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Provisioning tactics of great tits (*Parus major*) in response to long-term brood size manipulations differ across years

Kimberley J. Mathot[1,2*], Anne-Lise Olsen[3], Ariane Mutzel[1,2,4], Yimen G. Araya-Ajoy[1†], Marion Nicolaus[1,2‡], David F. Westneat[4], Jonathan Wright[3], Bart Kempenaers[2] and Niels J. Dingemanse[1,5]

[1]Research Group Evolutionary Ecology, Max Planck Institute for Ornithology, 82319 Seewiesen, Germany

[2]Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, 82319 Seewiesen, Germany

[3]Center for Biodiversity Dynamics (CBD), Department of Biology, Norwegian University of Science and Technology (NTNU), N-7491 Trondheim, Norway

[4]Department of Biology and Center for Ecology, Evolution, and Behavior, University of Kentucky, Lexington, Kentucky 40506-0225, USA

[5]Behavioural Ecology, Department of Biology, Ludwig-Maximilians University of Munich (LMU), Planegg-Martinsried, Germany

[†]Current address: Center for Biodiversity Dynamics (CBD), Department of Biology, Norwegian University of Science and Technology (NTNU), N-7491 Trondheim, Norway

[‡]Current address: Rijksuniversiteit Groningen, Conservation Ecology Group, Groningen Institute for Evolutionary Sciences, Groningen, NL

*Author for correspondence: mathot@ualberta.ca
Current address: Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

Authorship statement

KJM, AM, A-LO, MN, JW, BK, and ND designed the experiment. KJM, AM, A-LO, MN, YAA, and ND performed the field work. AM and ALO coordinated the video analyses and compiled the database. KJM, YAA and NJD performed the statistical analyses with input from all coauthors. KJM and DFW wrote the manuscript. All coauthors contributed to revisions.

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Data accessibility

All data used in the analyses presented in this paper will be deposited on Dryad upon publication of the paper.

Lay summary: Parents adjust their provisioning behaviour in response to offspring demand, but the way they do this depends on ecological conditions. Parent great tits (*Parus major*) responded to experimentally increased brood demand by working harder and decreasing prey selectivity in a year with favourable ecological conditions. In a more challenging year, parents did not meet increased offspring demand by shifts in average behaviour, and instead exhibited shifts in the variance in their behaviour.

Title: Provisioning tactics of great tits (*Parus major*) in response to long-term brood size manipulations differ across years

Abstract: Parents provisioning their offspring can adopt different tactics to meet increases in offspring demand. In this study, we experimentally manipulated brood demand in free living great tits (*Parus major*) via brood size manipulations and compared the tactics adopted by parents in two successive years (2010 and 2011) with very different ecological conditions. In 2011, temperatures were warmer, there were fewer days with precipitation, and caterpillars (the preferred prey of great tits) made up a significantly larger proportion of the diet. In this 'good' year, parents responded to experimental increases in brood demand by decreasing mean inter-visit intervals (IVIs) and reducing prey selectivity, which produced equal average long-term delivery of food to nestlings across the brood size treatments. In 2010, there was no evidence for effects of brood size manipulations on mean IVIs or prey selectivity. Consequently, nestlings from enlarged broods experienced significantly lower long-term average delivery rates compared with nestlings from reduced broods. In this 'bad' year, parents also exhibited changes in the variance in inter-visit intervals (IVIs) as a function of treatment that were consistent with variance-sensitive foraging theory: variance in IVIs tended to be lowest for reduced broods and highest for enlarged broods. Importantly, this pattern differed significantly from that observed in the ‘good’ year. We therefore found some support for variance-sensitive provisioning in the year with more challenging ecological conditions. Taken together, our results show that variation in brood demand can result in markedly different parental foraging tactics depending on ecological conditions.

Keywords: brood demand, brood size manipulation, heterogeneous residual variance, *Parus major*, provisioning behaviour, variance-sensitivity, risk-sensitivity

Introduction

In many organisms, parents care for offspring and they adjust this care in response to cues that reflect the benefits and/or the costs of parental care (e.g. Clutton-Brock, 1991; Leonard and Horn, 1998; Nakagawa and Schielzeth, 2017; Royle et al., 2012; Westneat et al., 2011; Williams, 1966; Winkler, 1987; Wright et al., 1998; Wright and Leonard, 2010). In birds, parents provisioning young in the nest can employ a variety of tactics to cope with increases in brood demand (Wright et al., 1998; Ydenberg, 2008). Parents can increase the time and/or energy allocated to the current brood at the cost of their own expected future fitness (Moreno et al., 1995; Ydenberg, 2008). For example, they might switch from a net energy maximization (i.e. the difference between energy provisioned to young and energy expended by the parent) to a gross energy maximization (i.e. total energy provisioned to young, ignoring costs associated with provisioning effort) (Lifjeld, 1989). The decision to increase provisioning can show different forms, because parents can reduce the time allocated to other activities (e.g. nest defense, Markman et al., 1995; self-feeding, Martins and Wright, 1993) and in this way they can increase their provisioning rate and/or they can bring larger or higher quality items per delivery (e.g. Wright, 1998) (Figure 1a).

Parents may also shift the relative nutritional quality versus energetic quantity of food provided. Prey items that provide the best energetic returns may not be the same as those containing the optimal combination of nutritional compounds for offspring growth (see Wright et al., 1998 and references therein). If so, parents working to meet increased brood demand may reduce prey selectivity, and increase the rate of energy delivery to the nest at a cost of reduced nutritional value via increased frequency of visits to the nest and/or increased energy delivered per visit (Figure 1b).

Though less commonly appreciated, parents can also adopt strategic shifts in their use of provisioning options that are associated with higher variance in prey delivery (i.e. variance-sensitivity, a.k.a. risk-sensitivity) as a way of mitigating increased brood demand (Westneat et al., 2013; Ydenberg, 1994, 2008). Variance in prey delivery generates an important selective force when it causes deviations in energy delivery above and below the expected mean delivery, because these deviations can have asymmetrical effects on offspring fitness (Figure 2). When offspring are in a low energy state or on a negative energy budget, they likely experience a convex (accelerating) utility function (left side in Figure 2). If so, they will benefit disproportionately when variance in intake is increased because of the disproportionate impact of higher than expected delivery on fitness (i.e., mean fitness is higher than the fitness of the mean intake). Parents would thus maximize their expected fitness return by preferring foraging options that increase variance in return. In contrast, when offspring are in a high energy state or on a positive energy budget, they likely experience diminishing returns with a concave (decelerating) utility function (right side in Figure 2). They then will benefit disproportionately from reduced variance in intake (i.e., fitness from the mean intake is higher than the mean fitness from the distribution of intakes). Parents are said to be “variance sensitive” if they use variance as a cue when making provisioning decisions (Ydenberg, 2008). Optimality theory predicts that parental variance-sensitivity will be adaptive, because changes in variance in energy delivery according to the state of the offspring increase offspring fitness. When faced with offspring that are experiencing a convex utility function (e.g. offspring in poor condition), parents should be "variance-prone" and seek foraging options that are more variable and variance in delivery should increase. Conversely, when faced with offspring experiencing a concave utility function (e.g. offspring in good condition), parents should be "variance-averse" and seek less variable foraging options, and variance in delivery to the nest should decrease (Figure 1c).

Shifts in variance in energy delivery to offspring could come about in several ways that depend upon the underlying prey distributions (i.e., variance in encounter rates with particular prey types) (Sutherland and Anderson, 1987). For example, foragers can alter the variance in energy gain by strategically altering their probability of rejecting or accepting lower ranking prey types (Weissburg, 1991). Variance in prey encounter rates may also differ across foraging patches (Sutherland and Anderson, 1987), and foragers may be able to manipulate variance in prey encounter rates by choosing locations with more or less variability or by altering patch departure times (Stephens and Charnov, 1982). All of these would alter the variance in returns per trip that are experienced by offspring.

Assessing variance sensitivity and the specific ecological conditions by which it comes about requires manipulations of offspring demand on parents (Ydenberg, 2008). Brood size manipulations are the most commonly used method for manipulating brood demand (Ydenberg, 2008). For adults provisioning young, having more young logically increases the required energy because, all else being equal (i.e. food availability, energetic costs imposed by weather conditions, etc.), more young require more energy. The extent to which the increased energy demands of enlarged broods translate to increased probability of experiencing meaningful energetic shortfalls will depend on ecological conditions (e.g. prey availability and/or ambient conditions that influence nestling energy expenditure; Moore, 2002). When enlarged broods do experience an increased probability of energetic shortfall, parents should generally increase their relative preference for prey with more variable encounter rates (Moore, 2002; Ydenberg, 2008) (see Figure 1c and Figure 2).

Here we report the results of a two-year study during which we altered offspring demand on parent great tits (*Parus major*) using brood size manipulations. We estimated changes in mean inter-visit intervals (IVIs), mean load size, mean short-term delivery (load size/time for each provisioning visit), and the relative contribution of caterpillars (the preferred prey of great tits, Naef-Daenzer et al., 2000; Wilkin et al., 2009) to the diet. Additionally, we quantify variances in IVIs, load size and short-term delivery experienced by nestlings. We also estimated the effect of experimentally manipulated brood demand on measures of long-term provisioning: provisioning rate (visits per parent per 30 minute observation) and long-term delivery (sum of load sizes per 30 minute). We evaluated the extent to which changes in means and variances in provisioning behaviour followed predictions from the three strategic options outlined above for coping with increased brood demand: increase provisioning effort, shift in energetic quantity relative to nutritional quality, or variance sensitivity (Figure 1). A fortuitous difference in ecological conditions (detailed in Nicolaus et al., 2015) between the two years allowed us to compare the strategies adopted by parents across the two study years in light of these contrasting ecological conditions.

Materials and Methods

Study population

This study was carried out in a nestbox population of great tits (*Parus major*) located in southwestern Germany. The study site consists of 12 plots covering a total area of approximately 120 ha. Each plot is comprised of 50 nestboxes arranged in a regular grid (50 m between adjacent nestboxes). All nestboxes were monitored throughout the breeding season (*circa* March to August) by visiting them at least twice per week in order to record lay date (date of first egg, back calculated assuming 1 egg laid per day), clutch size, onset of incubation, hatching and fledging date and the number of young fledged (see Nicolaus et al., 2015 for more details).

When nestlings were 3 days old, we performed brood size manipulations (BSMs) such that parents received either a reduced brood (net change of -3 nestlings), a control brood (net change of 0 nestlings, but nestlings still swapped between nests), or an enlarged brood (net change of +3 nestlings). Nestlings were exchanged between nests of the same age and with a similar average nestling body mass. After the manipulation, half of the nestlings in all manipulated nests came from another nest. Nests for which there was no suitable matching brood were left unmanipulated and are not discussed further here (see Nicolaus et al., 2015 for further details on the BSMs). BSMs were performed blind with respect to parental traits (e.g., behaviour, morphology) that may in turn have affected their response to the BSM.

Furthermore, BSMs were stratified across natural brood sizes, so there were no BSM-related differences in pre-manipulation brood size.

Provisioning behaviour

Provisioning behaviour was monitored at a total of 83 nestboxes that received BSMs (N = 42 in 2010 and N = 41 in 2011). This represents less than 20% of all first broods in each year (N = 223 first broods in 2010, N = 216 first broods in 2011). To record provisioning behaviour, small infrared cameras (CDD Bird Box Camera with IR Night Vision 420TV lines) were installed in nestboxes when nestlings were 10 days old by exchanging the side door of the nestbox with a small wooden box containing the camera. Nests were raised circa 2 cm by placing a piece of foam beneath the nest material to ensure that the entire nest cup could be filmed. Additionally, a clear piece of Plexiglas was placed between the nest and the side compartment that contained the infrared camera to prevent parents from sitting in the side compartment (Supplementary Figure S1). The following day (nestling day 11), nestlings were weighed and given unique markings on the top of their heads with acrylic paint (as part of another experiment).

On nestling day 12, at approximately 8h00, a portable recording device (Archos 5 Internet Media Tablet) and power supply were connected to the nestbox camera using 20 m long cables. This allowed the cameras to be turned on to start recordings at a distance from the nestbox. Observations began 30 minutes after camera installation. For observation period 1, the observer walked up to the nestbox (within 1 m) before starting the recording device. The observer then left the immediate vicinity of the nestbox (> 100 m) for 30 minutes (the duration of observation period 1) before returning to interrupt and resume the recording (at 20 m distance from the nestbox) for another 30 minutes (observation period 2). The observer again left the vicinity of the nestbox for the duration of observation period 2. The difference in close (within 1 m) versus far (circa 20 m) approach to the nestbox between observation period 1 and 2 was part of another experiment to investigate potential effects of short human disturbances at the nestboxes on provisioning behaviour (Mutzel et al., *In preparation*). Importantly, Mutzel et al. (*In preparation*) found no evidence of year-specific effects of these two disturbance levels on parental provisioning behaviour, suggesting that any year-specific differences observed in the present analyses as a function of the BSM are not due to year-specific responses to these two disturbance treatments. Following the two observation periods included in the present study, additional provisioning data were collected as part of another experiment on provisioning behaviour under different levels of perceived nest predation threat (Mutzel et al., *In preparation*).

For each parental visit to the nestbox, the following data were extracted from the videos: bird identity (male or female parent, determined from plumage characteristics), the time (to the nearest second) that a bird entered the nestbox, the load size relative to parent’s bill volume (e.g. 1 = volume of bill, 2 = twice the volume of the bill, scored to the nearest 0.1 bill volumes) and the time the individual left the nest (to the nearest second). Prey items were classified as preferred (i.e. caterpillar), or non-preferred (Naef-Daenzer et al., 2000; Wilkin et al., 2009). The combined effects of load size and prey type were used to assess evidence for changes in energetic value of prey delivered to the nest (e.g. Wright et al., 1998). For the data used in the present study, 5 observers recorded the timing of nest visits, and 2 observers recorded prey type and load size, from the videos. The two observers for prey type and load sizes were trained until among-observer consistency was high (Pearson's product moment correlation = 0.90, N = 173).

From these data, we calculated inter-visit intervals (IVIs) and inter-feed intervals (IFIs). IVIs represent the interval between successive provisioning visits to the nest by the same parent, and were calculated as (nestbox entry time for visit N) – (nestbox entry time for visit N-1). IFIs represent the interval between successive provisioning visits, regardless of the identity of the parent. Thus, short-term delivery to the brood was estimated for each provisioning visit as load size/IFI.

We also estimated the combined effects of changes in means and variances in short-term provisioning decisions (IVIs and load sizes) on long-term provisioning rates (sum of visits by each parent over the total observation time), and long-term nest level delivery (sum of load sizes by either parent over the total observation time) (see Bateson and Kacelnik, 1996 for discussions of different rate currencies).

Statistical analyses

Brood size manipulations

To verify that the brood size manipulations (carried out on nestling day 3) resulted in differences in brood size on the day that provisioning behaviour was filmed (nestling day 12), we used a mixed effects model with natural clutch size (within-year centered), and the unique combination of year and treatment (6 levels: 2010R, 2010C, 2010E, 2011R, 2011C, 2011E) as fixed effects. Plot (12 levels, 11 of which were present in both years) was included as a random effect. We did not have sufficient replication of nestboxes (only 2 nestboxes were replicated across years) or parent IDs (only 4 parent ids replicated across years) to meaningfully include these as random effects. We used square-root transformed brood size in our analyses (to approach a normal distribution) and modelled these transformed data with Gaussian errors. Analyses were performed using data from all BSM nests for which we observed provisioning behaviour (2010: N = 15 reduced, N = 13 control, N = 14 enlarged; 2011: N = 14 reduced, N = 13 control, N = 14 enlarged). We tested for a year × treatment interaction by comparing the effect of treatment (difference in brood size between reduced and enlarged broods) across the two study years. These analyses revealed year-specific effects of the BSM on realized brood sizes on the day of provisioning observations (see results). The two years were therefore treated separately in all subsequent analyses by modelling provisioning behaviour as a function of year-specific brood size manipulations (i.e. 6-level factor: 2010R, 2010C, 2010E, 2011R, 2011C, 2011E).

Provisioning behaviour

Visit-level decisions

We tested whether there was evidence for differences in means and variances in visit-level provisioning behaviour across the two study years as a function of the BSM. We assess this from the perspective of each parent and of the nestlings. To do this for parent level decisions, we constructed univariate mixed effects models with IVI, load size or prey type (preferred or non-preferred) as the response variable. Prey type was analyzed to test for changes in prey selectivity. Caterpillars typically make up the majority of prey items provisioned to young great tits and are thought to represent the most profitable prey type (energy per unit time) because they are provisioned in higher frequencies than expected based on natural abundances (Naef-Daenzer et al., 2000; Wilkin et al., 2009). Thus, within a given year, a decrease in the proportion of caterpillars with increasing brood demand would be consistent with expansion of the diet to include non-preferred prey types to cope with increased demand. We coded each provisioned prey as being preferred (1 = caterpillars) or non-preferred (0 = others), and constructed a binary mixed effect model with prey type (preferred or non-preferred) as the response variable.

Each of these parental visit-level decisions (IVI, load size, and prey type) was modelled as a function of the combination of year and treatment (6 level factor: 2010R, 2010C, 2010E, 2011R, 2011C, 2011E) and individual parent (2010: 71 levels, 2011: 79 levels), nestbox (2010: 41 levels, 2011: 40 levels) and block identity (the unique combination of nestbox and observation period: each nestbox had up to two unique observation period identities as described above ; 2010: 78 levels, 2011: 79 levels) were fitted as random effects. The number of levels for nestboxes in 2010 and 2011 are lower than the total number of nests observed because of problems with video recording or insufficient visits (i.e. less than 2 visits per parent) to calculate parental IVI at 2 nests in 2010, and 1 nest in 2011. To test whether there were treatment-related differences in the variance in IVI or load size, residual variances were modelled for each year by treatment combination (Cleasby and Nakagawa, 2011; Hadfield, 2010; Westneat et al., 2015). Heterogeneous errors cannot be modelled for binary data, therefore, we do not assess BSM-related effects on variances in prey types provisioned.

We also assessed the combined effects of parental IVI and load size decisions on means and variances in short-term delivery received by each nestling. Short-term delivery was estimated for each visit regardless of the identity of the parent as load size/IFI (units: bill volumes/second). As with the analyses for parent-level data, the unique combination of year and BSM treatment was included as a fixed effect. We additionally included brood size as a fixed effect to account for the average effect of brood size on delivery independent of BSM treatment. Note that because delivery was ln-transformed prior to analyses, the estimated brood size effect on delivery is non-linear on the observed scale. A significant Year:BSM effect on delivery over and above the effect of brood size would indicate differences in per-nestling delivery as a function of the manipulations. Nestbox and block indentity were included as random effects, and residual variance was modelled for each year by treatment combination. Parent identity was not included as a random effect because the response variable was constructed from the combined effects of both parents at a nest.

IVI and short-term delivery were ln-transformed, and load size was square root transformed prior to analyses. All of the above models were then constructed with Gaussian error distributions.

Long-term consequences of visit-level decisions

Variance-sensitive foraging theory predicts changes in preference or aversion to variance in response to changes in the long-term expectation of energy shortfall of nestlings. Because our short-term measures of provisioning were transformed prior to analyses using non-linear transformations, back-transformation cannot be used to translate the mean on the latent scale to the mean on the observed scale (Nakagawa and Schielzeth, 2017). Although methods are available to approximate the mean on the observed scale (e.g. 2nd order Taylor expansions or simulations, see Nakagawa and Schielzeth, 2017), we instead calculated long-term provisioning rates (for each parent individually) directly from the raw data (i.e., number of visits per parent per 30 minute observation). Along similar lines, extrapolating visit-level rates to infer long-term average rates produces biased estimates, and the magnitude of bias depends on the specific data structure (for discussion and examples, see Bateson and Kacelnik, 1996; Templeton and Lawlor, 1981; Welsh et al., 1988). Therefore, we also calculated long-term average nest-level delivery from the raw data (i.e., sum of load sizes delivered per 30 minute observation for both parents combined).

To analyze BSM-related effects on parent level long-term average provisioning effort, we modelled (as above) long-term visit rates per parent (sum of visits by a given parent) as a function of a 6 level factor representing the unique combination of year and treatment (2010R, 2010C, 2010E, 2011R, 2011C, 2011E). Nestbox, Block ID (a unique combination of nestbox and observation period) and parent ID were also included as random effects. Although our dependent variable constituted count data, counts of visits do not arise from a Poisson process because provisioning visits by the same parent are not independent of one another. Consequently, we did not analyse these data using Poisson error distributions, but instead used ln (n+1) transformed counts of parental visit for analyses with Gaussian error distributions.

To analyze BSM-related differences in long-term delivery experienced per nestling, we modelled long-term nest-level delivery (sum of load sizes from both parents per 30 minute observation) as a function of a 6 level factor representing the unique combination of year and treatment (2010R, 2010C, 2010E, 2011R, 2011C, 2011E). We included absolute brood size to assess the average care received per nestling. Thus, significant Year:BSM effects on delivery over and above the effect of brood size would indicate differences in per-nestling delivery as a function of the manipulations. Nestbox and Block ID (a unique combination of nestbox and observation period) were included as random effects. Nestling-level visit rate was normally distributed and therefore was not transformed.

All mixed effects models were fitted in the R statistical environment version 3.2.3 (R Development Core Team, 2015). Models to estimate year and BSM specific values for both means and residual variances (IVI, load size and short term delivery) were fitted using Monte Carlo Markov chains in the MCMCglmm package (Hadfield, 2010), which retrieves posterior distributions of the estimated parameters. Details of parameter estimates are provided in the electronic supplementary material (see Supplementary Text S1). Multivariate mixed-effects models were also constructed in ASREML to validate the Bayesian analyses by implementing an alternative REML-approach, which corroborated our findings (Results not shown).

We did not model heterogeneous residual errors for measures of long-term provisioning (long-term provisioning rate and long-term delivery per nestling) because we had only two measures per individual parent (or per nestbox), and therefore no power to detect heterogeneous residual errors. These models were constructed using the lmer function from the lme4 package in R (Bates et al., 2015). We used the 'sim' function of the 'arm' package to simulate values of the posterior distribution of the model parameters (Gelman and Su, 2015).

We evaluated support for treatment effects based on estimated effects sizes and their 95% credible intervals (Cumming and Finch, 2005; Nakagawa and Cuthill, 2007). This approach is advocated to avoid drawing dichotomous conclusions (e.g. accept or reject the null hypothesis) based on data which can show a continuous range of support (or lack of support) for a given interpretation (Cohen, 1990; Wasserstein and Lazar, 2016). As a reference for readers less familiar with CIs: a 95% CI is roughly equivalent to a value of $p \leq 0.05$ when the null distribution is outside the bounds of the CI (i.e. testing for a difference between two groups, H1: $\beta \neq 0$, with no *a priori* prediction for whether the difference would be positive or negative), or $p \leq 0.025$ when there is a directional prediction (Cumming and Finch, 2005) (e.g. H1: $\beta > 0$). We use the terms "strong support for an effect" or "significant" when the 95% CI does not overlap zero, moderate support when the estimated effect is removed from zero but the 95% CI overlaps zero by up to 15%, and no support for an effect (or support for lack of an effect) when the estimate is centered on zero.

Results

Brood size manipulations

In both study years, reduced broods were significantly smaller than enlarged broods on the day of filming (control broods were intermediate to the reduced and enlarged broods)

(Table 1, Figure 3). The overall variation in brood size produced via the BSM (i.e. difference in number of nestlings between enlarged and reduced treatments) was greater in 2011 (β = 1.03, 95% CI = 0.82, 1.23) compared with 2010 (β = 0.69, 95% CI = 0.49, 0.88); the presence of a year-difference was strongly supported (Year × Treatment interaction: β = 0.34, 95% CI = 0.05, 0.62, Figure 3). There was also an effect of natural clutch size on brood size on the day of filming (Table 1).

Effects of the BSM on mean visit-level provisioning behaviour

On average, mean IVIs were shorter in 2010 compared with 2011 (Table 2, Figure 4a), and there was moderate support for a difference in effect of the BSM across the years (β = 0.26, 95% CI = -0.09, 0.69, Bayesian p-value = 0.09). Post-hoc year-specific analyses support year-related differences in IVIs in response to the BSM. In 2010, there was no support for BSM-related differences in mean IVIs (difference between reduced and enlarged broods: β = 0.05, 95% CI = -0.23, 0.33). In contrast, in 2011, there was strong support for IVIs decreasing across the BSM categories (difference between reduced and enlarged broods: β = 0.32, 95% CI = 0.02, 0.58).

Average load size was smaller in 2010 compared with 2011 (Table 2, Figure 4b), and there was also moderate support that the effects of the BSM on load sizes differed across the two years (β = 0.06, 95% CI = -0.05, 0.20, Bayesian p-value = 0.15). In 2010, there was moderate support that load sizes increased across BSM categories (difference between reduced and enlarged broods: β = 0.07, 95% CI = -0.01, 0.16, Bayesian p-value = 0.05), but there was no support for any BSM differences in load size in 2011 (difference between reduced and enlarged broods: β = 0.02, 95% CI = -0.06, 0.11).

Caterpillars made up a more substantial portion of the diet in 2011 compared with 2010 (Table 2). In 2010, the proportion of caterpillars did not differ as a function of the BSM (difference between reduced and enlarged broods: β = 0.20, 95% CI = -0.52, 1.08). In contrast, in 2011, the proportion of caterpillars was greater in reduced broods compared with both control (β = 1.02, 95% CI = 0.13, 1.82) and enlarged (β = 0.94, 95% CI = 0.06, 1.63) broods.

Short-term delivery rates increased significantly with increasing current brood size (β = 0.12, 95% CI = 0.07, 0.18). After accounting for the effect of brood size, short-term delivery per nestling was similar in both study years and across the BSM treatment (Table 2, Figure 4c). There was no evidence for BSM-related differences in mean short-term delivery (load size/IFI, controlling for current brood size) in either 2010 (difference between reduced and enlarged broods: β = -0.22, 95% CI = -0.46, 0.15) or 2011 (difference between reduced and enlarged broods: β = -0.05, 95% CI = -0.42, 0.36) implying no BSM-related differences in per nestling delivery.

Effects of the BSM on variance in visit-level provisioning behaviour

We found strong support for an effect of the BSM on variance in IVIs that differed across the two study years (difference between enlarged and reduced treatment between 2010 and 2011: σ^2 = 0.25, 95% CI = 0.02, 0.47) (Table 3, Figure 4d). There was strong support for variances in IVIs decreasing across BSM categories in 2011 (σ^2 = -0.19, 95% CI = -0.37, -

0.01), which is opposite to the pattern predicted by variance-sensitive foraging theory. However, in 2010, BSM-related differences in residual variance in IVIs shifted significantly in the direction predicted by variance-sensitive foraging theory (year x treatment interaction). Reduced broods had the lowest residual variance in IVIs and enlarged broods had the highest residual variance in IVIs, although the difference was relatively weak (difference between reduced and enlarged broods: σ^2 = 0.05, 95% CI = -0.07, 0.17, Bayesian p-value = 0.22).

We found no support for BSM effects on variance in load sizes in either 2010 (difference between reduced and enlarged broods: σ^2 = 0.01, -0.01, 0.02) or 2011 (difference between reduced and enlarged broods: σ^2 = 0.01, 95% CI = -0.01, 0.03) (Table 3, Figure 4e). By contrast, we observed year-specific patterns of variance in short-term delivery rates experienced by nestlings as a function of the BSM (Table 3, Figure 4f). In 2010, the variance in prey delivery experienced per nestling did not differ between control and enlarged broods (σ^2 = 0.05, 95% CI = -0.22, 0.36), but there was strong support for nestlings from reduced broods experiencing lower variance in short term delivery rates compared with nestlings from enlarged broods (σ^2 = -0.23, 95% CI = -0.45, -0.01) and moderate support for nestlings from reduced broods experiencing lower variance in short-term delivery rates compared with nestlings from control broods (σ^2 = -0.15, 95% CI = -0.40, 0.04). In contrast, in 2011, variance in short-term delivery did not differ systematically across the BSM categories (Table 3), and the residual variance in short-term delivery was nearly identical between reduced and enlarged broods (σ^2 = -0.001, 95% CI = -0.002, 0.000). Overall, there was strong support that the effect of the BSM (difference between reduced and enlarged broods) on residual variance in short-term deliveries differed across years ($\sigma^2 = 0.22$, 95% CI = 0.01, 0.45).

Consequences of visit-level decisions for long-term provisioning

Long-term provisioning rates were similar across the two study years (Table 4, Figure 5a) and showed changes as a function of the BSM. In 2011, parents increased their average provisioning rates in response to the BSM (difference between enlarged versus reduced broods; β = 0.83, 95% CI = 0.22, 1.12), but there was only moderate support for an increase in provisioning rates across BSM in 2010 (difference between reduced and enlarged broods: β = 0.31, 95% CI = -0.10, 0.75) (Table 4).

Long-term nest-level delivery increased significantly with increasing brood size (β = 0.30, 95% CI = 0.16, 0.46). After controlling for brood size, there was moderate support for year-specific differences in long-term deliveries per nestling as a function of the BSM (β = 0.46, 95% CI = -0.47, 1.63, Bayesian p-value = 0.14) (Table 4, Figure 5b). In 2010, there was moderate support for the interpretation that long-term delivery per nestling decreased across the BSM levels (difference between reduced and enlarged broods: β = -0.52, 95% CI = -1.29, 0.43, Bayesian p-value = 0.14). In contrast, there was no support for BSM-related differences in long-term delivery in 2011 (difference between reduced and enlarged broods: β = 0.03, 95% CI = -0.97, 1.09), suggesting that delivery per nestling did not differ as a function of the BSM in that year.

Discussion

Parents provisioning offspring can adopt a variety of (non-exclusive) tactics to cope with changes in brood demand. We used brood size manipulations in great tits and found that the tactics adopted by parents to cope with increased brood demand differed across two years. In 2010, there was no evidence of BSM-related shifts in mean IVIs or prey selectivity. As a result, there was moderate support that nestlings from enlarged broods experienced lower long-term delivery compared with nestlings from reduced broods. In contrast, in 2011, parents exhibited BSM-related shifts in both mean IVI and prey selectivity and there was no support for BSM-related differences in long-term delivery experienced by nestlings. Moreover, we found strong evidence that BSM-related differences in variance in IVI and in delivery per trip differed across years. Shifts in variances in IVIs and delivery per trip were consistent with stronger variance-sensitive behaviour in 2010 compared with 2011. The difference between years was not a variable we had considered going into the experiment, but the consequences are important and suggest a potential role of ecological conditions in mediating the tactics adopted by parents to cope with increased brood demand.

Are shifts in behaviour the result of shifts in ecology?

Parental responses to the brood size manipulations differed across the two study years. We interpret this as evidence that ecological conditions play an important role in shaping parental provisioning decisions. However, the same brood size manipulations in the two study years did not have the same effect on brood size on the day of filming (Table 1, Figure 3). In 2010, the net effect of the brood size manipulation was much smaller compared with 2011. Therefore, an alternative interpretation for the year-related differences in parental provisioning behaviour as a function of the BSM is that parents were responding to year-related differences in the effects of the BSM treatment. However, analyses using brood size on the day of filming, rather than BSM category, produced qualitatively similar results (see ESM Text S2 and Table S1), indicating that parents responded to variation in nestling demand (i.e. number of nestlings) differently across the two years, which supports our interpretation that parental provisioning decisions were shaped by year-specific ecological conditions.

Although replication of ecological conditions is needed to draw strong conclusions regarding which specific aspects of the ecological conditions shaped the across year differences in parental provisioning decisions (Hurlbert, 1984), the comparison between the two years is intriguing. Ecological conditions in the two study years may have played an important role in shaping the options available to parent great tits to cope with increasing brood demand. The 2010 season appears to have been a bad one for breeding great tits in our population (see Nicolaus et al., 2015, and ESM Text S3) and the more challenging ecological conditions may have limited the options available to parents. Average daytime temperatures in our study area were colder compared with 2011 (ESM Figure S2a), and rainfall was more frequent (ESM Figure S2b). There was also higher nestling mortality in 2010 (ESM Figure S3), suggesting that parents struggled to meet the energy requirements of their broods in that year.

In the year with these more challenging conditions (2010), caterpillars, the preferred prey of great tits (Naef-Daenzer et al., 2000; Wilkin et al., 2009), made up a substantially smaller proportion of the diet compared with the good year (2011) (Table 2). This could reflect a lower availability of caterpillars in 2010, or may indicate that parents were overall less selective to compensate for higher brood requirements in that year, for example if the lower temperature increased the energy requirements of nestlings via increased thermoregulatory costs (Sanz and Tinbergen, 1999). The latter seems unlikely, because if that were the case, we would have expected a higher overall variance in prey type or size in 2010 compared with 2011, which would have been expected from reduced selectivity and a reduction in the minimum quality/size threshold for accepting prey items. We would expect that parent great tits would still accept large and/or high quality prey when encountered, resulting in a wider range of prey sizes being accepted, thereby reducing the mean but increasing the variance in size of provisioned items. In contrast, we observed that variance in load size was lower in 2010 compared with 2011 (see Table 3, Figure 4e). Therefore, differences in the size and type of prey provisioned across the two study years probably reflect a lower availability of large, preferred prey types in 2010.

There was only moderate support for an increase in long-term average provisioning rates as a function of the BSM in 2010. This increase in long-term average provisioning rate was not accompanied by any BSM-related differences in either mean IVI or in prey type (Table 2). There was moderate support for an increase in load size with increasing brood demand. Taken together, the tendency to increase long-term provisioning rates and mean load size per visit across the BSM categories suggests that parent great tits may have attempted to meet increased brood demand in 2010 via increased provisioning effort.

In 2011, there was strong support for BSM-related difference in mean IVI, but no support for BSM-related differences in load size. Additionally, there was strong support for prey selectivity being greatest for parents provisioning reduced broods (i.e. they provisioned a significantly greater fraction of preferred prey to the young). Thus, the BSM-related increase in long-term average provisioning rates in 2011 came about via a combination of increased effort (BSM-related changes in IVI) and a decrease in selectivity (for enlarged broods). The greater overall increase in provisioning rates in 2011 compared with 2010 may have occurred because the more favourable ecological conditions associated with that year meant that parents had more options available for increasing provisioning rates. The greater overall availability of caterpillars in 2011 implied that increased prey selectivity was a viable option for parents provisioning reduced broods in that year, and the more favourable temperatures may have meant that parents did not require as much time for self-feeding or brooding the young for thermoregulation, making it possible to increase long-term provisioning effort for enlarged broods to a greater extent compared with parents provisioning enlarged broods in the more challenging year (2010).

There was moderate support for long-term average delivery experienced by nestlings varying as a function of the BSM in 2010, but there was no support for such an effect in 2011. In 2010, the more challenging year in terms of ecological conditions, delivery to the nest decreased as a function of experimentally increased brood demand after controlling for current brood size. This indicates that the per nestling delivery was lower in enlarged broods, and suggests that the brood size manipulation did indeed place nestlings from enlarged broods on a negative energy budget relative to nestlings from control and reduced broods. This was not the case in 2011, when parents apparently fully compensated for increased brood demand as there was no evidence for BSM-related differences in long-term average delivery after controlling for number of nestlings. Analyses of nestling mortality rates as a function of the BSM in each year corroborate our interpretation that the BSM produced meaningful changes in the probability of energy shortfall in 2010 but not in 2011. In 2010, nestling mortality increased significantly across BSM categories, but there were no BSM-related differences in nestling mortality in 2011 (ESM Table S2).

Mechanisms underlying variance in provisioning behaviour

We observed year-specific BSM-related differences in residual variance in parental inter-visit intervals (IVIs) and in short-term delivery rates experienced by nestlings. The results were consistent with 2010 exerting stronger variance-sensitive provisioning compared with 2011. In 2010, residual variance in parental IVIs tended to be smallest for reduced broods and greatest for enlarged broods. More importantly, the combined effects of both parents resulted in significantly greater residual variance in short-term delivery experienced per nestling in enlarged compared with reduced broods. Our study was not designed to assess the potential mechanism(s) that parent great tits used that may have caused differences in the variance in their prey encounter rates. Nevertheless, the results here suggest that this did not come about via changes in prey selectivity (either size or type, Table 2). In contrast to our results, two previous experimental studies of variance-sensitive provisioning found that brood demand-related shifts in the variance in prey delivery were associated with changes in the size and type of prey delivered (Moore, 2002; Whittingham and Robertson, 1993). Differences in the foraging ecologies of the species involved may explain the different findings. Both previous reports of brood-size dependent variance-sensitive provisioning involved species where parents could choose between foraging in alternative, discrete habitat types that differed in prevailing prey type (e.g. common terns foraging in a small pond or large lake: Moore, 2002; red-winged blackbirds foraging in woodland or marsh: Whittingham and Robertson, 1993; see Ydenberg, 2008). Great tits, however, forage in what appears to be a single habitat type, deciduous forest. While it is likely that prey are distributed unevenly across this habitat and that parent great tits are making use of this heterogeneity in their decision-making (Naef-Daenzer, 2000), we cannot assess this with our data.

If great tits do not exhibit shifts in prey selectivity or foraging habitat, how were BSM-related differences in the variance in prey delivery rates achieved? One possibility is that great tits strategically adjust their patch departure decisions (Stephens and Charnov, 1982). However, this has only been explicitly considered for cases where animals obtain diminishing returns in a patch (i.e. consume/load multiple prey items per patch), and it is unclear that this can be extended to single prey loaders such as great tits (and with no obvious evidence of prior patch depletion from parental self-feeding). Detailed observations of parents on provisioning trips (e.g. when using feeders) may provide some insights into how BSM-related differences in variance are achieved.

Interestingly, BSM-related differences in the variance in IVIs in 2011 ran counter to the patterns observed in 2010: variance in provisioning behaviour decreased with increasing brood demand. We suggest that the patterns of decreasing variance in parental IVIs observed in 2011 is not the result of variance-sensitive provisioning decisions by parents for two reasons. First, the observed shifts in mean parental behaviour in 2011 meant that there were no treatment-related differences in average long-term delivery experienced per nestling. Since all nestlings in all treatments appear to have received the same long-term rate of food delivery, and since there were no BSM-related differences in mortality, nestlings from all BSM treatments should have been at a similar location on the utility curve in Figure 2, and hence no BSM-related changes in preference (or aversion) for variance were expected.

Second, residual variance in short-term delivery experienced at the level of nestlings did not vary as a function of the BSM in 2011. Variance-sensitive behaviour by parents is expected when deviations in energy above and below the mean energy delivery have asymmetric fitness consequences for offspring (Figure 2). Variance-sensitive responses will only have fitness consequences for offspring if the combined effect of each parent's individual response to variation in brood demand results in shifts in the variance in energy delivery experienced at the level of the nestling. Thus, the lack of BSM-related differences in variance in nestling-level delivery suggests that the BSM-related patterns in parental IVIs in that year were not due to parents adaptively adjusting the variance in delivery in response to non-linear utility functions of nestlings. Nonetheless, we cannot rule out that parents did exhibit adaptive variance-sensitive responses to variation in brood demand, but that these effects were slight in 2011 compared with the ones observed in 2010 and therefore masked by other processes influencing variance in parental IVIs.

What processes might have generated the observed pattern of decreasing variance in IVIs with increasing brood demand in 2011? One possible explanation is that the decrease in variance with brood size may have been a by-product of parental strategic decisions to decrease prey selectivity as a way of increasing mean energy delivery (via reduced IVIs) (see Weissburg, 1991 for worked examples). However, this seems unlikely as additional analyses of our data (not shown) demonstrated that residual variances in IVI did not differ as a function of prey type in the present study. Alternatively, parents may divide their time between parenting and other activities in a more variable manner between trips when brood demand is reduced (see also Westneat et al., 2017). For example, parents with small broods in good years may be able to forage intensively for a while close to the nest, and once their brood has been adequately fed they are free to devote some time to territory defense (Markman et al., 1995) and/or foraging for themselves (Martins and Wright, 1993). This could be a sensible strategy if territory defense and/or sampling new and different foraging patches requires additional travel further from the nest and is therefore best done separately from any continuous provisioning back at the nest. In this way, provisioning rates would decrease and simultaneously the variance in IVI would be higher in reduced broods, but only in good years. However, a more comprehensive quantification of parental behaviour (e.g. detailed observations on the time allocated to provisioning versus other activities) as a function of year and BSM are obviously required to establish how changes in parental effort affect mean provisioning rates and variance in IVIs. Additionally, field experiments that manipulate variability in food reward (e.g. Ratikainen et al., 2010) would be useful to disentangle the effects of multiple co-occurring processes on residual variance in parental provisioning.

Conclusions

We found that great tit parents respond in several ways to changes in brood demand, and that their responses likely depend on a complex mix of factors. Differing ecological conditions are the most likely reason for the year-specific parental responses. Parents faced with increased brood sizes increased long-term average visit rates in both years, but the increase was greater in the good year (2011) than in the bad (2010). In 2010, the increased long-term average provisioning rate was consistent with an increase in provisioning effort, while in 2011 it was consistent with a combination of increased effort and reduced selectivity. Great tit parents exhibited behaviour consistent with predictions from variance-sensitive foraging theory, but only in the bad year (2010). This supports an earlier claim that variance-sensitive decisions are favoured most strongly under more challenging ecological conditions (Moore, 2002). One of the most exciting implications of having manipulated brood size over two years with such different ecological conditions is that it revealed the intriguing possibility that conditions can strongly affect parental tactics for coping with increased brood demand. For example, decisions regarding the use of one strategy (e.g. shifting energetic quantity of prey at the expense of their nutritional quality) might influence the value of then also adopting other strategies (e.g. working harder or variance-sensitivity) (see also Ratikainen et al., 2012). The potential for such overlapping and interactive effects of the different strategic options involving both the means and variances in rewards highlights the need to adopt a more systems-level approach to the study of parental care decisions (i.e. studying integrated, multi-trait phenotypes) across an array of ecological conditions.

Data accessibility

All data used in the analyses presented in this paper will be deposited on Dryad upon publication of the paper.

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Figure legends:

Figure 1: Graphical illustration of the predicted outcomes from three non-mutually exclusive strategies for coping with changes in brood demand (R= reduced, C = control, and E = enlarged broods). Predicted effects of brood demand on means are illustrated with solid black lines (directional prediction) or grey filled wedges (when the predicted response can vary from no change to a directional effect). Solid grey lines reflect cases where there is no *a priori* predicted directional effect on means. Predicted effects on variances are illustrated with dotted lines where *a priori* predictions exist. All else being equal, a) when parents increase effort, increased energy delivery to the nest arises via decreased IVIs and/or increased energy per visit. This may be achieved via increased prey selectivity, or by increasing the time/energy devoted to provisioning. b) When parents trade off energetic quantity versus nutritional quality, increased energy delivery to the nest arises via decreased IVIs and/or increased energy delivery per visit, which are the result of decreasing prey selectivity (or prey shifts). c) When parents display variance sensitivity, variance in the rate of energy delivery is predicted to increase with increasing brood demand via an increase in variance in IVI and/or an increase in variance in prey size. There is no universal prediction regarding the effect of brood demand on mean IVI or mean energy delivered per visit when animals exhibit variance-sensitivity. Similarly, there is no universal prediction for how variance sensitivity should affect prey selectivity (in some cases, higher variance arises through increased selectivity, in other cases it can be achieved through decreased selectivity). Effects on means depend on characteristics of the prey (e.g. energy content, encounter rate, etc.).

Figure 2: Illustration of the non-linear relationship between food delivery and offspring fitness, which forms the basis of the theoretical argument for variance sensitivity of parents to prey encounter rates when feeding offspring. On the left side of the graph, a positive deviation (black whisker) from the mean food delivery (blue circle) has a larger benefit compared with the cost of an equal magnitude negative deviation (b > c) (e.g. when nestlings are in poor condition). Thus, parents are expected to be variance-prone. The right side of the graph illustrates a scenario where a positive deviation above the mean delivery (red circle) has a smaller benefit compared to the cost of an equal magnitude negative deviation (c > b) (e.g. when nestlings are in good condition), hence, parents should be variance-averse. Note that we assume that brood size manipulations will result in systematic reductions in the amount of food per nestling per unit of time, leading to an increased likelihood that parents become variance-prone.

Figure 3: Brood size on day of filming for reduced (R), control (C) and enlarged (E) broods. Values presented are means ± 1 s.e. calculated from raw data.

Figure 4: Effects of brood size manipulation on (I) means (top row) and (II) variances (bottom row) in visit-level provisioning behavior. Shown are: a) and d) inter-visit intervals (IVIs), b) and e) load size, c) & f) short-term delivery (load size/inter-feed interval/brood size). Note that statistical analyses of data in c) & f) were of total short-term delivery with current brood size as a covariate. Top panel depicts means ± 1 s.e. (calculated from raw data). The lower panel illustrates the residual variances estimates (σ ± 95% CI) extracted from models (see methods for further details). Data from 2010 is shown with filled circles, and data from 2011 is shown with hollow circles.

Figure 5: Effects of brood size manipulations (BSMs) on measures of long-term provisioning. Shown are: a) long-term provisioning rate (number of visits by each parent per 30 minute observation) and b) long-term nestling level delivery (sum of load sizes delivered by both parents per 30 minute observation divided by brood size. Note that statistical analyses of long-term nestling level delivery included current brood size as a covariate, but ratios (long-term delivery/brood size) are used here for illustrative purposes. In b) delivery/nestling is used for illustrative purposes. Values shown are means ± 1 s.e. calculated from raw data.

Table 1: Brood size (square-root ("Sqrt") transformed) on the day of the provisioning observations (nestling age 12) as a function of initial clutch size and the brood size manipulation (BSM) for each year (see Fig. 3 for non-transformed brood sizes). Estimated means (β) or variances (σ^2) are reported with their 95% credible intervals (CI).

	Sqrt brood size
Fixed effects	β (95% CI)
2010	
Reduced	1.94 (1.75, 2.18)
Control	2.29 (2.10, 2.54)
Enlarged	2.63 (2.42, 2.84)
2011	
Reduced	2.15 (1.94, 2.34)
Control	2.63 (2.42, 2.87)
Enlarged	3.17 (2.96, 3.36)
Natural clutch size[1]	0.06 (0.01, 0.11)
Random effects	**σ^2 ± 95% CI**
Plot	0.06 (0.01, 0.14)
Residual	0.07 (0.05, 0.10)

[1] Clutch size centered within year.

Table 2: Effects of brood size manipulations (BSM) on means of visit-level provisioning behaviour. Variation in parental decisions [mean inter-visit interval (IVI, in seconds), load size (bill volumes), and prey type (preferred or non-preferred)], the net consequence of combined parental decisions for nestlings [short-term delivery (prey size/IFI, controlling for brood size)] in relation to the brood size manipulation in each year. IVI and delivery data were ln transformed, and load size was square root transformed. Data were modelled with Gaussian (IVI, prey size, delivery) or binomial (prey type) errors. Values presented are estimated means (β) and their 95% credible intervals (CI).

	Parental visit-level behavior			Ln(Nestling-level Delivery)
	Ln IVI	Sqrt load size	Prey type[1]	
Fixed effects	β ± 95% CI	β ± 95% CI	β ± 95% CI	β ± 95% CI
Brood size	NA	NA	NA	0.12 (0.07, 0.18)
2010				
Reduced	4.90 (4.70, 5.09)	0.92 (0.86, 0.98)	-1.83 (-2.39, -1.25)	-5.24 (-5.52, -4.96)
Control	4.85 (4.64, 5.05)	0.97 (0.91, 1.03)	-1.96 (-2.55, -1.30)	-5.14 (-5.56, -4.80)
Enlarged	4.85 (4.66, 5.06)	1.00 (0.94, 1.06)	-2.05 (-2.67, -1.45)	-5.06 (-5.47, -4.62)
2011				
Reduced	5.19 (4.95, 5.40)	1.16 (1.10, 1.23)	1.47 (1.02, 2.22)	-5.13 (-5.47, -4.76)
Control	5.09 (4.87, 5.30)	1.14 (1.07, 1.22)	0.61 (0.06, 1.21)	-5.18 (-5.64, -4.78)

Enlarged	4.88 (4.70, 5.06)	1.18 (1.11, 1.23)	0.74 (0.20, 1.24)	-5.11 (-5.70, -4.53)

Footnotes

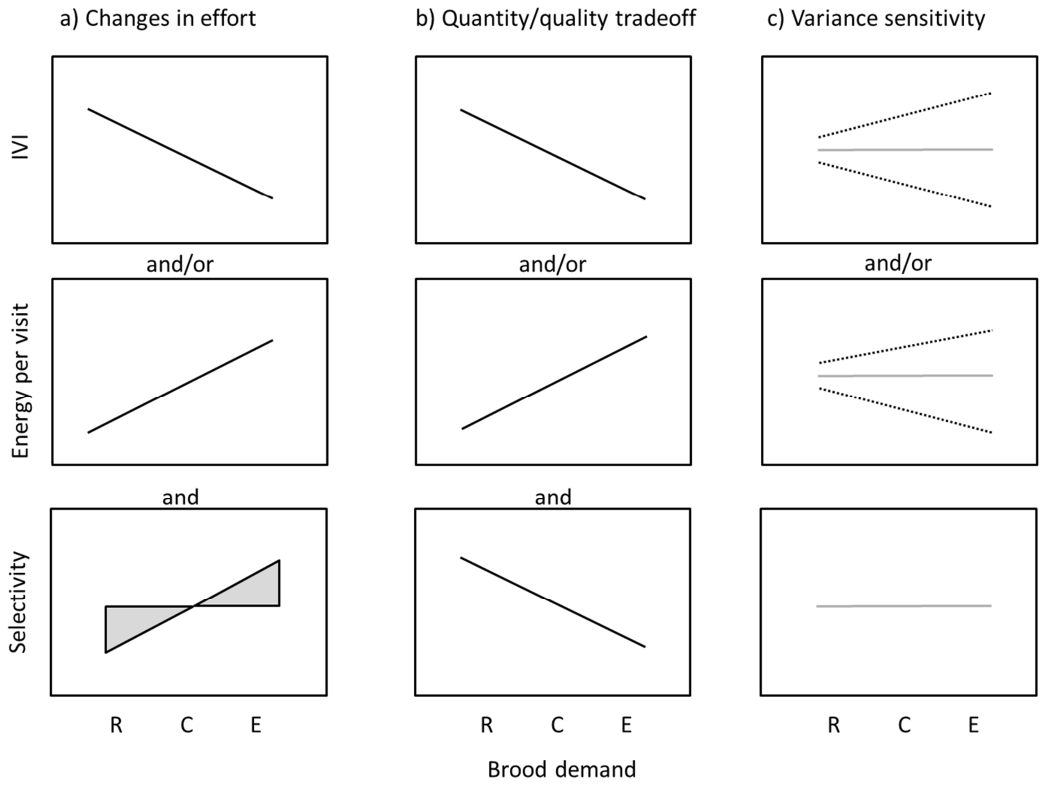
1. Prey type was modelled with binomial errors. Preferred prey (i.e. caterpillars) were coded as 1, and non-preferred prey (i.e. others) were coded as 0. Estimates are in ln (odds ratios): therefore, an estimate of 0 represents an equal proportion of preferred and non-preferred prey in the diet; an estimate of 0.69 represents cases where preferred prey are twice as frequent as non-preferred prey, and an estimate of -0.69 represents cases where non-preferred prey are provisioned twice as much as preferred prey.

Table 3: Effects of brood size manipulations (BSM) on variances of visit-level provisioning behaviour, obtained from the same models as in Table 2. Variance components of inter-visit interval (IVI, in seconds), load size (bill volumes), and short-term delivery (prey size/IFI, controlling for brood size) in relation to the brood size manipulation in each year. IVI and delivery data were ln transformed and load size was square-root transformed. Values presented are residual variances (σ^2) and their 95% credible intervals (CI).

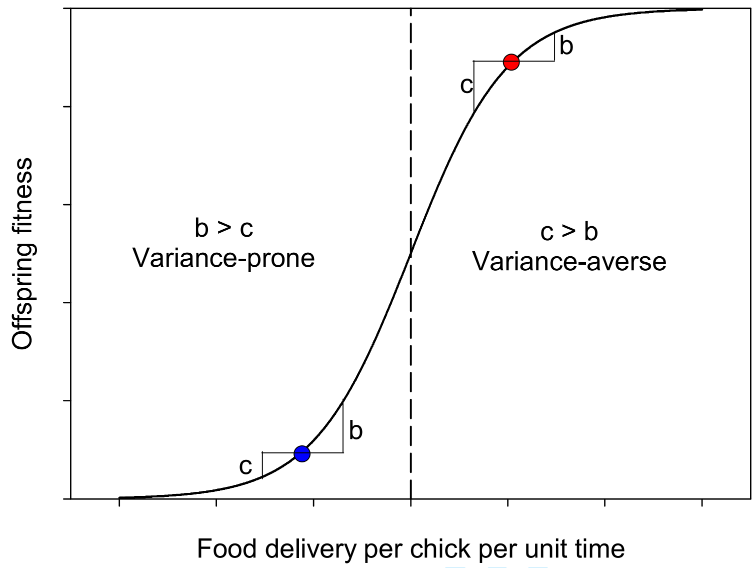
	Parent-level behaviour		**Ln (Nestling-level**
Treatment	**Ln IVI**	**Sqrt load size**	**Delivery)**
	σ^2 ± 95% CI	**σ^2 ± 95% CI**	**σ^2 ± 95% CI**
2010			
Reduced	0.55 (0.46, 0.64)	0.05 (0.04, 0.06)	0.88 (0.73, 1.04)
Control	0.56 (0.47, 0.67)	0.06 (0.05, 0.07)	1.04 (0.89, 1.22)
Enlarged	0.60 (0.51, 0.69)	0.05 (0.04, 0.05)	1.11 (0.96, 1.28)
2011			
Reduced	0.77 (0.61, 0.92)	0.09 (0.07, 0.10)	1.06 (0.87, 1.29)
Control	0.63 (0.52, 0.75)	0.09 (0.07, 0.10)	1.15 (0.95, 1.37)
Enlarged	0.57 (0.50, 0.65)	0.08 (0.07, 0.09)	1.04 (0.92, 1.16)

Table 4: Long-term consequences of visit-level decisions: long-term parental provisioning rate (ln of visits per 30 minute observation), and long-term delivery per nestling (sum of load sizes per 30 minute observation, controlling for brood size).

	Long-term provisioning rate per parent	**Long-term delivery per nestling**
Fixed effects	**β ± 95% CI**	**β ± 95% CI**
Brood size	NA	0.30 (0.16, 0.46)
2010		
Reduced	1.55 (1.21, 1.80)	3.36 (2.94, 3.99)
Control	1.67 (1.36, 2.03)	3.29 (2.75, 3.82)
Enlarged	1.86 (1.48, 2.13)	3.01 (2.53, 3.61)
2011		
Reduced	1.52 (1.13, 1.76)	4.27 (3.53, 4.75)
Control	1.65 (1.26, 1.92)	3.65 (3.21, 4.29)
Enlarged	2.12 (1.90, 2.50)	4.19 (3.58, 4.81)


a) Changes in effort
b) Quantity/quality tradeoff
c) Variance sensitivity
IVI
and/or
Energy per visit
and
Selectivity
R
C
E
Brood demand

796 **Figure 1**



797

798 **Figure 2**

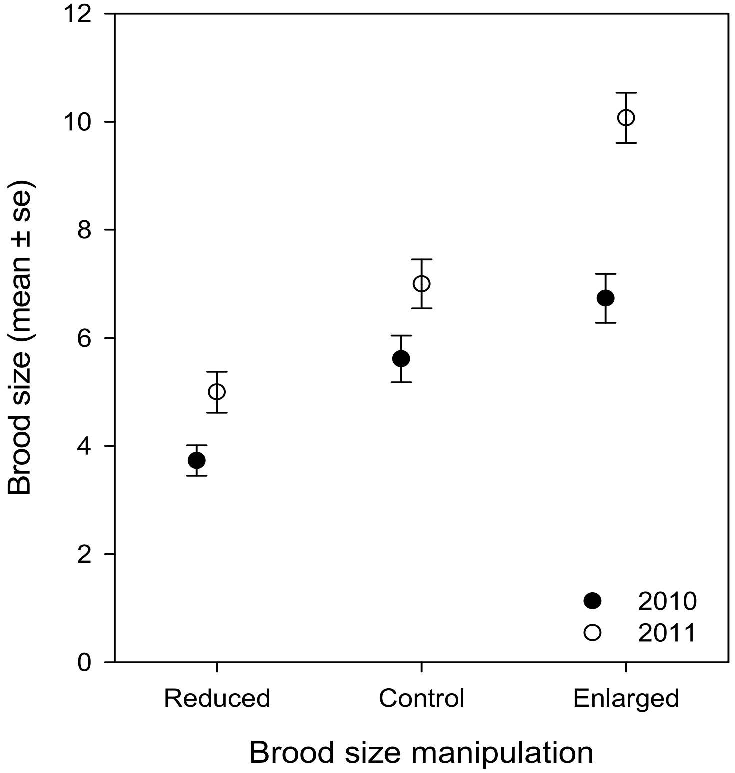

Brood size (mean ± se)
0
2
4
6
8
10
12
Reduced
Control
Enlarged
Brood size manipulation
● 2010
○ 2011

Figure 3

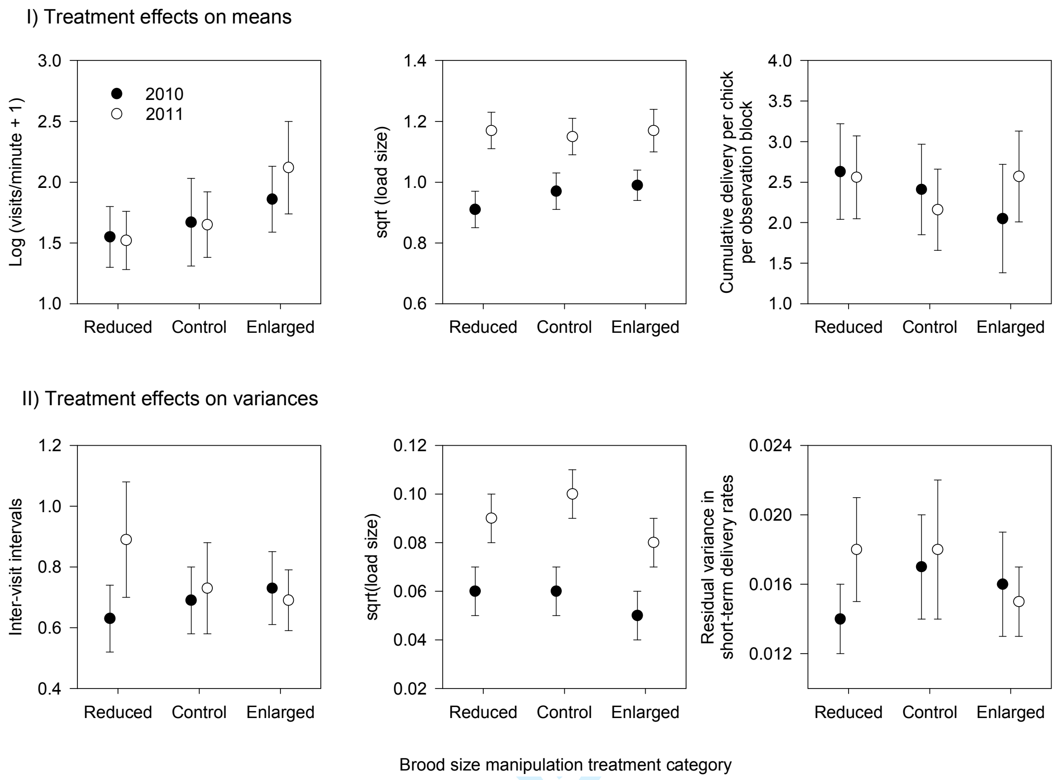
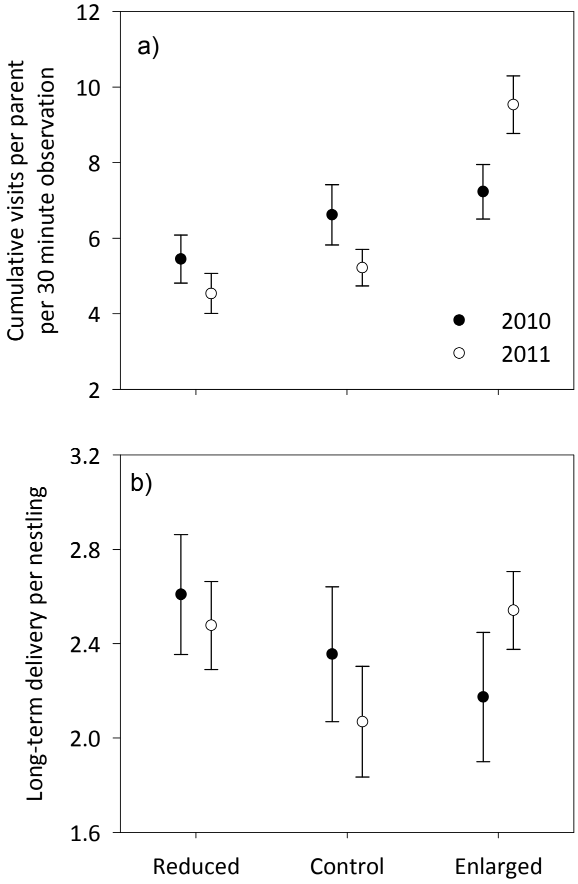

I) Treatment effects on means
Log (visits/minute + 1)
3.0
2.5
2.0
1.5
1.0
● 2010
○ 2011
sqrt (load size)
1.4
1.2
1.0
0.8
0.6
Cumulative delivery per chick per observation block
4.0
3.5
3.0
2.5
2.0
1.5
1.0
Reduced
Control
Enlarged
II) Treatment effects on variances
Inter-visit intervals
1.2
1.0
0.8
0.6
0.4
sqrt(load size)
0.12
0.10
0.08
0.06
0.04
0.02
Residual variance in short-term delivery rates
0.024
0.020
0.016
0.012
Reduced
Control
Enlarged
Brood size manipulation treatment category

Figure 4



803

804 **Figure 5**

Electronic Supplementary Material

Contents

Text S1: Parameter estimation method

We ran each analysis for a range of prior settings to ensure that our estimates were not influenced by the choice of prior. The different prior settings produced very similar estimates for all the parameters estimated (results not shown); analyses presented in the main text use an inverse wishart prior where nu = 0.002. Models were run for 103,000 iterations, with a burn-in period of 3000 and thinning interval of 100. This produced a sample of 1000 estimates for each model. These estimates were used to calculated the most likely value for each parameter (the mode of the distribution), as well as its 95% credible interval.

Text S2: Year differences in parental responses to current brood size

The brood size manipulation (BSM) had different effects on brood size on the day of filming in the two study years (main text Table 1 and Figure 3). Therefore, the year-related differences in parental response to BSM could be due to either to year-specific ecology condition, or year-specific effects of the BSM on realized brood size. To address these two possibilities, we repeated the analyses presented in Tables 2 and 3 of the main text using as predictor variables brood size on the day of filming (instead of BSM), year, and the brood size: year interaction. If among-year differences in response to the BSM were due to the fact that the BSM had different effects on brood size in the two years, then we expect brood size to predict parental behaviour, but we do not expect a year x brood size interaction effect. Because average brood size differed across the two study years, we centered brood size within-years prior to analyses to break the correlation between year and brood size.

In all cases where we interpreted support for year-specific effects of the BSM on mean levels of parental provisioning (IVI, load size, prey type) in the main text, analyses using current brood size, year, and their interaction (rather than year-specific BSM) showed moderate to significant support for the year x brood size interaction (Bayesian p-values: IVI = 0.062, load size = 0.041, prey type = 0.017) (see Table S1). Further, consistent with analyses using a variable combining year and BSM as a fixed effect (YBSM, a fixed effect with 6 levels, see Table 3, main text), there was no support for an interaction between year and brood size on the nestling level delivery (Bayesian p-value = 0.27). Modelling brood size as a fixed effect rather than the Year: BSM also had no effect on the estimated residual variances relative to the analyses presented in the main text. These findings indicate that between-year differences in the realized effect of the BSM on the number of nestlings cannot account for year-related differences in the effect of the BSM categories on parental provisioning decisions, and corroborate the interpretation that year-specific ecological conditions shape the response of parent great tits to variation in brood demand.

Text S3: Year differences in ecological conditions

To describe the differences in the ecological conditions across the two study years, we considered average daily temperature and daily probability of rainfall, two variables previously shown to influence the energetic requirements of great tit nestlings (Radford *et al.* 2001). Weather data were obtained from the Rothenfeld weather station located in the center of the study area (http://www.gkd.bayern.de/). We tested for between-year differences in average daily temperature (^{o}C) and total daily probability of precipitation (rain = 1, no rain= 0) throughout the breeding season using a generalized linear model (glm). Data were included for the months of

April, May and June, to cover the period from egg laying to nestling fledging for our first broods. In 2010, weather data was unavailable for 4 days during this period, resulting in N = 87 days of weather data for 2010 and N = 91 days of weather data for 2011. Year, April day (days since April 1st), and their interaction were included as fixed effects. Temperature was modelled with Gaussian errors and probability of precipitation was modelled with binomial errors. Analyses using daily precipitation (in mm) gave qualitatively similar results to analyses of daily probability of rainfall, and we present only the latter analyses here.

We also investigated annual differences in nestling mortality, both before and after the brood size manipulations. To control for annual differences in clutch size, we modelled mortality as a two-column matrix comprised of the number of nestlings dead and the number of nestlings alive (using the "cbind" function). For mortality prior to the manipulations, these values were the number of nestlings that died between hatching and nestling day 3 (dead) and the number of nestlings that survived until day 3 (alive). For mortality after the brood size manipulation, these values were the number of nestlings that died between day 3 and fledging (dead), and the number of nestlings that survived from day 3 until fledging (alive). For analyses of mortality prior to the BSM, mortality was modelled as a function of year, and plot was included as a random effect. For analyses of post-manipulation mortality, we modelled mortality as a function of year-specific treatment (6-level factor: 2010 Reduced, 2010 Control, 2010 Enlarged, 2011 Reduced, 2011 Control, 2011 Enlarged). Models were fitted with a binomial error distribution (coded as family = "multinomial2").

Analyses of temperature and precipitation data confirmed earlier work suggesting that 2010 was a more challenging season to great tits breeding in our study populations compared with 2011 (Nicolaus *et al.* 2015). At the start of the breeding season, average daily temperatures were 3.8°C

(95% CI = 1.68, 5.96) higher in 2011 compared with 2010. Average daily temperatures increased across the breeding season (April to June) in both years (2010: β = 0.13°C per day, 95% CI = 0.09, 0.16; 2011: β = 0.07°C, 95% CI = 0.04, 0.10, Fig. S2a), but the increase was greater in 2010. Thus, year differences in temperatures were greatest early in the breeding season (Fig. S2a).

The 2010 breeding season was also more challenging with regards to precipitation (Fig. S2b). At the beginning of the breeding season, there was moderate support for the interpretation that the daily probability of precipitation was greater in 2010 compared with 2011 (odds ratio β = 1.54, 95% CI = -0.24, 2.90). The daily probability of precipitation increased in 2011 (β = 0.04, 95% CI = 0.02, 0.05), but there was no evidence for a seasonal increase in 2010 (β = 0.01, 95% CI = -0.01, 0.02). Thus, as with year differences in temperature, year differences in precipitation were greatest early in the breeding season (Fig. S2b).

The year differences in ecological conditions were also reflected in year differences in nestling mortality. Prior to manipulations, mortality was higher in 2010 compared with 2011 (mean % mortality: 3.5% versus 0.2%, Fig. S3a). This corresponded to an estimated difference in odds ratios of β = 3.58, 95% CI = 1.60, 5.70). Post-manipulation mortality was also higher in 2010 (Fig. S2b, mean % mortality: 55% in 2010 versus 31% in 2011). Additionally, mortality increased across BSM categories in 2010 (i.e. enlarged broods had higher mortality than reduced broods without overlap in 95% CIs), but not in 2011 (Table S1 and Fig. S3b).

Table S1: Variation in mean inter-visit interval (IVI, in seconds), load size (bill volumes), and prey type (preferred or non-preferred), and short-term delivery experienced at the level of nestlings (load size/IFI/brood size) in relation to brood size (within-year centered), year, and their interaction. IVI and delivery data were ln transformed, and load size was square-root transformed. Data were modelled with Gaussian (IVI, load size, delivery) or binomial (prey type) errors. Year-BSM-specific residual variances were fitted for IVI, load size and delivery, but not for prey type, as it is not possible to fit heterogeneous residual errors to binomial data. Values presented are estimated means (β) and their 95% credible intervals (CI).

	Ln IVI	**Sqrt load size**	**Prey type[1]**	**Ln delivery**
Fixed effects	**β ± 95% CI**	**β ± 95% CI**	**β ± 95% CI**	**β ± 95% CI**
Intercept[2]	4.85 (4.74, 4.95)	0.96 (0.93, 1.00)	-8.31 (-14.75, -1.76)	-6.12 (-6.23, -6.00)
Brood size	-0.05 (-0.09, 0.01)	0.01 (0.00, 0.03)	0.23 (-0.65, 1.39)	-0.03, -0.09, 0.02)
Year (2011)	0.12 (-0.01, 0.26)	0.19 (0.14, 0.24)	11.82 (2.25, 20.82)	-0.05 (-0.21, 0.09)
Brood size: Year (2011)	-0.05 (-0.11, 0.02)	-0.02 (-0.04, 0.00)	-1.12 (-2.61, 0.11)	0.02 (-0.04, 0.09)
Residual variance	**σ^2 ± 95% CI**	**σ^2 ± 95% CI**	**σ^2 ± 95% CI**	**σ^2 ± 95% CI**
2010				
Reduced	0.55 (0.46, 0.65)	0.054 (0.046, 0.062)	NA	0.88 (0.74, 1.03)
Control	0.56 (0.48, 0.64)	0.058 (0.049, 0.068)	NA	1.05 (0.88, 1.21)
Enlarged	0.60 (0.50, 0.69)	0.046 (0.040, 0.053)	NA	1.11 (0.96, 1.28)
2011				
Reduced	0.76 (0.60, 0.93)	0.09 (0.07, 0.10)	NA	1.05 (0.87, 1.26)
Control	0.63 (0.51, 0.76)	0.09 (0.08, 0.11)	NA	1.15 (0.96, 1.36)
Enlarged	0.57 (0.49, 0.63)	0.08 (0.07, 0.09)	NA	1.04 (0.90, 1.17)

1. Prey type was modelled with binomial errors. Preferred prey (i.e. caterpillars) were coded as 1, and non-preferred prey (i.e. others) were coded as 0. Estimates are in ln (odds ratios): therefore, an estimate of 0 represents an equal proportion of preferred and non-preferred prey in the diet; an estimate of 0.69 represents cases where preferred prey are twice as frequent as non-preferred prey, and an estimate of -0.69 represents cases where non-preferred prey are provisioned twice as much as preferred prey.

2. Intercept estimated at within-year centered brood size of zero, and year = 2010.

Table S2: Nestling mortality as a function of year and BSM. Nestling mortality was modelled using as the ln odds ratio of dying versus surviving (dead, alive) between the brood size manipulation day and fledging. Values presented are estimated means (β) or variances (σ^2) and their 95% credible intervals (CI).

	Mortality (odds ratio of dying)[1]
Fixed effects	**β ± 95% CI**
2010	
Reduced	-0.48 (-1.65, 0.92)
Control	0.85 (-0.50, 2.27)
Enlarged	2.41 (1.10, 3.60)
2011	
Reduced	-1.93 (-3.27, -0.46)
Control	-1.81 (-3.26, 0.48)
Enlarged	-0.84 (-2.18, 0.40)
Random effects	**σ^2 ± 95% CI**
Plot	1.55 (0.26, 3.43)
Residual	8.95 (5.63,12.77)

[1] Estimates are in ln (odds ratios): therefore, an estimate of 0 represents an equal proportion of nestlings that died and survived in the specified interval (i.e. 50% mortality); an estimate of 0.69 represents cases where dying is twice as likely as surviving, and an estimate of -0.69 represents cases where surviving is twice as likely as dying.

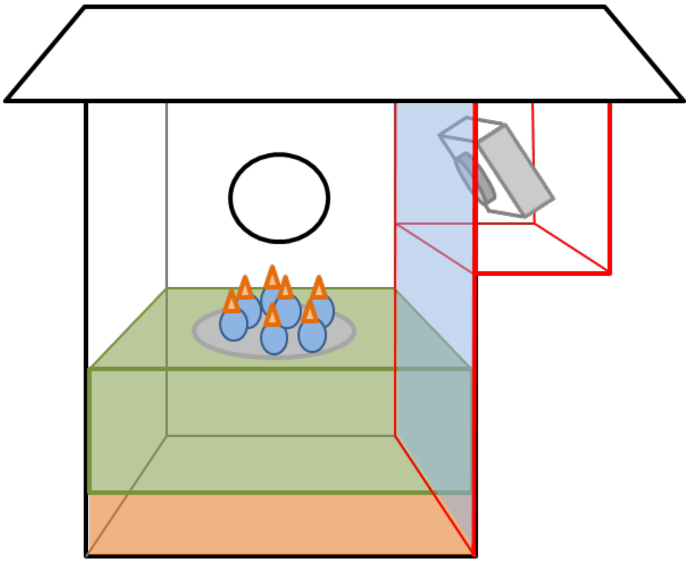


Figure S1: Schematic overview of nestbox during provisioning trials. The side door (illustrated in red) with camera (illustrated in grey) was installed two days before provisioning videos were recorded, and was replaced with the original door after recordings were complete. A sheet of clear plexiglass (illustrated in blue) was placed between the nest and the side door in order to prevent parents from sitting within the side compartment that housed the camera, which would have obscured views from the camera. Additionally, a small piece of foam (illustrated in orange) was placed below the nesting material (illustrated in green) to ensure that the full nestcup was visible in recordings.

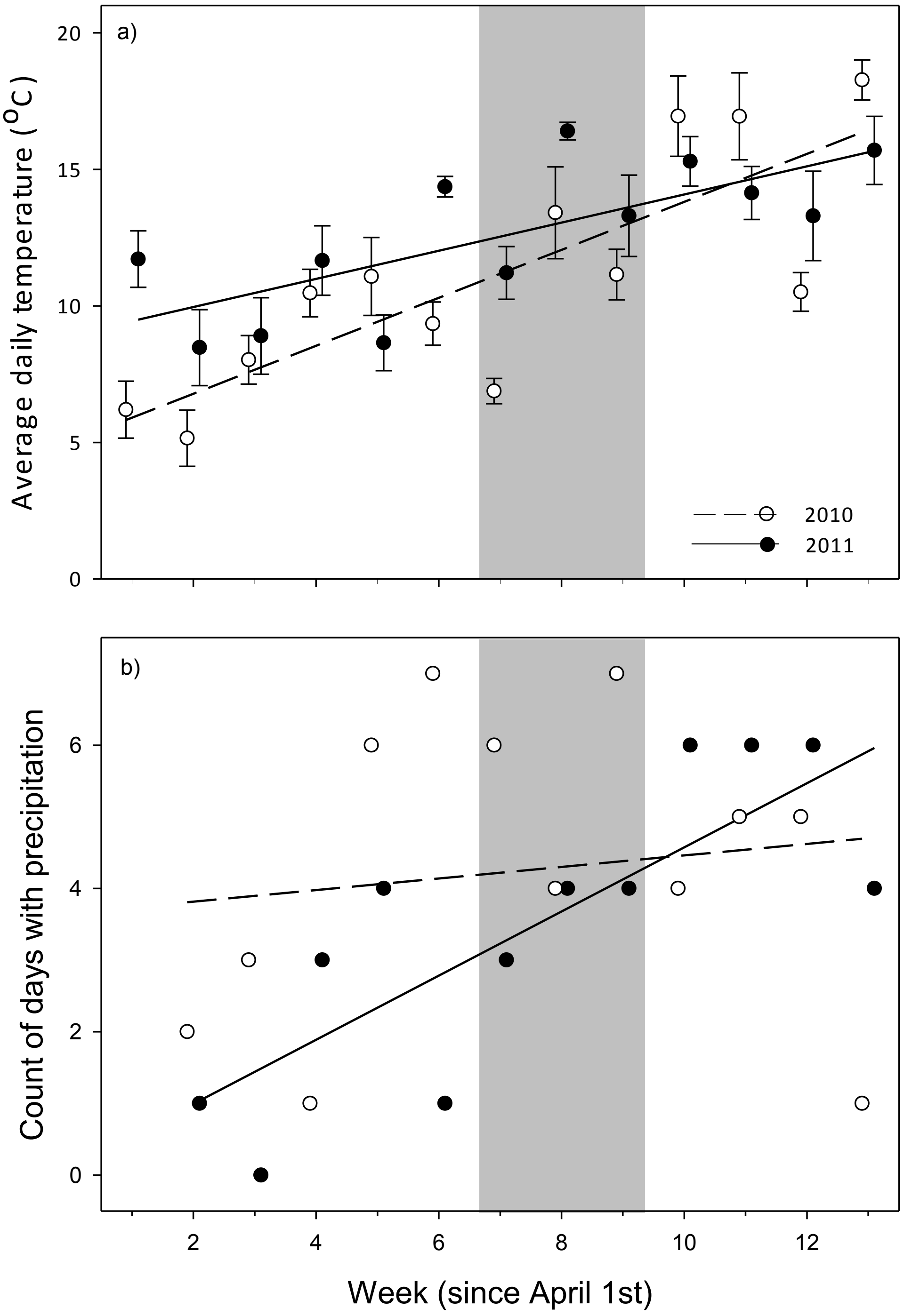


Figure S2: Annual differences in a) temperature and b) precipitation throughout the breeding seasons in 2010 and 2011. In a) values presented are weekly means ± 1 s.e. In b) values presented are counts of days with precipitation in each week. Week 1 is not shown in Fig. 3b) because of missing data from the weather station. The weeks during which provisioning behavior was observed are indicated with grey shading. Lines are best fits to the raw data.

Supplementary References

Nicolaus, M., Mathot, K.J., Araya-Ajoy, Y.G., Mutzel, A., Wijmenga, J.J., Kempenaers, B. & Dingemanse, N.J. (2015) Does coping style predict optimization? An experimental test in a wild passerine bird. *Proceedings of the Royal Society B Biological Sciences,* **282,** 20142405.

Radford, A.N., McCleery, R.H., Woodburn, R.J.W. & Morecroft, M.D. (2001) Activity patterns of parent Great Tits *Parus major* feeding their young during rainfall. *Bird Study,* **48,** 214-220.