

Exploratory behaviour and foraging strategies in Mediterranean blue tits

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Abstract

Exploratory behaviour and foraging strategies in Mediterranean blue tits. Animal behaviour is potentially a mechanism of individual diet specialization. To explore this possibility we assessed exploratory behaviour (EB) and foraging data for a population of blue tits *Cyanistes caeruleus*. Our results suggest that: 1) foraging differs between sexes; 2) the prey type selected by females depends on the provisioning rates of their mate, and adjustment of this prey-choice differs between EB phenotypes; and 3) foraging behaviour in males shows a trend towards linkage to their EB phenotype, with faster-exploring males obtaining marginally larger caterpillars but provisioning less frequently than slower-exploring males. Lastly, environmental variables contributed substantially to the diet composition of offspring. For this reason, we cannot suggest that EB dominates, but it may contribute to a diet specialization process in our study population.

Key words: Behaviour, Diet specialization, Prey choice, Intersexual differences

Resumen

Comportamiento exploratorio y estrategias de búsqueda de alimento en herrerillos Mediterráneos. El comportamiento animal tiene la capacidad de ser un mecanismo de especialización individual de la dieta. Para comprobarlo, se estudió el comportamiento exploratorio (EB por su sigla en inglés) y se obtuvieron datos sobre búsqueda de alimento en una población de herrerillo común, *Cyanistes caeruleus*. Los resultados muestran que 1) existen diferencias en la búsqueda de alimento entre sexos; 2) el tipo de presa elegido por las hembras depende de la frecuencia de aprovisionamiento de su pareja y este ajuste de la elección de la presa difiere entre los fenotipos de EB; y 3) existe una tendencia que relaciona el comportamiento de búsqueda de alimentos de los machos con su EB, por la que los machos con un comportamiento exploratorio más rápido obtienen orugas marginalmente más grandes, pero alimentan a sus pollos menos veces que los exploradores más lentos. Por último, las variables ambientales contribuyeron sustancialmente a la composición de la dieta de los pollos de herrerillo. Por ello, no podemos sugerir que el EB sea el principal factor determinante de los procesos de especialización de la dieta en la población estudiada, pero sí que puede contribuir a dichos procesos.

Palabras clave: Comportamiento, Especialización en dieta, Elección de presa, Diferencias intersexuales

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Introduction

Animal behaviour may be a mechanism of individual diet specialization. A relationship between behavioural phenotypes and foraging strategies can imply that selection pressures differ among individuals within a population (Toscano et al., 2016). Studies on consistent behavioural differences between individuals (termed animal personality; Réale et al., 2010) have gained traction over the last two decades, steadily increasing our understanding of how behavioural traits in avian species relate to one another or to various fitness parameters. Diet studies in common passerine species have been fairly common since the 1970s, but most early studies are limited to descriptive statistics that provide rough information on prey proportions and often include broad categories of prey types (Eguchi, 1980; Blondel et al., 1991). In later diet studies, there has been a shift to a more thorough description in the offspring diet (García-Navas and Sanz, 2011; García-Navas et al., 2013), but to date, few studies have addressed in detail the intrapopulation variability in offspring diet composition (or parental prey preference).

Not only environmental variables but also social factors have been related to diet variability across taxa (Blondel et al., 1991; Naef-Daenzer et al., 2000; Sih and Christensen, 2001; Marshall et al., 2015). In passerines, possibly the most widely studied parameters associated with nestlings' diet are those linked to the calendar date (Dias and Blondel, 1996). It is well known that insectivorous birds aim to synchronize the period in which their offspring have the greatest energetic demand with the phenological moment when their main caterpillar prey species peaks (Blondel et al., 1991; García-Navas and Sanz, 2011; but see Naef-Daenzer et al., 2000). Caterpillar phenology, their availability or their scarcity, and their size seem to have an effect in the diet of nestlings. García-Navas et al. (2013), for example, found that in blue tits *Cyanistes caeruleus*, a great abundance of noctuid caterpillars fosters the use of this resource, and for great tits *Parus major*, hairy caterpillars of the *Malacosoma* genus were fed to the offspring of late nests. In this latter example, the researchers also highlight that males were significantly more likely than females to feed their offspring hairy caterpillars, and they suggest that personality traits may be responsible for this difference.

Individual personality is a potential driver of dietary specialization because different behavioural phenotypes may contribute to creating differences in foraging behaviour. Along this line, Toscano et al. (2016) suggest a series of pathways relating personality traits to foraging behaviour, such as foraging activity (related to activity and prey search), risk-dependent foraging, social foraging, and physiological drivers (i.e. hormonal control). Other studies have assessed direct or indirect relationships between behavioural traits and provisioning rates (Mutzel et al., 2013; David et al., 2015; Serrano-Davies et al., 2017) or spatial foraging behaviour (Minderman et al., 2010; van Overveld and Matthysen, 2010). To date, however,

the relationship between avian behaviour and offspring diet composition remains understudied.

Exploratory behaviour (EB) refers to the way an individual interacts with a new object or environment. It has been widely used to study personality in passerines because it is a relatively easy trait to measure. Furthermore, it has proven to correlate with other personality traits (Verbeek et al., 1996; Mutzel et al., 2013) and to life-history traits (Dingemanse et al., 2004; Velasco et al., 2022). In blue tits, EB has been linked to local migration patterns (Nilsson et al., 2010), spatial aspects of foraging (Herborn et al., 2010), survival (Velasco et al., 2022), habitat selection and provisioning rate (Serrano-Davies et al., 2017).

In this study we assessed the phenotypic relationship between EB and provisioning strategies. We measured EB *in situ* in a population of blue tits in central Spain and we recorded the diet of their nestlings over two consecutive reproductive seasons. As intrapopulation differences in EB between sexes (Velasco et al., 2022) were observed in a previous study, we hypothesized that prey choice and provisioning effort would differ between males and females. Individuals with different behavioural phenotypes were expected to have different foraging strategies (Toscano et al., 2016). Therefore, we also hypothesized that the variability in EB between individuals would affect the diet composition of offspring. Because tortricid caterpillars (*Tortrix* spp. and *Archips* spp.) in our study area are superabundant, it could be expected that faster—and also shallower explorers (Verbeek et al., 1994) supply a higher proportion of tortricids to their offspring. In contrast, as noctuid and geometrid caterpillars are cryptic (but likely more caloric; García-Navas et al., 2013), slower and more thorough explorers are expected to supply higher proportions of these prey (Verbeek et al., 1994; García-Navas et al., 2013).

Material and methods

This research is part of an ongoing project in which two populations of blue tits have been monitored since 2005. These blue tits breed in the nest boxes situated in two study plots within the country estate of Quintos de Mora (Toledo, Spain). The study plots (Val: Arroyo de Valdeyernos 39° 26' 12" N, 4° 05' 37" W; and GG: Barranco de Gil García 39° 22' 43" N, 4° 07' 31" W) are located in forests dominated by Pyrenean and Portuguese oaks (*Quercus pyrenaica* and *Q. faginea* respectively). In each area, there are 100 nest boxes, and an average of 65% of these boxes are occupied by blue tits each year. Data for this study are derived from the fieldwork of 2018 and 2019 breeding seasons. Laying dates for the blue tits vary between years, but monitoring tasks commonly begin in the second fortnight of March, and often extend into June. Nest box monitoring includes: detecting nests, determining laying and hatching dates, ringing adults and offspring, and taking biometric measures. The hatch day is defined as 'day 0' for each nest. Adults are captured on day 8 using spring traps inside the

nest boxes, and nestlings are ringed and measured on day 13. All the individuals are fitted with uniquely numbered aluminium rings (if not previously banded), and a EURING age class is assigned based on plumage characteristics (Demongin, 2016).

Novel environment exploratory tests

After the adults were banded and measured on day 8, 379 individuals were tested for exploratory behavior using an in situ Novel Environment (NE) test (Stuber et al., 2013). These tests are the same as those described by Velasco et al. (2022), but a brief summary is provided here. Tested individuals had access to a test box through a sliding pane that was connected to a small wooden box (holding room) to it. The individuals stayed in this holding room for 1 minute to homogenize their stress levels prior to the NE test. Once access to the test box was allowed, latency time was obtained (time to enter the test box). The maximum value for latency was two minutes, after which the bird was 'flushed' into the test box. The EB was then recorded for 5 minutes. After this time, the individuals were set free without further contact with the researchers. In 2018, all the exploratory tests included in this analysis took place between 14 IV and 28 V. In 2019, the exploratory tests took place between 19 III and 7 V.

During visualization, the test box was virtually (not physically) divided into six sections to determine the spatial distribution of EB. The first two minutes of the test were visualized to determine the exploratory variables: number of movements, number of area changes and number of areas explored. All the exploratory videos were observed by the same researcher (ACV). A principal components analysis (PCA) including the latency and the exploratory variables returned two axes or principal components (PC) with eigenvalues > 1. The PCs were centered and scaled prior to further analysis.

Provisioning behavior

The original nest box was replaced by a nest box adapted to hold a handycam (Sony HDR–XR550V; Sony Corp., Tokyo, Japan; see fig. 1s in supplementary material) one day prior to recording (day 10) to habituate birds to this setup. On day 11, the cameras were placed in the extra compartment of the adapted nest box, allowing us to film the entrance of the nest box in infrared light. A minimum of two–and a half hours was recorded per nest, but the first hour was discarded to avoid an artificially reduced provisioning rate due to nest manipulation disturbance (Hinde, 2006; García–Navas et al., 2013). No nest was deserted after recording. For the following hour, every time a bird entered the box, the following information was noted: time of entry, time of exit, sex of the bird (male or female), prey order (Arachnida, Lepidoptera, Other or Unidentified), prey family (only for caterpillars: Noctuidae, Geometridae, Tortricidae, Other or Unidentified) and prey length and width (only for caterpillars). All the provisioning videos were processed by the same researcher (ACV).

The sex of the visiting adult was easily identifiable from the rings. The leg on which the aluminum ring was fitted and an additional PVC ring on the opposite leg facilitated this. The PVC rings are also frequently readable in our recordings (see video 1s for an example in supplementary material). In this study we only used the videos that allowed identification of both provisioning individuals ($N = 119$ pairs). Caterpillars were measured using a pixel ruler (MB–ruler, MB–softwaresolutions). This measure was converted to centimeters using the nest box entrance diameter (3.5 cm) as a reference. We assumed a cylinder to be a relatively good approximation to the caterpillar volume and used the length and width of these prey to obtain their volume (cm^3 ; Slagsvold and Wiebe, 2011).

The category 'Lepidoptera' included –from most common to least common– caterpillars, pupae and moths. The category 'Other' in prey order (6% of the total identified observations) included Diptera, Coleoptera, Hemiptera, Hymenoptera or Orthoptera. Some items, especially if very small, were impossible to identify to Order level (approx. 7% of the preys) or to Family level (approx. 10% of the caterpillars). The category 'Other' in the case of caterpillar families (7% of the identified caterpillars) almost entirely included Lycaenidae caterpillars. We took into account potential differences in diet composition due to prey phenology by including the laying date in the analyses (see 'Statistical analysis' section below).

Statistical analysis

All statistical analyses were performed in R 3.1.2 (R Core Team, 2020). Mann Whitney U–tests were used to explore differences in the response variables between sexes. For this test, we excluded individuals with only one provisioning event ($N = 226$ individuals). The descriptive statistics of the foraging behaviour for both sexes can be found in table 1s in supplementary material. The potential relationships between individual EB and the following individual provisioning behavior variables was assessed: provisioning frequency (number of visits per hour), proportion of lepidoptera over the total number of prey, proportion of arachnids over the total number of prey, proportion of noctuids over the total number of caterpillars, proportion of geometrids over the total number of caterpillars, proportion of tortricids over the total number of caterpillars, and average volume of the caterpillars. All the proportions were analyzed as logistic models with logit link function, while the error distribution of provisioning frequency and prey volume followed a Gamma distribution (log link function). An information–theoretic approach (Akaike Information Criterion (AIC); Zuur et al., 2009) was used to compare models. For each response variable, all models with $\Delta\text{AIC} \leq 2$ were considered equivalent (see tables 2s–7s in supplementary material). From these equivalent models, estimates were averaged and unconditional standard errors and confidence intervals were obtained (Burnham and Anderson, 2002).

Table 1. Results of the model averaging the equivalent best-ranked GLMs ($\Delta AIC \leq 2$) relating female prey choice at Order level to exploratory behaviour and extrinsic variables. Parameter estimates and their corresponding unconditional standard errors (USE) were obtained through model averaging of the best ranked equivalent models ($\Delta AIC \leq 2$; see table 2s in supplementary material): E, estimate; EB, exploratory behaviour; P.Freq., provisioning frequency; – indicate variables that were included in the analysis but that failed to appear within the best ranked equivalent models.

Tabla 1. Resultados de promediar los modelos lineales generalizados equivalentes al mejor modelo ($\Delta AIC \leq 2$) que relacionan la elección de presas a nivel de orden por las hembras con el comportamiento exploratorio de estas y con variables extrínsecas. Las estimaciones de los parámetros y sus correspondientes errores estándar no condicionales (USE) se obtuvieron calculando el promedio de los modelos equivalentes al mejor modelo ($\Delta AIC \leq 2$; véase la tabla 2s del material suplementario): E, estimación; EB, comportamiento exploratorio; P.Freq., frecuencia de aprovisionamiento; – indican variables que se incluyeron en el análisis, pero que no aparecieron en los modelos equivalentes al mejor modelo.

	E ± USE	$\Sigma\omega(AIC)$	95 % CI		E ± USE	$\Sigma\omega(AIC)$	95 % CI
♀ Order Lepidoptera (%)				♀ Order Arachnida (%)			
Area: Val	–	–	–	–0.02 ± 0.17	0.019	–0.36, 0.32	
Brood size	0.00 ± 0.03	0.024	–0.06, 0.07	–	–	–	
♀ EB PC1	0.00 ± 0.06	0.020	–0.11, 0.11	–0.03 ± 0.11	0.048	–0.24, 0.19	
♀ EB PC2	–0.06 ± 0.17	0.056	–0.39, 0.26	0.14 ± 0.26	0.130	–0.36, 0.65	
♀ Age: > 1 year	0.08 ± 0.28	0.057	–0.48, 0.64	–0.05 ± 0.26	0.040	–0.56, 0.45	
Relative lay date	0.00 ± 0.01	0.020	–0.01, 0.01	0.00 ± 0.01	0.039	–0.02, 0.02	
♂ P.Freq.	0.00 ± 0.01	0.019	–0.02, 0.02	0.00 ± 0.01	0.019	–0.02, 0.02	
Year: 2019	–	–	–	0.00 ± 0.16	0.019	–0.31, 0.31	

The nest can be considered a working unit (Both et al., 2005; Hinde, 2006; Mutzel et al., 2013): individuals breeding together affect each other's behavior. These pair-effects may not necessarily work in both directions (Schuett et al., 2010). Because of this, models were fitted separately for the sexes to include the parameters of the breeding partner in the models. Furthermore, only nests for which the EB of both individuals was known were used ($N = 119$ pairs). Because this study took place over two consecutive years, some individuals were repeated (15 females and 18 males), but only 4 couples remained the same in both years. Removing the repeated couples did not produce different results.

In addition to individual exploration scores (covariates, two principal components), all models included brood size (covariate), relative laying date (covariate, relativized to the average laying date of each area each year), individual age (factor with two levels: yearling or older), year (factor with two levels) and area (factor with two levels). The provisioning frequency of the breeding partner was also included in all analysis (covariate). Individuals were expected to adjust their provisioning frequency to the size of the available prey, so when analyzing this variable, the individuals' average prey volume was included as a covariate. Initially, the EB score of the partner was included in all models, as was habitat effect (number of trees in a radius of 25 m), but these terms were non-significant in all cases and

were removed from the models. The variance inflation factor (VIF) was calculated for every model to test for collinearity between variables. Quadratic effects and potential two-way interactions between the explanatory variables were explored, but only those with $P < 0.05$ were included in the models. To facilitate the interpretation of our results, female EB PC1 was transformed to a categorical variable in the figures using the standard deviation (SD) so as to classify them into slower-explorers ($EB < SD$), faster-explorers ($EB > SD$) and intermediate explorers (EB within the SD).

Results

Exploratory PCA scores were the same as those obtained in a previous study (Velasco et al., 2022), but a brief summary is included here. Two principal components with eigenvalues > 1 were obtained and used in further analysis. Forty-seven percent of the variance in EB was explained by the first principal component (PC1) and 26% of the variance was explained by the second component (PC2). PC1 conformed a slow-fast continuum, with higher values in individuals with a higher number of movements and area changes, and taking less time to explore a minimum of three areas. The PC2 axis was referred to as daring-timid as it reflects the latency to enter the test-box: higher values indicate longer latency (more timid EB).

Table 2. Results of model averaging the equivalent best-ranked GLMs ($\Delta AIC \leq 2$) relating male prey choice at Order level to exploratory behaviour and extrinsic variables. Parameter estimates and their corresponding unconditional standard errors (USE) were obtained through model averaging of the best ranked equivalent models ($\Delta AIC \leq 2$; see table 3s in supplementary material): E, estimate; EB, exploratory behaviour; P.Freq., provisioning frequency; – indicate variables that were included in the analysis but that failed to appear within the best ranked equivalent models.

Tabla 2. Resultados de promediar los modelos lineales generalizados equivalentes al mejor modelo ($\Delta AIC \leq 2$) que relacionan la elección de presas a nivel de orden por los machos con el comportamiento exploratorio de estos y con variables extrínsecas. Las estimaciones de los parámetros y sus correspondientes errores estándar (USE) no condicionales se obtuvieron calculando el promedio de los modelos equivalentes al mejor modelo ($\Delta AIC \leq 2$; véase la tabla 3s del material suplementario): E, estimación; EB, comportamiento exploratorio; P.Freq., frecuencia de aprovisionamiento; – indican variables que se incluyeron en el análisis, pero que no aparecieron en los modelos equivalentes al mejor modelo.

	E ± USE	$\Sigma\omega(AIC)$	95% CI		E ± USE	$\Sigma\omega(AIC)$	95% CI
♂ Order Lepidoptera (%)				♂ Order Arachnida (%)			
Area: Val	0.58 ± 0.55	0.166	–0.50, 1.66	–	–	–	–
Brood size	0.01 ± 0.04	0.024	–0.06, 0.07	–	–	–	–
♂ EB PC1	0.00 ± 0.05	0.015	–0.10, 0.09	0.01 ± 0.09	0.032	–0.18, 0.19	
♂ EB PC2	0.00 ± 0.06	0.016	–0.12, 0.12	0.00 ± 0.12	0.032	–0.23, 0.24	
♂ Age: > 1 year	–	–	–	–	–	–	–
Relative lay date	0.00 ± 0.01	0.042	–0.02, 0.02	–	–	–	–
♀ P.Freq.	0.01 ± 0.02	0.046	–0.03, 0.04	–	–	–	–
Year: 2019	0.02 ± 0.15	0.019	–0.28, 0.31	0.00 ± 0.24	0.032	–0.48, 0.48	

Males in our study area brought a significantly higher proportion of spiders ($W = 5,071$; $P < 0.001$) and geometrid caterpillars ($W = 5,530$; $P = 0.003$), and had higher provisioning frequencies than females ($W = 4,840$; $P < 0.001$).

Offspring diet composition

For both sexes, EB was part of the best-fit models for all the response variables (tables 2s, 3s, 5s and 6s in supplementary material). None of the analysed variables had a strong relationship with the type of prey brought to the nest at an Order level (tables 1, 2). After model-averaging, only the first principal component of exploratory behaviour in females (female EB PC1) was significantly related to offspring diet composition. A significant interaction between female EB PC1 and the frequency of male visits revealed that when the male provisioning rate was high, faster-exploring females fed their nestlings more geometrids than slower-exploring ones (fig. 1; table 3). Similarly, a significant interaction between female EB PC1 and male provisioning frequency indicated that slower-exploring females brought a higher proportion of tortricids to the nest when they paired with males that fed their young at high frequencies (fig. 2; table 3). When females paired with a male with a low visit frequency,

slower-exploring females brought a lower proportion of tortricids than faster-exploring females (fig. 2). Although non-significant through model averaging, female EB PC2 had certain importance in the geometrid and tortricid proportion models. A trend indicated that more timid females (higher EB PC2) were more likely to bring geometrid caterpillars than their counterparts, which brought marginally higher proportions of tortricid caterpillars (table 3).

Consistently for both sexes, environmental variables related significantly (and in opposite directions) to the proportion of noctuid and tortricid caterpillars (tables 3, 4). Birds that bred relatively early brought higher proportions of tortricid caterpillars than later breeders, but later breeders brought a higher proportion of noctuids than early breeders (tables 3, 4). The proportion of tortricid caterpillars was significantly higher in 2019 than in 2018, and the opposite was true for the proportion of noctuids. For females, but not for males, the proportion of geometrids was significantly higher in 2019 than in 2018 (table 3).

Provisioning effort

Females' EB was unrelated to the provisioning effort in both regarding visits rate and prey volume (table 5). For males, although non-significant after model ave-

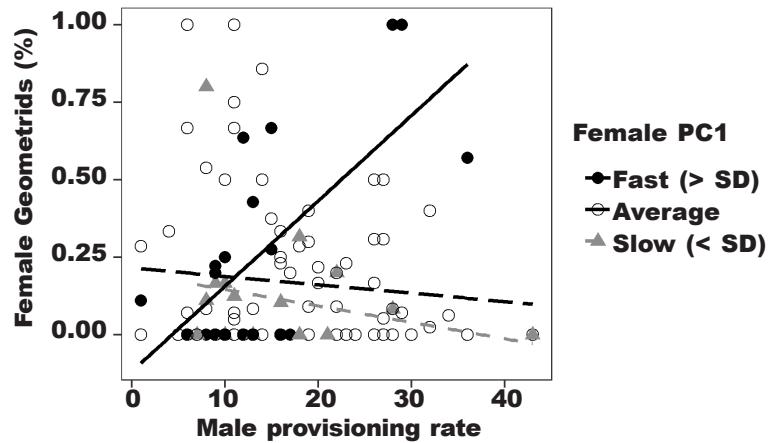


Fig. 1. Relationship between the proportion of geometrids obtained by females and the provisioning rate of males (/h), mediated by female exploratory behaviour (EB PC1): fast females, black circles, continuous line (EB > SD); slow females, grey triangles, short-dashed line (EB < SD); intermediate females, empty circles, long-dashed line; SD, standard deviation.

Fig. 1. Relación entre la proporción de geométridos obtenidos por las hembras y la frecuencia de aprovisionamiento de los machos (/h), mediada por el comportamiento exploratorio de las hembras (EB PC1: hembras rápidas, círculos negros, línea continua (EB > SD); hembras lentas, triángulos grises, línea discontinua con trazos cortos (EB < SD); hembras intermedias, círculos vacíos, línea discontinua con trazos largos; SD, desviación estándar.

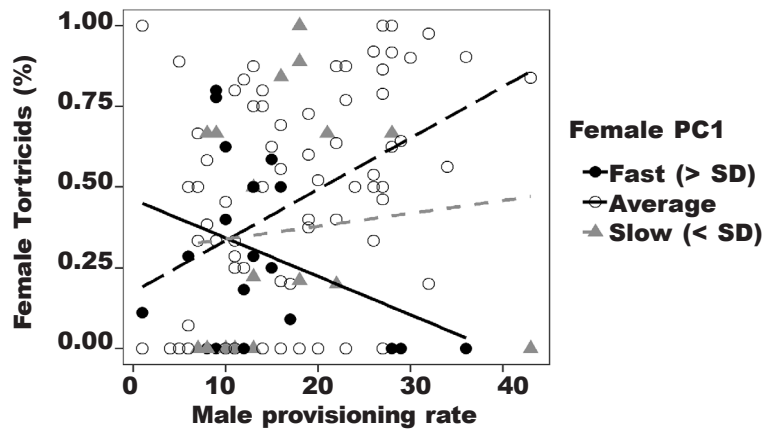


Fig. 2. Relationship between the proportions of tortricids brought to the nest by females and the male provisioning frequency, mediated by female exploratory behaviour (EB PC1): fast females, black circles, continuous line (EB > SD); slow females, grey triangles, short-dashed line (EB < SD); intermediate females, empty circles, long-dashed line; SD, standrad deviation.

Fig. 2. Relación entre la proporción de tortricidos llevados al nido por las hembras y la frecuencia de aprovisionamiento de los machos, mediada por el comportamiento exploratorio de las hembras (EB PC1: hembras rápidas, círculos negros, línea continua (EB > SD); hembras lentas, triángulos grises, línea discontinua con trazos cortos (EB < SD); hembras intermedias, círculos vacíos, línea discontinua con trazos largos; SD, desviación estándar.

Table 3. Results of model averaging the equivalent best-ranked GLMs ($\Delta AIC \leq 2$) relating female caterpillar prey choice to exploratory behaviour and extrinsic variables. Parameter estimates and their corresponding unconditional standard errors (USE) were obtained through model averaging of the best ranked equivalent models ($\Delta AIC \leq 2$; see table 4s in supplementary material): E, estimate; EB, exploratory behaviour; P.Freq., provisioning frequency; – indicate variables that were included in the analysis but that failed to appear within the best ranked equivalent models. Values in bold highlight significant variables (unconditional 95% confidence interval (CI) does not include zero).

Tabla 3. Resultados de promediar los modelos lineales generalizados equivalentes al mejor modelo ($\Delta AIC \leq 2$) que relacionan la elección de orugas por las hembras con el comportamiento exploratorio de estas y con variables extrínsecas. Las estimaciones de los parámetros y sus correspondientes errores estándar (USE) no condicionales se obtuvieron calculando el promedio de los modelos equivalentes al mejor modelo ($\Delta AIC \leq 2$; véase la tabla 4s del material suplementario): E, estimación; EB, comportamiento exploratorio; P.Freq., frecuencia de aprovisionamiento; – indican variables que se incluyeron en el análisis pero que no aparecieron dentro de los modelos equivalentes mejor clasificados. Los valores en negrita resaltan las variables significativas (el intervalo de confianza (IC) incondicional del 95% no incluye el cero).

	E ± USE	$\Sigma\omega(AIC)$	95% CI	E ± USE	$\Sigma\omega(AIC)$	95% CI
♀ Noctuid caterpillars (%)						
Area: Val	0.45 ± 0.47	0.303	–0.46, 1.37			
Brood size	–0.01 ± 0.04	0.051	–0.09, 0.08			
♀ EB PC1	–0.01 ± 0.07	0.044	–0.16, 0.13			
♀ EB PC2	–	–	–			
♀ Age: > 1 year	0.03 ± 0.20	0.045	–0.36, 0.42			
Relative lay date	0.07 ± 0.02	0.356	0.02, 0.11			
♂ P.Freq.	0.00 ± 0.01	0.060	–0.03, 0.03			
Year: 2019	–2.04 ± 0.49	0.356	–3.01, –1.08			
♀ Geometrid caterpillars (%)						
Area: Val	–0.19 ± 0.42	0.184	–1.01, 0.63	♀ Tortricid caterpillars (%)		
Brood size	0.02 ± 0.07	0.081	–0.11, 0.15	0.10 ± 0.41	0.000	–0.71, 0.91
♀ EB PC1	–0.64 ± 0.42	0.378	–1.51, 1.07	0.42 ± 0.34	0.193	–0.23, 1.11
♀ EB PC2	0.43 ± 0.29	0.127	–0.13, 0.99	–0.27 ± 0.26	0.162	–0.77, 0.23
♀ Age: > 1 year	–	–	–	–0.26 ± 0.48	0.050	–1.20, 0.67
Relative lay date	–	–	–	–0.05 ± 0.02	0.162	–0.10, –0.01
♂ P.Freq.	–0.06 ± 0.04	0.378	–0.14, 0.02	0.04 ± 0.03	0.156	–0.02, 0.10
Year: 2019	1.73 ± 0.73	0.378	0.29, 3.16	1.35 ± 0.45	0.162	0.47, 2.23
♀ EB PC1*						
♂ P.Freq.	0.06 ± 0.03	0.378	0.00, 0.11	0.02 ± 0.01	0.156	–0.04, –0.00

raging, EB PC1 had certain relevance in both models (table 6): (1) slower-exploring males had marginally higher provisioning rates than faster-exploring males, and (2) slower-exploring males tended to bring smaller caterpillars than faster-exploring ones.

Brood size related significantly to the provisioning rate in both sexes, indicating that birds with larger brood sizes had a higher number of visits per hour (tables 5, 6). Females with higher provisioning rates brought significantly smaller caterpillars (table 5). Caterpillar volume was significantly related consistently across sexes to the relative laying date and year of

the study. For both males and females, prey volume was larger in later broods than in earlier ones and in 2018 than in 2019 (tables 5, 6).

Discussion

This study presents evidence of how provisioning and foraging strategies in blue tits differ between sexes. Female with opposite EB phenotypes adapted differently to their partner’s provisioning behaviour by modifying their caterpillar prey choice. Males’ EB was

Table 4. Results of model averaging the equivalent best-ranked GLMs ($\Delta AIC \leq 2$) relating male caterpillar prey choice to exploratory behaviour and extrinsic variables. Parameter estimates and their corresponding unconditional standard errors (USE) were obtained through model averaging of the best ranked equivalent models ($\Delta AIC \leq 2$; see table 5s in supplementary material): E, estimate; EB, exploratory behaviour; P.Freq., provisioning frequency; – indicate variables that were included in the analysis but that failed to appear within the best ranked equivalent models. Values in bold highlight significant variables (unconditional 95% confidence interval (CI) does not include zero).

Tabla 4. Resultados de promediar los modelos lineales generalizados equivalentes al mejor modelo ($\Delta AIC \leq 2$) que relacionan la elección de presas a nivel de orden por los machos con el comportamiento exploratorio de estos y con variables extrínsecas. Las estimaciones de los parámetros y sus correspondientes errores estándar (USE) no condicionales se obtuvieron calculando el promedio de los modelos equivalentes al mejor modelo ($\Delta AIC \leq 2$; véase la tabla 5s del material suplementario): E, estimación; EB, comportamiento exploratorio; P.Freq., frecuencia de aprovisionamiento; – indican variables que se incluyeron en el análisis pero que no aparecieron dentro de los modelos equivalentes mejor clasificados. Los valores en negrita resaltan las variables significativas (el intervalo de confianza (IC) incondicional del 95% no incluye el cero).

	E ± USE	$\Sigma\omega(AIC)$	95% CI	E ± USE	$\Sigma\omega(AIC)$	95% CI
♂ Noctuid caterpillars (%)						
Area: Val	–	–	–			
Brood size	–0.01 ± 0.05	0.051	–0.10, 0.08			
♂ EB PC1	–	–	–			
♂ EB PC2	0.04 ± 0.13	0.062	–0.22, 0.30			
♂ Age: >1 year	0.08 ± 0.30	0.072	–0.51, 0.67			
Relative lay date	0.09 ± 0.02	0.349	0.04, 0.13			
♀ P.Freq.	0.00 ± 0.01	0.047	–0.03, 0.02			
Year: 2019	–1.95 ± 0.49	0.349	–2.90, –0.99			
♂ Geometrid caterpillars (%)			♂ Tortricid caterpillars (%)			
Area: Val	–1.26 ± 0.50	0.335	–2.23, –0.28	0.51 ± 0.47	0.321	–0.40, 1.43
Brood size	0.07 ± 0.10	0.189	–0.13, 0.27	–	–	–
♂ EB PC1	0.01 ± 0.06	0.023	–0.11, 0.13	–0.01 ± 0.06	0.043	–0.14, 0.12
♂ EB PC2	–0.02 ± 0.10	0.052	–0.21, 0.18	–0.04 ± 0.13	0.104	–0.30, 0.23
♂ Age: > 1 year	–	–	–	–	–	–
Relative lay date	0.00 ± 0.01	0.023	–0.02, 0.01	–0.07 ± 0.02	0.376	–0.11, –0.02
♀ P.Freq.	–0.01 ± 0.03	0.094	–0.06, 0.04	0.00 ± 0.02	0.040	–0.03, 0.04
Year: 2019	–0.22 ± 0.42	0.216	–1.05, 0.60	1.27 ± 3.53	0.376	1.27, 3.53

weakly related to prey choice, but gained importance in provisioning frequency and prey volume models. In addition to this, this study presents significant differences between the foraging habits of the sexes. These results contrast with previous research on blue tits that failed to detect differences in prey choice between males and females (Blondel et al., 1991; García-Navas et al., 2013). We found that males provisioned their offspring more frequently and brought overall a higher proportion of spiders and geometrid caterpillars than females. This can be due to differences in the exploratory behaviour between sexes described in previous research (Velasco et al.,

2022). A plausible explanation is that our slower-exploring males allocate less time to 'fast-associated' behaviours (such as male-male aggressiveness or nest defence; Schuett et al., 2010; Stuber et al., 2013), consequently increasing their parental care (Boon et al., 2007).

This study presents evidence of how EB links to offspring provisioning strategies and, consequently, to foraging strategies and prey choice. The results show that the relationship between EB and foraging behaviour differs between sexes, and in the case of females, this link was mediated by the provisioning frequency of their breeding male. Schuett et al. (2010)

Table 5. Results of model averaging the equivalent best-ranked GLMs ($\Delta AIC \leq 2$) relating female provisioning effort to exploratory behaviour and extrinsic variables. Parameter estimates and their corresponding unconditional standard errors (USE) were obtained through model averaging of the best ranked equivalent models ($\Delta AIC \leq 2$; see table 6s in supplementary material): E, estimate; EB, exploratory behaviour; P.Freq., provisioning frequency; – indicate variables that were included in the analysis but that failed to appear within the best ranked equivalent models. Values in bold highlight significant variables (unconditional 95% confidence interval (CI) does not include zero).

Tabla 5. Resultados de promediar los modelos lineales generalizados equivalentes al mejor modelo ($\Delta AIC \leq 2$) que relacionan el esfuerzo de aprovisionamiento de las hembras con el comportamiento exploratorio de estos y con variables extrínsecas. Las estimaciones de los parámetros y sus correspondientes errores estándar (USE) no condicionales se obtuvieron calculando el promedio de los modelos equivalentes al mejor modelo ($\Delta AIC \leq 2$; véase la tabla 6s del material suplementario): E, estimación; EB, comportamiento exploratorio; P.Freq., frecuencia de aprovisionamiento; – indican variables que se incluyeron en el análisis pero que no aparecieron dentro de los modelos equivalentes mejor clasificados. Los valores en negrita resaltan las variables significativas (el intervalo de confianza (IC) incondicional del 95% no incluye el cero).

	E ± USE	$\Sigma\omega(AIC)$	95% CI	E ± USE	$\Sigma\omega(AIC)$	95% CI
♀ Provisioning rate (visits/h)				♀ Average caterpillar volume (cm ³)		
Area: Val	0.07 ± 0.10	0.128	–0.26, 0.12	0.06 ± 0.09	0.195	–0.24, 0.13
Brood size	0.12 ± 0.04	0.343	0.04, 0.19	0.02 ± 0.04	0.195	–0.06, 0.11
♀ EB PC1	–	–	–	–	–	–
♀ EB PC2	0.05 ± 0.11	0.050	–0.17, 0.28	–	–	–
♀ Age: >1 year	–	–	–	–	–	–
Relative lay date	–0.01 ± 0.01	0.102	–0.02, 0.01	0.02 ± 0.01	0.414	0.00, 0.03
Year: 2019	–	–	–	–0.31 ± 0.10	0.414	0.11, 0.5
♀ Prey volume	–2.21 ± 0.98	0.343	–4.13, –0.28			

suggest that female mate choice promotes consistency in male behavioural traits (confirmed in our study population; Velasco et al., 2022) because this facilitates females to adapt to the predictable behaviour of their mate (Sanz et al., 2000). This agrees with the results presented in this study: females selected their prey based on the provisioning frequency of their breeding pair, mediated by their own EB.

In our population, the frequency of male provisioning was unrelated to the rate of female provisioning, but it affected the female's prey choice, mediated by female EB. When males had a low provisioning frequency, slower-exploring females brought a lower proportion of tortricids than faster-exploring females (fig. 2), but the opposite is observed for the proportion of geometrids (fig. 1). Faster-exploring females provided a higher proportion of geometrids and a lower proportion of tortricids when they paired with a high-frequency provisioning male than when their mate had a low-frequency of visits. Meanwhile, average- and slow-exploring females obtained higher proportions of tortricids when mating with a male with high provisioning rates compared to females with this same EB phenotype that pair with a low-frequency provisioning male. Thus, when mating with inattentive males, why do slower females provide a higher

proportion of geometrid caterpillars? and why do faster females do the opposite and provide a higher proportion of tortricids? Naef-Daenzer et al. (2000) and García-Navas et al. (2013) suggest different costs regarding search efforts, associated with different prey types and sizes. Without the interaction between the provisioning behaviour of the males, slower-exploring females bring a higher percentage of geometrid caterpillars to the nest, while faster-exploring females bring a higher proportion of tortricids. Thus, our results suggest that geometrids are the preferred prey of slower females, while tortricids are the preferred item of faster females. When offspring are underfed due to a poor-providing male, females will forage for caterpillars they find easier to find so as to reduce foraging costs (Naef-Daenzer et al., 2000). This difference between females of different behavioural phenotypes suggests a pathway for diet specialization regarding the EB. Agreeing with previous literature, our results indicate that faster- and slower-exploring females differ in foraging strategies (Drent and Marchetti, 1999), and these differences could lead to a disparity between the costs of foraging associated to different EB phenotypes. Exploring the spatial distribution of foraging activities could prove interesting to disentangle time-allocation aspects

Table 6. Results of model averaging the equivalent best-ranked GLMs ($\Delta AIC \leq 2$) relating male provisioning effort to exploration behaviour and extrinsic variables. Parameter estimates and their corresponding unconditional standard errors (USE) were obtained through model averaging of the best ranked equivalent models ($\Delta AIC \leq 2$; see table 7s in supplementary material): E, estimate; EB, exploratory behaviour; P.Freq., provisioning frequency; – indicate variables that were included in the analysis but that failed to appear within the best ranked equivalent models. Values in bold highlight significant variables (unconditional 95% confidence interval (CI) does not include zero).

Tabla 6. Resultados de promediar los modelos lineales generalizados equivalentes al mejor modelo ($\Delta AIC \leq 2$) que relacionan el esfuerzo de aprovisionamiento de los machos con el comportamiento exploratorio de estos y con variables extrínsecas. Las estimaciones de los parámetros y sus correspondientes errores estándar (USE) no condicionales se obtuvieron calculando el promedio de los modelos equivalentes al mejor modelo ($\Delta AIC \leq 2$; véase la tabla 7s del material suplementario): E, estimación; EB, comportamiento exploratorio; P.Freq., frecuencia de aprovisionamiento; – indican variables que se incluyeron en el análisis pero que no aparecieron dentro de los modelos equivalentes mejor clasificados. Los valores en negrita resaltan las variables significativas (el intervalo de confianza (IC) incondicional del 95% no incluye el cero).

	E ± USE	$\Sigma\omega(AIC)$	95% CI	E ± USE	$\Sigma\omega(AIC)$	95% CI
♂ Provisioning rate (visits/h)				♂ Average caterpillar volume (cm ³)		
Area: Val	0.10 ± 0.19	0.132	–0.27, 0.47	0.00 ± 0.19	0.043	–0.37, 0.37
Brood size	0.09 ± 0.04	0.440	0.01, 0.17	0.03 ± 0.04	0.477	–0.05, 0.1
♂ EB PC1	–0.04 ± 0.07	0.126	–0.18, 0.11	0.04 ± 0.07	0.347	–0.10, 0.18
♂ EB PC2	0.02 ± 0.10	0.035	–0.16, 0.21	–0.03 ± 0.10	0.111	–0.22, 0.15
♂ Age: >1 year	0.01 ± 0.24	0.031	–0.45, 0.47	–0.09 ± 0.24	0.129	–0.55, 0.37
Relative lay date	–0.01 ± 0.01	0.210	–0.03, 0.01	0.02 ± 0.01	0.526	0.01, 0.04
Year: 2019	0.41 ± 0.24	0.440	–0.07, 0.89	–0.73 ± 0.20	0.526	–1.12, –0.34
♂ Prey volume	–1.34 ± 1.32	0.440	–3.92, 1.25			

related to differences in behavioural traits (Herborn et al., 2010; van Overveld and Matthysen, 2010).

In research performed in our study area a decade ago, blue tits were found to prefer noctuid and tortricid caterpillars (García-Navas and Sanz, 2011; García-Navas et al., 2013), the latter becoming the main prey type during tortricid outbreaks. García-Navas et al. (2013) found no intersexual differences regarding prey preference and provisioning frequency, and found that geometrids were overall underexploited by blue tits. Our results regarding prey choice suggest that, indeed, tortricid caterpillars are exploited in the years they are superabundant (see 2019 data in table 1s in supplementary material), and otherwise, noctuids are commonly preyed upon by both sexes. The difference between our study and previous studies is related to geometrid caterpillars. While females rarely exploit this prey, males obtain a substantial proportion of these caterpillars. We suggest that the shift in the EB described in our previous research (Velasco et al., 2022; males becoming slower explorers) is linked to the shift in their prey choice. A link between behavioural traits and foraging has already been described (Verbeek et al., 1994; Drent and Marchetti, 1999; van Overveld and Matthysen, 2010; Betini and Norris, 2012), and

slower explorers are observed to be more adaptable to changing environments, and to be more likely to explore alternative food resources. Nonetheless, we failed to find a direct relationship between male EB and the proportion of geometrid caterpillars brought to the nest. We consider that, while males in our area are indeed slower explorers than females (Velasco et al., 2022), there is not enough variability within male EB PC1 to conclude that slower-exploring males bring higher percentages of these caterpillars than faster ones. Nonetheless, the case of geometrid caterpillars in our study area is particularly interesting because –unlike tortricids and noctuids– we found that the proportion of preyed geometrid caterpillars was practically unrelated to phenological variables, suggesting an active choice for this type of prey.

Although male EB was part of various models predicting prey choice, the relevance of these terms remained weak throughout the analysis. In the case of males, environmental variables conditioned prey choice more relevantly than EB. Only in the case of tortricid caterpillars did male EB acquire certain relevance, and a tendency (although non-significant) seems to arise: daring males tended to bring higher proportions of tortricid caterpillars. This trend

also existed for females. It is possible that daring (potentially bolder) individuals tend to have more “straightforward” foraging strategies, and prey more often on caterpillars that are easily detectable and more readily available (Drent and Marchetti 1999; van Overveld and Matthysen, 2010). Lastly, in provisioning effort models (visit rates and prey volume), male EB variables also remained statistically non-significant through model averaging. However, the first principal component of male EB was relevant in the majority of the equivalent top-fit models for prey volume, suggesting that a trend exists in which faster-exploring males are more prone to obtain bigger caterpillars than slower-exploring ones. Slower-explorers are described to invest more in parental care than faster-explorers (Boon et al., 2007). Thus, we suggest that the tendency of faster-explorers provisioning bigger prey may be a compensation mechanism mitigating their decrease in parental attentiveness (lower visit rate), but further research is needed to confirm this.

In conclusion, exploratory behaviour seems to condition foraging strategies differently across sexes. The relationship between parental EB and offspring diet is complex and depends in some cases on the interaction between the members of the breeding pair. Regardless, in blue tits, environmental variables seem to contribute substantially to the diet composition of offspring. While interesting, we cannot suggest that EB is currently leading a diet specialization process in our studied species, although it may contribute to this.

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Supplementary material

Fig. 1s. Camera-adapted nest boxes used during the study to record the diet of blue tit offspring. Regular nest-boxes were replaced with camera-adapted nest-boxes the day before the recording date.

Fig. 1s. Cajas nido adaptadas a la cámara utilizadas durante el estudio para grabar la dieta de los pollos de herrerillo común. Las cajas habituales fueron reemplazadas por las cajas adaptadas el día anterior a la filmación.



Video 1s. An adult blue tit fitted with an aluminium ring on the right leg and PVC on the left leg (K14; female) brings a pupa to the nestlings.

Video 1s. Un adulto de herrerillo común con una anilla de aluminio en la pata derecha y una de PVC en la izquierda (K14; hembra) trae una pupa a los pollos.

Table 1s. Descriptive statistics of the variables used in the study, by year and area. Numbers represent the average value (M) \pm the standard deviation (SD). Laying date 1 = 1 IV. Area names: GG, barranco de Gil García; Val, arroyo de Valdeyernos. Prey types are expressed as a proportion, provisioning frequency represents the number of visits per hour and prey volume is measured in cm³.

Tabla 1s. Estadística descriptiva de las diferentes variables usadas en el estudio, por año y área. Los números representan el valor medio (M) \pm la desviación estándar (SD). Fecha de puesta = 1 IV. Nombre de las áreas: GG, barranco de Gil García; Val, arroyo de Valdeyernos. El tipo de presa está expresado como proporción, la frecuencia de aprovisionamiento representa el número de visitas por hora y el volumen de las presas está medido en cm³.

Females				Prey Order		Caterpillar Family			Provisioning effort	
Year	Area	Laying date	Brood size	Lepidoptera	Arachnida	Noctuidae	Geometridae	Tortricidae	Frequency	Prey volume
2018	GG	26.04 \pm 9.72	7.41 \pm 2.04	0.79 \pm 0.17	0.07 \pm 0.11	0.54 \pm 0.31	0.00 \pm 0.00	0.23 \pm 0.28	9.27 \pm 5.12	0.18 \pm 0.08
	Val	32.50 \pm 8.73	6.70 \pm 2.34	0.82 \pm 0.15	0.10 \pm 0.13	0.59 \pm 0.27	0.12 \pm 0.14	0.24 \pm 0.28	11.10 \pm 10.53	0.12 \pm 0.05
2019	GG	1.48 \pm 11.78	6.78 \pm 2.39	0.82 \pm 0.19	0.06 \pm 0.07	0.12 \pm 0.20	0.32 \pm 0.30	0.49 \pm 0.35	13.18 \pm 8.22	0.26 \pm 0.16
	Val	10.84 \pm 12.01	6.24 \pm 2.58	0.81 \pm 0.19	0.08 \pm 0.11	0.23 \pm 0.27	0.17 \pm 0.26	0.51 \pm 0.30	11.89 \pm 7.41	0.11 \pm 0.06
Total		14.14 \pm 10.91	6.71 \pm 2.39	0.81 \pm 0.18	0.07 \pm 0.10	0.31 \pm 0.32	0.18 \pm 0.26	0.41 \pm 0.33	11.71 \pm 7.97	0.15 \pm 0.10

Males				Prey Order		Caterpillar Family			Provisioning effort	
Year	Area			Lepidoptera	Arachnida	Noctuidae	Geometridae	Tortricidae	Frequency	Prey volume
2018	GG			0.72 \pm 0.16	0.17 \pm 0.16	0.53 \pm 0.29	0.38 \pm 0.27	0.07 \pm 0.11	11.73 \pm 5.02	0.19 \pm 0.05
	Val			0.87 \pm 0.13	0.07 \pm 0.13	0.60 \pm 0.32	0.15 \pm 0.27	0.14 \pm 0.11	10.85 \pm 6.70	0.11 \pm 0.05
2019	GG			0.78 \pm 0.14	0.16 \pm 0.14	0.17 \pm 0.27	0.30 \pm 0.19	0.48 \pm 0.26	18.33 \pm 8.58	0.24 \pm 0.15
	Val			0.87 \pm 0.09	0.08 \pm 0.09	0.25 \pm 0.23	0.10 \pm 0.12	0.59 \pm 0.28	19.41 \pm 9.89	0.10 \pm 0.05
Total				0.81 \pm 0.14	0.12 \pm 0.12	0.33 \pm 0.32	0.23 \pm 0.22	0.38 \pm 0.32	16.18 \pm 8.90	0.14 \pm 0.09

Table 2s. Fitted models for prey order (females) based on Akaike Information Criterion (AIC) with $\Delta AIC \leq 2$: A, area; Bs, brood size; EB PC1 and EB PC2, first and second principal components of exploratory behaviour; RLD, relative lay date; M.Freq., male visit frequency; df, degrees of freedom; ^a normalized probability that the model with the lowest AIC is preferred over the current one.

Tabla 2s. Modelos ajustados para el Orden de presa (hembras) basados en el Criterio de Información de Akaike (AIC) con $\Delta AIC \leq 2$: A, área; Bs, tamaño de cría; EB PC1 y EB PC2, primer y segundo componentes principales del comportamiento exploratorio; RLD, fecha relativa de puesta; M.Freq., frecuencia de las visitas del macho; df, grados de libertad; ^a probabilidad normalizada de que se prefiera el modelo con el AIC más bajo al actual.

Model	Intersect	A	Bs	EBPC1	EBPC2	Age	RLD	M.Freq.	Year	df	AIC	$\Delta(AIC)$	$\omega(AIC)$	p^a
♀ Lepidoptera (%)														
F.1.1.1	1.464									1	77.9	0.00	0.052	
F.1.1.2	1.249					+				2	78.7	0.81	0.035	0.598
F.1.1.3	1.444				-0.254					2	78.7	0.84	0.034	0.605
F.1.1.4	1.232		0.035							2	79.4	1.55	0.024	0.684
F.1.1.5	1.235				-0.252	+				3	79.6	1.69	0.022	0.703
F.1.1.6	1.451			0.030						2	79.8	1.91	0.020	0.722
F.1.1.7	1.464						-0.001			2	79.8	1.95	0.020	0.722
F.1.1.8	1.362							0.006		2	79.8	1.97	0.019	0.732
♀ Arachnida (%)														
F.1.2.1	-2.049				0.316					2	38.7	0.00	0.050	
F.1.2.2	-2.062									1	38.8	0.02	0.050	0.500
F.1.2.3	-2.011			-0.166						2	40.0	1.31	0.026	0.658
F.1.2.4	-2.011			-0.129	0.284					3	40.4	1.66	0.022	0.694
F.1.2.5	-2.064						-0.007			2	40.6	1.83	0.020	0.714
F.1.2.6	-1.823					+				2	40.6	1.84	0.020	0.714
F.1.2.7	-1.817				0.314	+				3	40.6	1.84	0.020	0.714
F.1.2.8	-2.051				0.311		-0.005			3	40.6	1.91	0.019	0.725
F.1.2.9	-2.089							0.002		2	40.6	1.91	0.019	0.725
F.1.2.10	-1.897	+			0.339					3	40.7	1.95	0.019	0.725
F.1.2.11	-2.092								+	2	40.7	1.96	0.019	0.725

Table 3s. Fitted models for prey order (males) based on Akaike Information Criterion (AIC) with $\Delta AIC \leq 2$: A, area; Bs, brood size; EB PC1 and EB PC2, first and second principal components of exploratory behaviour; RLD, relative lay date; F.Freq., female visit frequency; df, degrees of freedom; ^a normalized probability that the model with the lowest AIC is preferred over the current one.

Tabla 3s. Modelos ajustados para el orden de las presas (machos) basados en el criterio de información de Akaike (AIC) con $\Delta AIC \leq 2$: A, área; Bs, tamaño de cría; EB PC1 y EB PC2, primer y segundo componentes principales del comportamiento exploratorio; RLD, fecha relativa de puesta; F.Freq., frecuencia de las visitas de la hembra; df, grados de libertad; ^a probabilidad normalizada de que se prefiera el modelo con el AIC más bajo al actual.

Model	Intersect	A	Bs	F.Freq.	RLD	EBPC1	EBPC2	Age	Year	df	AIC	$\Delta(AIC)$	$\omega(AIC)$	p^a
♂ Lepidoptera (%)														
M.2.1.1	1.136	+								2	64.8	0.00	0.039	
M.2.1.2	0.745	+		0.034						3	65.5	0.67	0.028	0.582
M.2.1.3	1.469									1	65.6	0.73	0.027	0.591
M.2.1.4	1.139	+			-0.011					3	65.7	0.88	0.025	0.609
M.2.1.5	0.778	+	0.052							3	65.8	0.96	0.024	0.619
M.2.1.6	0.971	+							+	3	66.3	1.45	0.019	0.672
M.2.1.7	1.120			0.031						2	66.4	1.57	0.018	0.684
M.2.1.8	1.473				-0.011					2	66.5	1.65	0.017	0.696
M.2.1.9	1.133	+					-0.038			3	66.7	1.84	0.016	0.709
M.2.1.10	1.101	+				-0.051				3	66.8	1.92	0.015	0.722
♂ Arachnida (%)														
M.2.2.1	-1.951									1	33.4	0.00	0.087	
M.2.2.2	-1.942					0.032				2	35.4	2.00	0.032	0.731
M.2.2.3	-1.947						0.021			2	35.4	2.00	0.032	0.731
M.2.2.4	-1.934								+	2	35.4	2.00	0.032	0.731

Table 4s. Fitted models for caterpillar families (females) based on Akaike Information Criterion (AIC) with $\Delta AIC \leq 2$: A, area; Bs, brood size; EB PC1 and EB PC2, first and second principal components of exploratory behaviour; RLD, relative lay date; M.Freq., male visit frequency; df, degrees of freedom; N.I., variable not included in the model; ^a normalized probability that the model with the lowest AIC is preferred over the current model.

Tabla 4s. Modelos ajustados para las familias de las orugas (hembras) basados en el criterio de información de Akaike (AIC) con $\Delta AIC \leq 2$: A, area; Bs, tamaño de cría; EB PC1 y EB PC2, primer y segundo componentes principales del comportamiento exploratorio; RLD, fecha relativa de puesta; M.Freq., frecuencia de las visitas del macho; df, grados de libertad; N.I., variable no incluida en el modelo; ^a probabilidad normalizada de que se prefiera el modelo con el AIC más bajo al actual.

Model	Intersect	A	Bs	EBPC1	EBPC2	Age	RLD	M.Freq.	Year	EBPC1*M.Freq	df	AIC	$\Delta(AIC)$	$\omega(AIC)$	p^a
♀ Noctuidae (%)															
F.3.1.1	0.039	+					0.067		+	N.I.	4	98.4	0	0.103	
F.3.1.2	0.177	+					0.065	-0.012	+	N.I.	5	99.5	1.08	0.060	0.632
F.3.1.3	0.294						0.067		+	N.I.	3	99.7	1.31	0.053	0.660
F.3.1.4	0.379	+	-0.046				0.064		+	N.I.	5	99.8	1.41	0.051	0.669
F.3.1.5	-0.127	+				+	0.07		+	N.I.	5	100	1.63	0.045	0.696
F.3.1.6	0.096	+		-0.108			0.067		+	N.I.	5	100.1	1.71	0.044	0.701
♀ Geometridae (%)															
F.3.3.1	-2.308			-0.618				-0.049	+	0.056	5	75.4	0	0.088	
F.3.3.2	-2.136	+		-0.627				-0.049	+	0.056	6	75.5	0.13	0.082	0.518
F.3.3.3	-2.031	+		-0.624	0.502			-0.055	+	0.060	7	76	0.55	0.067	0.568
F.3.3.4	-2.253			-0.612	0.472			-0.055	+	0.059	6	76.2	0.75	0.060	0.595
F.3.3.5	-2.807		0.07	-0.68				-0.062	+	0.059	6	76.7	1.3	0.046	0.657
F.3.3.6	-2.587	+	0.077	-0.679				-0.06	+	0.059	7	77.3	1.85	0.035	0.715
♀ Tortricidae (%)															
F.3.3.1	-1.782			0.546	-0.289		-0.048	0.036	+	-0.048	7	134.6	0.00	0.075	
F.3.3.2	-1.576			0.573	-0.297	+	-0.054	0.036	+	-0.049	8	135.4	0.82	0.050	0.600
F.3.3.3	-1.244			-0.146	-0.233		-0.052		+		2	136.1	1.44	0.037	0.670
F.3.3.4	-1.673			0.548			-0.046	0.033	+	-0.046	6	136.4	1.77	0.031	0.708
F.3.3.5	-1.839	+		0.552	-0.299		-0.049	0.036	+	-0.048	8	136.5	1.88	0.029	0.721

Table 5s. Fitted models for caterpillar families (males) based on Akaike Information Criterion (AIC) with $\Delta AIC \leq 2$: A, area; Bs, brood size; EB PC1 and EB PC2, first and second principal components of exploratory behaviour; RLD, relative lay date; F.Freq., female visit frequency; df, degrees of freedom; ^a normalized probability that the model with the lowest AIC is preferred over the current one.

Tabla 5s. Modelos ajustados para las familias de orugas (machos) basados en el criterio de información de Akaike (AIC) con $\Delta AIC \leq 2$: A, área; Bs, tamaño de cría; EB PC1 y EB PC2, primer y segundo componentes principales del comportamiento exploratorio; RLD, fecha relativa de puesta; F.Freq., frecuencia de las visitas de la hembra; df, grados de libertad; ^a probabilidad normalizada de que se prefiera el modelo con el AIC más bajo al actual.

Model	Intersect	A	Bs	F.Freq	RLD	EB.PC1	EB.PC2	Age	Year	df	AIC	$\Delta(AIC)$	$\omega(AIC)$	p^a
♂ Noctuidae (%)														
M.4.1.1	0.351				0.088				+	3	100.1	0.00	0.117	
M.4.1.2	0.073				0.091			+	+	4	101.0	0.98	0.072	0.619
M.4.1.3	0.372				0.089		0.222		+	4	101.3	1.25	0.062	0.654
M.4.1.4	0.684		-0.046		0.085				+	4	101.7	1.64	0.051	0.696
M.4.1.5	0.476			-0.012	0.086				+	4	101.9	1.84	0.047	0.713
♂ Geometridae (%)														
M.4.2.1	-0.489	+							+	3	81.3	0.00	0.043	
M.4.2.2	-1.218	+	0.097						+	4	81.4	0.10	0.041	0.512
M.4.2.3	-1.336	+	0.160	-0.046						4	81.5	0.22	0.039	0.524
M.4.2.4	-1.490	+	0.106							3	81.7	0.37	0.036	0.544
M.4.2.5	-0.739	+								2	82.2	0.89	0.028	0.606
M.4.2.6	-1.201	+	0.151	-0.043					+	5	82.5	1.23	0.023	0.652
M.4.2.7	-0.496	+			-0.017				+	4	82.6	1.27	0.023	0.652
M.4.2.8	-0.489	+					-0.100		+	4	83.0	1.69	0.019	0.694
M.4.2.9	-0.438	+				0.063			+	4	83.1	1.81	0.017	0.717
M.4.2.10	-1.175	+	0.099			0.068			+	5	83.2	1.85	0.017	0.717
M.4.2.11	-1.201	+	0.095				-0.087		+	5	83.2	1.90	0.017	0.717
M.4.2.12	-1.327	+	0.161	-0.049			-0.123			5	83.2	1.93	0.016	0.729
M.4.2.13	-0.244	+		-0.025					+	4	83.3	1.99	0.016	0.729
♂ Tortricidae (%)														
M.4.3.1	-2.580	+			-0.067				+	4	110.0	0.00	0.106	
M.4.3.2	-2.756	+		0.016	-0.064				+	5	110.9	0.88	0.068	0.609
M.4.3.3	-2.590	+			-0.068		-0.138		+	5	111.0	0.99	0.064	0.624
M.4.3.4	-2.252				-0.065				+	3	111.3	1.32	0.055	0.658
M.4.3.5	-2.662	+			-0.068	-0.090			+	5	111.8	1.81	0.043	0.711
M.4.3.6	-2.761	+		0.015	-0.065		-0.134		+	6	111.9	1.94	0.040	0.726

Table 6s. Fitted models for provisioning effort (females) based on Akaike Information Criterion (AIC) with $\Delta AIC \leq 2$: A, area; Bs, brood size; EB PC1 and EB PC2, first and second principal components of exploratory behaviour; RLD, relative lay date; df, degrees of freedom; N.I., variable not included in the model; ^a normalized probability that the model with the lowest AIC is preferred over the current model.

Tabla 6s. Modelos ajustados para la frecuencia de aprovisionamiento cebas (hembras) basados en el criterio de información de Akaike (AIC) con $\Delta AIC \leq 2$: A, area; Bs, tamaño de cría; EB PC1 y EB PC2, primer y segundo componentes principales del comportamiento exploratorio; RLD, fecha relativa de puesta; df, grados de libertad; N.I., variable no incluida en el modelo; ^a probabilidad normalizada de que se prefiera el modelo con el AIC más bajo al actual.

Model	Intersect	A	Bs	EBPC1	EBPC2	Age	Prey volume	RLD	Year	df	AIC	$\Delta(AIC)$	$\omega(AIC)$	p^a
♀ Provisioning rate (visits/h)														
F.5.1.1	1.970		0.116				-2.219			4	724.4	0.00	0.107	
F.5.1.2	1.965	+	0.119				-2.335			5	724.9	0.50	0.084	0.560
F.5.1.3	1.983		0.110				-2.054	-0.005		5	725.6	1.23	0.058	0.648
F.5.1.4	1.979		0.115		0.053		-2.180			5	725.9	1.52	0.050	0.682
F.5.1.5	1.981	+	0.113				-2.167	-0.005		6	726.1	1.77	0.044	0.709
♀ Average caterpillar volume (cm ³)														
F.5.2.1	-1.859						N.I.	0.016	+	4	-325.0	0.00	0.124	
F.5.2.2	-2.045	+	0.027				N.I.	0.018	+	6	-324.6	0.44	0.100	0.554
F.5.2.3	-1.859	+					N.I.	0.016	+	5	-324.5	0.53	0.095	0.566
F.5.2.4	-2.014		0.022				N.I.	0.017	+	5	-324.5	0.54	0.095	0.566

Table 7s. Fitted models for provisioning effort (males) based on Akaike Information Criterion (AIC) with $\Delta AIC \leq 2$: A, area; Bs, brood size; EB PC1 and EB PC2, first and second principal components of exploratory behaviour; RLD, relative lay date; df, degrees of freedom; ^a normalized probability that the model with the lowest AIC is preferred over the current one.

Tabla 7s. Modelos ajustados para la frecuencia de aprovisionamiento (machos) basados en el criterio de información de Akaike (AIC) con $\Delta AIC \leq 2$: A, área; Bs, tamaño de cría; EB PC1 y EB PC2, primer y segundo componentes principales del comportamiento exploratorio; RLD, fecha relativa de puesta; df, grados de libertad; ^a probabilidad normalizada de que se prefiera el modelo con el AIC más bajo al actual.

Model	Intersect	A	Bs	RLD	EBPC1	EBPC2	Age	Prey volume	Year	df	AIC	$\Delta(AIC)$	$\omega(AIC)$	p^a
♂ Provisioning rate (visits/h)														
M.6.1.1	2.030		0.088	-0.007				-1.254	+	6	775.1	0.00	0.084	
M.6.1.2	2.030		0.096					-1.557	+	5	775.6	0.42	0.068	0.553
M.6.1.3	1.983		0.087	-0.007	-0.036			-1.137	+	7	776.1	0.96	0.052	0.618
M.6.1.4	1.974	+	0.091	-0.007				-1.301	+	7	776.2	1.04	0.050	0.627
M.6.1.5	1.967	+	0.100					-1.602	+	6	776.4	1.22	0.046	0.646
M.6.1.6	1.987		0.096		-0.032			-1.465	+	6	776.7	1.61	0.038	0.689
M.6.1.7	1.912	+	0.091	-0.007	-0.041			-1.172	+	8	776.8	1.71	0.036	0.700
M.6.1.8	2.037		0.087	-0.007		0.023		-1.244	+	7	776.9	1.74	0.035	0.706
M.6.1.9	2.023		0.088	-0.007			+	-1.250	+	7	777.1	1.99	0.031	0.730
♂ Average caterpillar volume (cm ³)														
M.6.2.1	-1.737		0.029	0.023	0.041			N.I	+	6	-379.3	0.00	0.116	
M.6.2.2	-1.764		0.029	0.023				N.I	+	5	-378.5	0.80	0.078	0.598
M.6.2.3	-1.665		0.028	0.022	0.039		+	N.I	+	7	-378.4	0.88	0.074	0.611
M.6.2.4	-1.743		0.029	0.023	0.040	-0.031		N.I	+	7	-378.1	1.15	0.065	0.641
M.6.2.5	-1.685		0.028	0.022			+	N.I	+	6	-377.8	1.48	0.055	0.678
M.6.2.6	-1.525			0.021	0.040			N.I	+	5	-377.6	1.73	0.049	0.703
M.6.2.7	-1.770		0.029	0.023		-0.034		N.I	+	6	-377.4	1.85	0.046	0.716
M.6.2.8	-1.736	+	0.029	0.023	0.041			N.I	+	7	-377.3	2.00	0.043	0.730