load})$ or
 276 the variance of $\log(\text{delivery})$ while the remaining predictors remain fixed.

277 The second interpretation of note is that if the response is modeled on the log scale, as we have
278 done with both load and IVI, then the variance on the natural scale will depend on the coefficient
279 from both the mean and variance portions of the model. Suppose, for example, that we have a
280 single predictor x used to model both the mean and variance of $\log(y)$ such that $\log(y_i) = \beta_0 +$
281 $\beta_1 x_i + \epsilon_i$ and $\log(\sigma_i^2) = \phi_0 + \phi_1 x_i$. We can interpret ϕ_1 to mean that the variance of
282 $\log(y)$ increases by ϕ_1 when x_1 increases by one unit. However, the variance of y on the natural
283 scale is

$$284 \quad \text{Var}(y) = (e^{\phi_0 + \phi_1 x} - 1)e^{(\phi_0 + 2\beta_0) + (\phi_1 + 2\beta_1)x}.$$

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

289 In our secondary analyses we modeled nestling begging intensity and parental mass changes. The
290 models of begging included log-transformed inter-feed interval (IFI; defined as time between
291 feedings by either parent; mean-centered within nest identity), brood size manipulation and
292 nestling age as fixed effects and nest identity as a random effect. Because begging was assessed
293 as an average intensity over all nestlings in a brood, we added a weighting variable to the
294 analysis to control for the necessary relationship of variance in mean values with changes in
295 brood size. To analyze changes in parental body mass we initially fitted models including the
296 fixed effects of brood size manipulation, individual mean-centered $\log(\text{IVI})$, parental sex, year,
297 nestling age and date and the respective 2-way interactions between sex and year with $\log(\text{IVI})$
298 and brood size manipulation treatment.

299 **Results**

300 Effects on mean parental behavior

301 We assessed the impact of the brood manipulation and any covariates on both the mean and
302 variance in the two main parental response variables, log(IVI) and log (load mass) per trip. We
303 first investigated the relationships between the two response variables. Mean load mass increased
304 with log(IVI), with this effect being stronger in 1999 (1998: $\beta = 0.06$, 95% CI: 0.02, 0.10; 1999:
305 $\beta = 0.14$, 95%CI: 0.11, 0.18; difference between 1998 and 1999: $\beta = 0.08$, 95% CI: 0.03, 0.13).
306 Residual variation in load mass also increased with log(IVI) ($\varphi = 0.04$, 95% CI: 0.01, 0.07). In
307 addition, we found that load masses were generally smaller in 1999 compared to 1998
308 (difference between 1999 and 1998: $\beta = -0.45$, 95% CI: -0.73, -0.17). For these reasons, we
309 included log(IVI) in all models of log(load mass), and we interpret all other effects in these
310 models as effects on delivery.

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

319 We included in our analyses of log(IVI) and log(load mass) the covariates of nestling age, date in
320 season and year. We found some evidence for an effect of nestling age on parental log(IVI) that

321 differed across sexes. Nestling age negatively affected male, but not female IVI, with males with
322 older broods tending to make shorter trips ($\beta = -0.04$, 95% CI: -0.09, 0.01; Table 1a, Table S1)
323 and therefore likely provisioning at higher rates. In contrast, there was no evidence for an effect
324 of nestling age on male or female delivery (Table 1a). In females, date negatively affected IVI,
325 with females recorded later in the season taking less time per trip, but delivering less food per
326 unit of time (Table 1a). In males, there was no effect of date on IVI ($\beta = 0.00$, 95% CI: -0.02,
327 0.03, Table S1), but males of later broods also delivered less food ($\beta = -0.05$, 95% CI: -0.09, -
328 0.01, Table S1). Yet, this decrease in food delivery later in the season was less pronounced
329 compared to females (Table 1a, Table S1).

330 We assessed the potential impact of nestling begging intensity and its interaction with the brood
331 manipulation using the data from 1999, the only year when begging intensity was also measured.
332 In both sexes, we found support for a negative effect of the average begging parents experienced
333 during their previous (t-1) visit to the nest on IVI (summarized in Table 2, full model results in
334 Table S2; Fig. 1a). Begging levels at visit t-2 also negatively affected IVI, and the effect of t-1 is
335 reduced slightly and the credible interval reached 0 (Table 2, Table S3). Begging at t-3 did not
336 predict IVI nor did it alter the effects of begging at t-1 and t-2 compared to the model when t-3
337 was not included (Table 2, Table S3). The effect of begging during the previous visit did not
338 differ between brood size manipulation groups (interaction BSM \times begging t-1: $\beta = 0.04$, 95%
339 CI: -0.06, 0.13); all parents decreased their IVIs at the same rate with increasing nestling begging
340 intensity. In females, there was no evidence for an effect of nestling begging on delivery,
341 whereas there was a positive effect of begging at visit t-1 on delivery in males ($\beta = 0.28$, 95% CI:
342 0.09, 0.46) (Table 2; Table S2; Fig. 1a). This resulted in males, but not females, having higher

343 delivery in response to increases in nestling begging at t-1. There was no additional effect of
344 begging at visit t-2 on delivery (Table 2, Table S3).

345 Patterns in residual variance in parental behavior

346 Our main goal in analyzing this dataset was to assess predictions from variance sensitivity theory
347 as applied to parental behavior. If increased offspring demand due to the manipulation of brood
348 size indicates to parents that the average delivery of food is not sufficient for their needs, then
349 theory predicts they should shift to a more variable patch and this would affect the realized
350 variance in delivery. Contrary to these predictions, we found no evidence that variance in
351 delivery was influenced by the brood size manipulation (Table 1b, Fig. 1b) and strong evidence
352 for lower residual variance in parental IVIs in enlarged compared to reduced broods (Table 1b,
353 Fig. 1b, 2). Older nestlings might demand more than younger nestlings, but we found no support
354 for residual variance in IVI or delivery differing for parents feeding older compared to younger
355 nestlings (Table 1b). There was some evidence for residual variance in delivery being higher in
356 males compared to females, but residual variance in IVI did not differ between the sexes (Table
357 1b).

358 The main cue parents are expected to use to assess the condition of their nestlings is the intensity
359 of their begging. We assessed the potential impact of nestling begging intensity and its
360 interaction with the brood manipulation using the data from 1999, the year when begging
361 intensity was measured. Contrary to predictions, residual variance in IVIs decreased with
362 increased begging in reduced ($\varphi = -0.22$, 95% CI: -0.35, -0.08), but not in enlarged broods ($\varphi =$
363 0.02, 95% CI: -0.13, 0.10; difference: $\varphi = -0.20$, 95% CI: -0.38, -0.02; Table S2, Fig. 1b; Fig. 3).
364 We did not detect any effects of begging on residual variance in delivery ($\varphi = -0.03$, 95% CI: -
365 0.18, 0.13; Table S2; Fig. 1b).

366 Effects on nestling begging

367 *Mean effects on nestling begging*

368 We also explored the factors that affected nestling begging behavior. Mean nestling begging
369 intensity during different parental visits to the same brood was strongly affected by the time
370 between feedings (by either parent), called the “inter-feed interval” or IFI. Mean begging became
371 more intense when the IFI was longer (Table 3a). There were no additional effects of the IFIs of
372 even earlier visits over and above the strong effects of the most recent IFI (e.g. t-1: $\beta = 0.01$,
373 95% CI: -0.01, 0.02).

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

378 *Patterns in residual variance in begging*

379 We also modeled the residual variance in mean begging intensity (i.e. within broods over
380 repeated trips) and we used brood size as a weighting variable to control for effects of sample
381 sizes on variance in averages. We found that mean begging intensity decreased with increasing
382 parental IFIs (Table 3b). Parental IFIs of previous visits did not affect residual variances in
383 average nestling begging over and above effects of IFIs of the present visit (e.g. t-1: $\varphi = -0.03$,
384 95% CI: -0.08, 0.02). Residual variances in average begging intensity were higher in
385 experimentally enlarged compared to reduced broods (Table 3b).

386 Parental body mass changes

387 *Mean effects on parental body mass*

388 Life history theory predicts mean effects on parental condition of increased work associated with
389 provisioning. We analyzed absolute mass as a repeatedly measured trait on those visits when it
390 could be measured, but the models failed to converge. Instead, we analyzed two other mass-
391 related variables. First, we explored possible influences on mean mass of the parent during the
392 parental care observation. We found no support for the idea that parents feeding enlarged broods
393 differed in body mass compared to parents feeding reduced broods ($\beta = -0.09$, 95% CI: -0.39,
394 0.19).

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

399 *Patterns in residual variance in parental body mass*

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

408 1998: $\varphi = 0.13$, 95% CI: 0.04, 0.22; Table 4). In contrast, there was no such effect of log(IVI) in
409 males in either year (1998: $\varphi = 0.03$, 95% CI: -0.06, 0.12; 1999: $\varphi = -0.09$, 95% CI: -0.19, 0.01;
410 Fig. 1b).

411 **Discussion**

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

421 Variance sensitivity theory (Caraco 1980; Stephens 1981) as applied to parental care (Ydenberg
422 1994; Ydenberg 2007) predicts that residual variance in provisioning should increase with a
423 sufficient increase in nestling demand, which itself would be driven by the experimental
424 manipulation of brood size. We thus expected that when faced with increased demand, parent
425 pied flycatchers might shift to foraging in patches of habitat or microhabitat that had either more
426 variable encounter rates with prey or more variable loads sizes due to differences in the prey
427 types encountered. Such shifts should produce an increase in the residual variation in IVI and/or
428 load size. Our analyses support the implicit assumption that the brood manipulation increased
429 demand on parents. Offspring in enlarged broods begged more intensely (Fig. 1a). Both this
430 increased begging within nests and the brood manipulation across nests led to a decrease in

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

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

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

454 common terns in a poorer year. The pied flycatchers in our population appeared to have
455 experienced very good conditions in both years of our study. Although nestling survival to 12
456 days old for the whole population was lower in 1999 compared to 1998, it was high overall
457 (1998 = 87% \pm 4%; 1999 = 70% \pm 7%) and there was no effect of the brood size manipulation on
458 nestling survival or fledging dates across all 55 manipulated nests (i.e. parental provisioning was
459 not monitored in the additional 18 nests) (all p-values>0.3). In agreement with this, nestling body
460 mass at 12 days was only slightly lower in enlarged broods overall ($F_{1,54}=6.2$; $P=0.017$), with
461 almost all of this differences being due to just the smallest nestlings being lighter in the enlarged
462 broods – i.e. most nestlings in enlarged broods were of comparable pre-fledging mass to those in
463 reduced brood sizes. This information leads us to the conclusion that parents in this system had
464 more than enough food available to them and had no problems almost fully compensating for the
465 experimental differences in brood size we imposed upon them. Although we enlarged brood
466 sizes to at or near the maximum observed brood size for this population, because of large
467 amounts of natural food available to parents, the enlargement may not have been sufficient to
468 place our subjects in the accelerating part of the fitness-delivery utility curve. Thus our subjects
469 may not have been sufficiently stressed to produce adaptive variance-prone parental
470 provisioning.

471 An inadequate manipulation cannot explain why parents of enlarged broods significantly reduced
472 the variance in IVI. Two potential effects of the increased brood demand on mean parental
473 behavior might have trickle-down effects on the residual variance (Mathot et al. submitted).
474 First, parents of enlarged broods may have shifted how they allocated their time. Life history
475 theory predicts that increased demand may indicate increased benefits of care (Drent and Daan
476 1980; Nur 1984), thereby favoring shifts of parental effort away from other activities and

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

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

500 away from non-provisioning behaviors, as opposed to any shift in prey preferences or variance-
501 aversion *per se*.

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

521 We also found that enlarged broods had more residual variance in begging intensity per nestling
522 than small broods. Most studies seem to indicate that begging reflects hunger (e.g., Leonard and

523 Horn 2006). If so, one possibility is that residual variance in begging is affected by the opposing
524 effects of increased hunger in larger broods but more frequent and less variable visits by parents.
525 This could produce sequences of visits in which more of the nestlings had recently been fed and
526 so were begging less compared to sequences in which all nestlings were hungrier and so begging
527 was greater. In smaller broods, despite more variable trip times by individual parents, individual
528 nestlings may have been fed more often and more regularly, leading to lower variance in begging
529 intensity.

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

542 Intriguingly, these same three processes (i. foraging effort reducing mass, ii. foraging for self
543 thereby increasing mass, and iii. excretion causing sudden but infrequent drops in mass), should
544 act to increase the residual variance in parental mass change with IVI. Our models produce a
545 mixed result. IVI had no effect on residual variance in males, but a significant positive effect in

546 females (Fig. 1b), and this effect differed between the two years. A sex difference in the variance
547 in mass change from trip to trip with respect to the length of the trip implies a different mix of
548 the three processes in males and females or some additional processes unique to one sex. One
549 possibility is that mass change is also linked with load size. Males tended to have higher residual
550 variance in these two variables than did females, so perhaps males were behaving in ways that
551 kept their mass constant and allowed other elements of provisioning behavior to vary, whereas
552 females were holding provisioning more constant and allowing their own mass to vary more,
553 which may mean they were also more sensitive to variation between years. Why the sexes would
554 differ in that way is not clear, but it might reflect slightly different roles, with males continuing
555 to attend to territory boundaries or interacting with neighbors during at least some trips away
556 from the nest may contribute indirectly to these sex-specific patterns (see Markman et al. 1995).
557 Our results cannot provide an answer, but suggest that more attention to sex-specific processes
558 away from the nest may influence in subtle ways the provision of care in biparental species (e.g.,
559 Markman et al. 2004).

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

569 the residual variance of both begging and parental mass changes. These more exploratory
570 analyses stimulate some new ideas and reaffirm the value of thoroughly exploring pattern in
571 repeatedly expressed traits such as provisioning behavior.

572

573 **Acknowledgements**

574 We would like to thank Duncan Brown and (the then) CCW for access to Abergwyngregyn
575 NNR, as well as Gabrielle Archard, Christian Both, Matt Davey, Kim Denny, Ioan Fazey,
576 Camilla Hinde, Adam Morrey, Roberta Spears, Jane Stott, Richard Yarnell and Yoram and
577 Shlomith Yom-Tov for assistance in the field. Christian Both, Camilla Hinde, and Kim Mathot
578 provided comments on earlier versions of the manuscript. During data analysis and preparation
579 of the manuscript, DFW, AM, and SB were supported by NSF grant IOS1257718, and JW was
580 partly supported by the Research Council of Norway through its Centres of Excellence funding
581 scheme, project number 223257.

582

583 **References**

584 Budden AE, Wright J (2001) Begging in nestling birds. In: Val Nolan J, Thompson CF (eds)

585 Current Ornithology Vol 16. Springer US, New York, NY, pp 83-118

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

587 Clutton-Brock TH (1991) *The Evolution of Parental Care*. Princeton University Press, Princeton,

588 New Jersey

589 Drent RH, Daan S (1980) The prudent parent - energetic adjustments in avian breeding. *Ardea*

590 68:225-252

591 Frey-Roos F, Brodmann PA, Reyer HU (1995) Relationships between food resources, foraging
592 patterns, and reproductive success in the water pipit, *Anthus sp. spinoletta*. Behav Ecol
593 6:287-295

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

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

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

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

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

604 Lee Y, Nelder JA (2006) Double hierarchical generalized linear models. Journal of the Royal
605 Statistical Society C-Applied Statistics 55:139-167

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

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

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

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

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

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

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

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

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

624 Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell
625 RD, Stairs RD (eds) *Analysis of Ecological Systems*. Ohio State University Press,
626 Columbus, OH, pp 154-177

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

629 Plummer M (2003) JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs
630 Sampling. In: *Proceedings of the 3rd International Workshop on Distributed Statistical*
631 *Computing (DSC 2003)*, Vienna, Austria

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

634 R Development Core Team (2016) *R: A Language and Environment for Statistical Computing*. R
635 Foundation for Statistical Computing, Vienna

636 Real LA, Ellner S (1992) Life-history evolution in stochastic environments - a graphical mean-
637 variance approach. *Ecology* 73:1227-1236

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

639 Ronnegard L, Shen X, Alam M (2010) hglm: A package for fitting hierarchical generalized linear
640 models. *R Journal* 2:20-28

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

643 Royle NJ, Smiseth PT, Kölliker M (2012) The Evolution of Parental Care. Oxford University
644 Press, Oxford

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

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

649 Smyth GK (1989) Generalized linear models with varying dispersion. *J R Stat Soc Ser B-*
650 *Methodol* 51:47-60

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

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

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

655 Stephens DW, Charnov EL (1982) Optimal foraging - some simple stochastic models. *Behav*
656 *Ecol Sociobiol* 10:251-263

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

658 Trivers RL (1972) Parental investment and sexual selection. In: Campell B (ed) Sexual Selection
659 and the Descent of Man, 1871-1971. Aldine-Atherton, Chicago, pp 136-179

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

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

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

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

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

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

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

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

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

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

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

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

684 Wright J, Leonard ML (2002) The Evolution of Begging: Competition, Cooperation and
685 Communication. Kluwer Academic, Dordrecht

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

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

690 Ydenberg RC (2007) Provisioning. In: Foraging. University of Chicago Press, Chicago, IL, pp
691 273-303

692

693 **Table 1.** Sources of variation in two different aspects of parental provisioning behavior in 1998 and
694 1999: inter-visit intervals (IVI) and load mass in two brood size manipulation groups. Because log(IVI) is
695 included in the log(load mass) analysis, all other effects are interpreted as effects on delivery (food per
696 unit of time). Estimates were derived from a Bayesian double GLM with random intercepts for nest
697 identity ($N = 27$) and individual ($N = 54$). BSM (brood size manipulation, factor with 2 levels: reduced (R),
698 enlarged (E)), mean-centered brood age (days), date (mean-centered), year (factor with 2 levels: 1998,
699 1999), and log-transformed IVI (centered within individuals) were fitted as fixed effects. Point estimates
700 are given with their 95% credible intervals (CI). Effects that were strongly supported by the model (95%
701 CI not overlapping zero) are indicated in bold. Effects on (a) means and (b) on the residual variance.

(a)	Log(IVI)	Log(Load mass)
<i>Means</i>	β (95% CI)	β (95% CI)
Intercept ¹	2.05 (1.99, 2.12)	-2.54 (-2.68, -2.39)
BSM (E-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(E-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 observations</i>	8740	4693

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

703

704 **Table 2.** Effects of begging in previous visits on parental IVI and load mass. Estimates were derived from
705 double GLMs including the same fixed and random effects as described for Table 1 with model 1
706 additionally including begging at t-1, model 2 including begging at t-1 and t-2, and model 3 begging at t-
707 1, t-2 and t-3. The effects of begging on load differed across sexes and are therefore given separately for
708 male and females. Effects that were strongly supported by the model (95% CI not overlapping zero) are
709 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 mass			
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)	-

710

711 **Table 3.** Sources of variation in average nestling begging intensity in two brood size manipulation
712 groups. Estimates were derived from a Bayesian double GLM with random intercepts for nest identity (N
713 = 13). BSM (brood size manipulation factor with 2 levels: reduced, enlarged), mean-centered brood age
714 (days), and log-transformed inter-feed interval (IFI, mean-centered within nest) were fitted as fixed
715 effects. Point estimates are given with their 95% credible intervals (CI). Effects that were strongly
716 supported by the model (95% CI not overlapping zero) are indicated in bold. Effects on (a) means and (b)
717 on the residual variance.

(a)	
<i>Means</i>	β (95% CI)
Intercept ¹	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	0.16 (0.00, 0.68)
(b)	
<i>Residual variances</i>	φ (95% CI)
Intercept ¹	-0.56 (-0.72, -0.40)
BSM(E-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

718 ¹ Reference category is BSM 'reduced'

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

	Mean	Residual variance
<i>Fixed effects</i>	β (95% CI)	φ (95% CI)
Intercept ¹	0.00 (-0.01, 0.01)	-2.00 (-2.25, -1.73)
BSM(E-R)	0.00 (-0.01, 0.01)	0.01 (-0.27, 0.28)
Log(IVI) ²	-0.03 (-0.04, -0.01)	0.25 (0.15, 0.35)
Sex (male-female)	0.00 (-0.01, 0.01)	0.04 (-0.18, 0.28)
Year (1999-1998)	0.01 (0.00, 0.02)	0.64 (0.37, 0.90)
Log(IVI) × year	-	-0.12 (-0.23, -0.01)
Log(IVI) × sex	-	-0.22 (-0.33, -0.11)
<i>Random effects</i>	σ^2 (95% CI)	σ^2 (95% CI)
Individual	0.00 (0.00, 0.01)	0.42 (0.33, 0.52)
Box	0.00 (0.00, 0.01)	0.12 (0.00, 0.28)

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

726 ²Reference category for residual variance part is sex 'female' and year '1998'

727

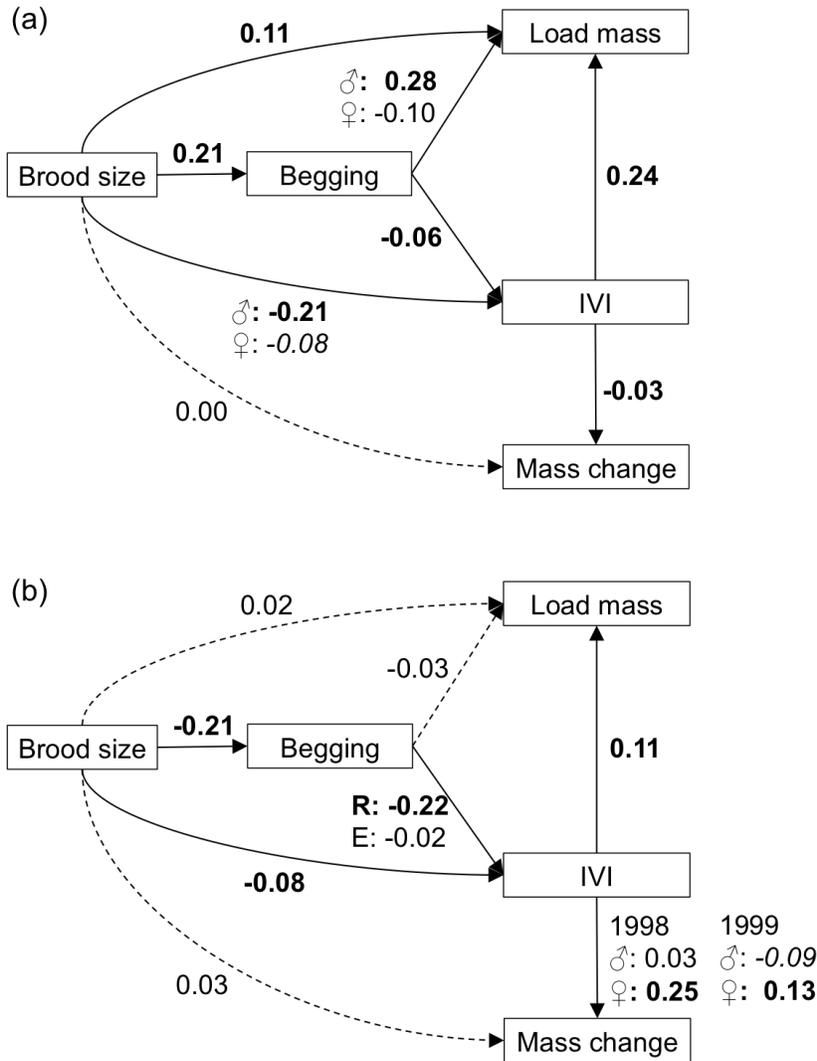
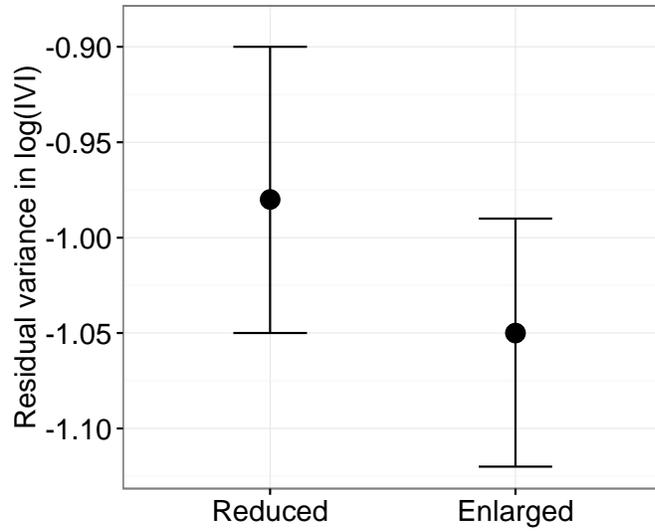


Figure 1. Summary of results from separate analyses of the impact of experimentally enlarged brood size on two aspects of parental provisioning behavior (IVI and load mass), average nestling begging at the previous visit (begging) and changes in parental body mass (mass change) across two consecutive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



729

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

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

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

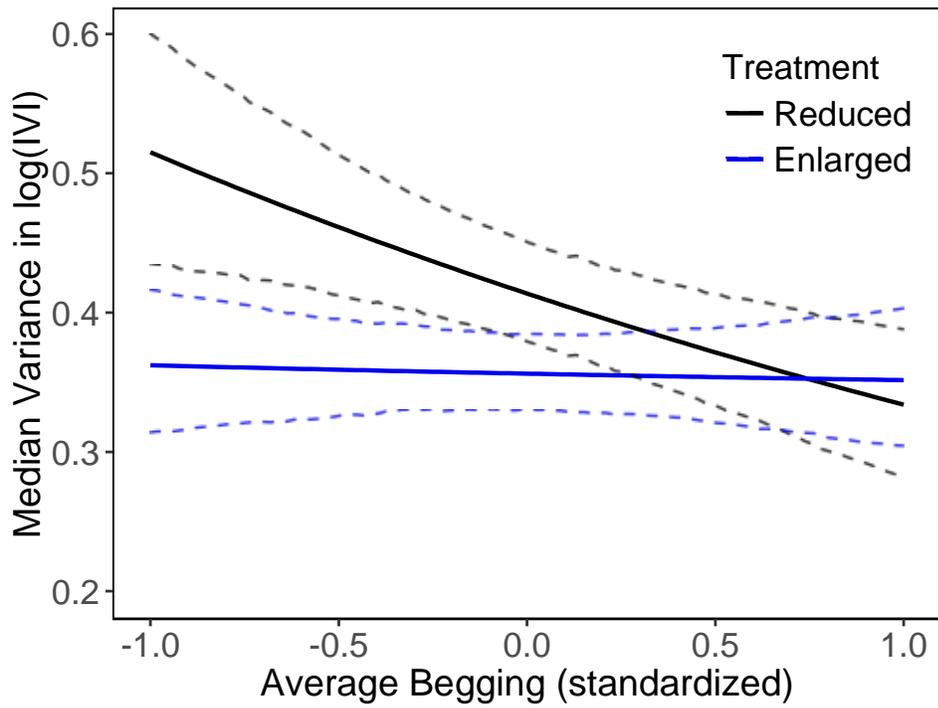


Figure 3. Effects of average begging intensity on residual variances in log-transformed IVI for reduced and enlarged broods. Thick lines indicate the posterior means, thin dashed lines indicate the 95% credible intervals.

734 Supplementary Material

735 **Table S1.** Effects on means in two different aspects of parental provisioning behavior in 1998 and 1999:
 736 inter-visit intervals, log(IVI), and log(load mass) (delivery with log(IVI) in model) in two brood size
 737 manipulation groups for females and males, respectively. Point estimates and their 95% credible
 738 intervals (CI) are retrieved from the full model described under Table 1 by retrieving and summing up
 739 the posterior samples from the respective estimates. Effects that were strongly supported by the model
 740 (95% CI not overlapping zero) are indicated in bold.

	Log(IVI)		Load mass	
	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 (E-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)

741 ¹ Reference category is BSM 'reduced' and year '1998'
 742

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

(a)	Log(IVI)	Log(Load mass)
<i>Means</i>	β (95% CI)	β (95% CI)
Intercept ¹	2.05 (1.94, 2.15)	-2.59 (-2.78, -2.39)
BSM(E-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(E-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</i> observations	4291	2451

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

753 **Table S3.** Same model as in Table 1a but with average begging at t-2 and t-3 subsequently added to the
754 mean part of the model (any interactions with BSM were not included). Adding begging t-2 to the
755 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(E-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(E-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

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

757

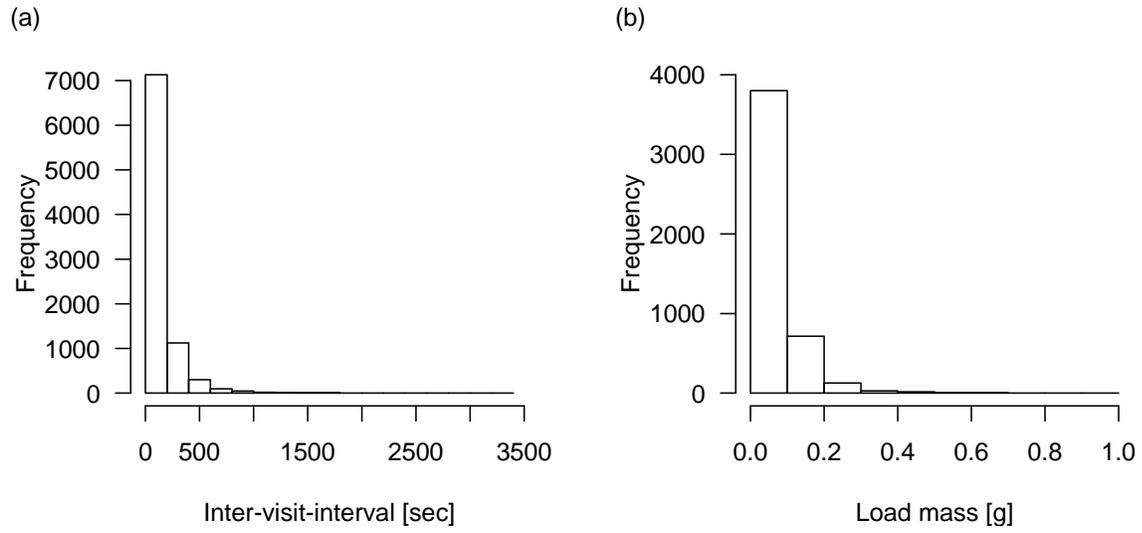


Figure 1. Distributions of natural scale measures of (a) inter-visit-interval and (b) load mass

758

759

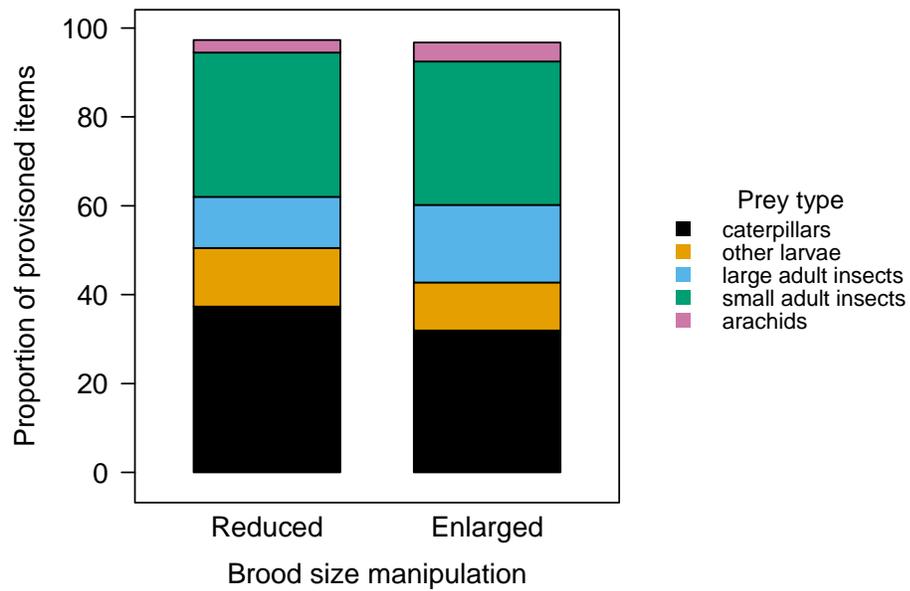


Figure S2. Proportion of different prey types delivered to nestlings in relation to brood size manipulation. Caterpillars consist of small green winter moth larvae while other larvae prey items comprise other colored larvae and pupae. Large adult insects are mostly flies and midges and small insects contain ants, weevils, etc.