



Provisioning challenge: self-consumption versus nestling provisioning, an experimental study

Laura Arco ^{a, *}, Manuel Martín-Vivaldi ^{a, b}, Juan Manuel Peralta-Sánchez ^c,
Natalia Juárez García-Pelayo ^a, Manuel Soler ^{a, b}

^a Department of Zoology, Faculty of Sciences, University of Granada, Granada, Spain

^b Unidad Asociada Coevolución: Cucos, Hospedadores y Bacterias Simbiontes, University of Granada, Granada, Spain

^c Department of Microbiology, Faculty of Sciences, University of Granada, Granada, Spain

ARTICLE INFO

Article history:

Received 17 March 2021

Initial acceptance 21 June 2021

Final acceptance 4 May 2022

MS. number: 21-00179R

Keywords:

central-place forager
food provisioning
parental decision
prey selection
reproductive investment
short-lived species
Upupa epops

A way of untangling the trade-off between investment in current offspring versus self-maintenance and future reproductive success is to determine how both parents allocate food between themselves and their offspring according to food availability. The hoopoe, *Upupa epops*, is an excellent model to test hypotheses about these decisions, since it is a central-place forager, a short-lived species and it reproduces successfully in captivity. We created different conditions of food availability (abundant/scarse) at two stages of the nestling period and provided different prey qualities in terms of digestibility and/or size. We hypothesized that parents would prioritize current offspring over their own maintenance. We predicted that (1) parents would offer their nestlings larger/more digestible prey, while they would eat smaller/less digestible prey and (2) when food was scarce, parents would not reduce the amount offered to nestlings. We found that both parents delivered high-quality prey to their nestlings at both stages and ate prey of lower digestibility in the early stage and smaller prey in the late stage. These results support the expectations for central-place foragers, as adults delivered the best prey to nestlings. When food availability was limited, parents at both nestling stages did not reduce the amount of consumed biomass. Despite nestlings receiving similar biomass in both treatments at the early stage, they experienced a reduction in biomass at the late stage when food was scarce. Therefore, hoopoes did not follow the typical strategy of a short-lived species, probably due to energy constraints related to a larger home range and prolonged nestling periods. In addition, females showed a more flexible response than males to changes in food availability, especially at the end of the breeding period. These sex-dependent responses could be related to different parental care investment at this stage when males take care of fledglings until independence and females are preparing for a second clutch.

© 2022 The Author(s). Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

In altricial birds, parental food provisioning is crucial for the survival and growth of their nestlings and constitutes a considerable part of the costs of parental care (Clutton-Brock, 1991; Drent & Daan, 1980). The costs of feeding the offspring may reduce the probability of survival of the parents and their future reproductive success (Alonso-Álvarez & Velando, 2012). Thus, parents should balance the allocation of food between themselves and their offspring to maximize their lifetime reproductive success. This leads to a trade-off between investment in offspring provisioning versus self-maintenance and future reproduction (Stearns, 1992).

Moreover, most birds show biparental care, so each parent benefits from the care provided by the other, whereas it pays only the cost of its own effort (Houston et al., 2005; Lessells & McNamara, 2012). Thus, each parent profits if it leaves the highest workload for its partner (Lessells, 1999; Royle et al., 2012). If there is a reduction in the partner's effort, parents can adjust their provisioning behaviour by following different evolutionarily stable strategies (Harrison et al., 2009; Johnstone & Hinde, 2006). In negotiation models, parents fully (Sanz et al., 2000) or partially (Rauter & Moore, 2004) compensate for this reduction by increasing their effort (McNamara et al., 1999), while in the matching strategy, parents adjust their effort in the same direction as their partner (Iserbyt et al., 2019; Johnstone & Hinde, 2006). In sealed bid models, parents invest an a priori fixed effort, independently of their partner's effort (Houston

* Corresponding author.

E-mail address: larco@ugr.es (L. Arco).

& Davies, 1985; Nakagawa et al., 2007). Therefore, the provisioning behaviour of a parent to its offspring is influenced by the effort of its partner (Hinde & Kilner, 2007).

Parental decisions about how to allocate food between themselves and their offspring are strongly influenced by avian life history traits, mainly by longevity (Stearns, 1992). Life history theory suggests that short-lived species will favour investment in their current offspring even at the expense of their own survival (Ghalambor & Martin, 2001; Hamel et al., 2010). In contrast, long-lived species will favour their own survival and/or their future reproduction (Ghalambor & Martin, 2001; Hamel et al., 2010). Brood size (Koenig & Walters, 2012; Musgrove & Wiebe, 2014) and food resource manipulations (Markman et al., 2002) can modify the reproductive costs of the parents. Both experimental approaches allow us to measure the ability or willingness of the parents to invest in current or future reproduction.

Brood enlargement experiments show parents in short-lived species increase provisioning rates more often than parents in long-lived species (89% versus 50%; Gow & Wiebe, 2014). However, absolute provisioning rates may be uninformative because short-lived species may instead react to increased brood demand by adjusting the allocation of prey quality, preferentially giving high-quality prey to offspring (Grieco, 2001, 2002). By contrast, long-lived species are expected to retain high-quality prey for themselves (Ballard et al., 2010; Stearns, 1992). Similarly, some supplementary feeding experiments found that parents in short-lived species invested the surplus in offspring, with effects on offspring growth and survival (Banbura et al., 2011; Granbom & Smith, 2006; Markman et al., 2002), while parents of long-lived species kept it for themselves, with effects on their own survival (Eldegard & Sonerud, 2010). However, these effects are not universal, with both short- and long-lived species violating the basic expectations (short lived: Dawson & Bortolotti, 2002; Krause et al., 2017; long lived: González et al., 2006).

In birds, the time and energy costs of transporting each prey also influence parental food allocation decisions (Mullers et al., 2009; Schoener, 1979). Parents provisioning offspring at the nest (central-place foragers) are expected to select prey to maximize their energy delivery per provisioning trip (Burke & Montevecchi, 2009; Stephens & Krebs, 1986). Therefore, parents may have to select larger or more digestible prey (high-quality or more profitable prey) for their nestlings, while reserving smaller or less digestible prey (low-quality or less profitable prey) for themselves (Kacelnik, 1984; Sonerud, 1989; Wilson et al., 2004). These circumstances can lead to dietary differences between parents and their nestlings, especially in single-prey loaders (Alonso et al., 2012; Danhardt et al., 2011).

The hoopoe, *Upupa epops*, a hole-nesting bird with biparental care, is a short-lived species (low annual survival probability 0.38), double brooded and an obligate single-prey loader (Cramp, 1998; Hoffmann et al., 2015; Martín-Vivaldi et al., 1999; Schaub et al., 2012). The hoopoe shows a clear sex-specific task specialization: while the female stays in the nest during the incubation period and the first week of the nestling period, the male collects and provides all food to the family (Arlettaz et al., 2010; Martín-Vivaldi et al., 1999). Afterwards, both parents collect food and feed the nestlings, although males continue to offer food to the females outside the nest. Previous studies on food provisioning in hoopoes showed that males carry mainly larger prey to the nest (Arlettaz et al., 2010; Fournier & Arlettaz, 2001; Ryser et al., 2016), whereas females carry smaller prey (Guillod et al., 2016). This indicates that parents follow different sex-specific foraging strategies (Guillod et al., 2016). Although the diet of nestlings has been well investigated, the type of prey consumed by parents is unknown. Moreover, Plard et al.

(2018) found that the sexes differ in their reproductive and survival costs when breeding under harsh environmental conditions. This work suggests that females prioritize the success of each reproductive event at the expense of their future reproduction and survival whereas males limit their reproductive effort within a breeding season (Plard et al., 2018).

These life history traits make the hoopoe an excellent model to test hypotheses about parental food provisioning decisions throughout the breeding cycle. First, since they deliver one prey item per trip (Cramp, 1998), hoopoes need to balance digestibility, size and destiny of each prey carried to the nest. Second, the parents differ in their parental tasks, sex-specific foraging strategies and reproductive costs (Guillod et al., 2016; Martín-Vivaldi et al., 1999; Plard et al., 2018), so the value of each prey for each sex may change throughout the nestling period. Third, the fact that they are short-lived species may influence parental provisioning decisions, especially when prey availability is limited in the environment (Hamel et al., 2010). Fourth, the successful reproduction of hoopoes in captivity (Martín-Vivaldi et al., 2014) and their behaviour as single-prey loaders allow the manipulation of every aspect of the quality (size and digestibility) and quantity of prey.

We aimed to investigate sex-specific differences in the allocation of prey between self-maintenance and nestling provisioning. In particular, we experimentally studied the decisions that males and females make for prey of different qualities (size and digestibility) during two stages of the nestling period (small and large nestlings) and in two food availability treatments (abundant/scarcely food). Most of the previous studies modified the hunger of the brood (by increasing or reducing brood size) or supplemented the nest with food (Gow & Wiebe, 2014; Ruffino et al., 2014). The novelty of our study is that we experimentally reduced the availability of food outside the nest. Therefore, parents experienced food limitations in the environment. In addition, the usual methods of determining food allocation between parents and their offspring, such as direct observations, prey quantification using nest cameras and biochemical analysis, among others (Beaulieu & Sockman, 2014; Hernández-Pliego et al., 2017; Robinson et al., 2015), have some limitations. None of these techniques provides a good assessment of the complete series of provisioning decisions made by parents for each prey, from its capture to its delivery to the nestlings or its own consumption. Our experimentally controlled approach fills this gap, as we provided prey one by one allowing us to follow the complete and exhaustive pathway of parental decisions.

Since the hoopoes should maximize their energy delivery per provisioning trip, we predicted that parents would selectively offer larger and more digestible prey to their nestlings, while eating smaller and less digestible ones (Prediction 1). This prediction is also in line with the hypothesis of short-lived species favouring their offspring and therefore sacrificing the best part of their diet to feed their nestlings. We hypothesized that short-lived hoopoe parents should prioritize current offspring rather than their own maintenance. Therefore, hoopoes would not reduce the amount of biomass offered to their nestlings when food was scarce (Prediction 2). We also predicted that, in periods of scarcity, parents would not change their selective provisioning strategy (Prediction 3). Finally, each sex differs in parental tasks, reproductive costs and foraging strategies, so we hypothesized that changes in food availability would differentially affect the reproductive investment of each sex. In harsh years hoopoe females experience interseasonal costs of reproductive success and survival (Plard et al., 2018), so we predicted that females would reduce their prey consumption when food was scarce more than males (Prediction 4).

METHODS

Housing and Experimental Set-up

The experiment was performed during the 2012 breeding season (March–July) on hoopoes from a population maintained in captivity since 2008. During the breeding season, pairs were kept in cages located in a pine forest in the Hoya de Guadix (37°21'N, 003°05'W, Granada province, southern Spain). We used 27 cages, 3 × 2 m and 2 m high, at least 50 m apart. All cages contained soil, were partially protected with a roof that provided shade and were equipped with one cork nestbox (40 × 20 cm and 20 cm high, 5.5 cm hole diameter). Nestboxes were filled up to 2 cm with chopped pine bark. An internal aluminium roof protected plastic poultry feeders (50 × 12 cm and 12.5 cm high) from sun and rain.

During autumn and winter, hoopoes were maintained, separated by sex, in facilities located at the University of Granada (Granada, Spain). These consisted of one large aviary (13.5 × 7 m and 4 m high) and three medium-sized cages (7 × 6 m and 3 m high), with an approximate density of 0.072 birds/m³. We housed females in the large aviary while males were housed in the medium-sized cages. The aviary and each cage were equipped similarly to the breeding cages, with aluminium roofs protecting plastic poultry feeders.

Breeding pairs were established in early March, when one male and one female were paired in each cage. Breeding birds were captured with mist-nets and transported to the breeding cages in opaque cloth bags to reduce stress. No bird experienced any harm during catching and transport. Cages were visited daily to feed the birds and monitor their health.

Hoopoes were fed daily with larvae and pupae of the flies *Calliphora* and *Sarcophaga* as well as vitamin-enriched meat (beef heart) ad libitum throughout the year. Water was not provided as hoopoes obtain sufficient from their diet.

The day before the control session, cages were prepared with the necessary equipment to habituate the adults. A carpet of 3 × 2 m was placed over the soil in the cage to prevent access to

wild prey or food remains from previous days. An opaque PVC pipe with a diameter of 4 cm and 1.80 m in length served to provide prey directly from outside the cage onto a 25 × 15 cm tray of white plastic. A 2 × 1 m wooden panel on one of the outer cage walls hid the researcher. The panel had two holes, one for the researcher to observe the inside of the cage and one for the PVC pipe in the cage (Fig. 1). A microcamera (540TVL SONY CCD Color) was installed inside the nestbox. A small monitor connected to the microcamera allowed the researcher to observe what happened inside the nestbox. In this way, it was possible to know in real time whether the female consumed the prey or offered it to one of the nestlings.

Experimental Procedure

Experiments were performed at two different stages of the nestling period. At nestling stage 1 (NS1 hereafter), day 4 after hatching of the first egg, females stay within the nest and the males provide all food to the family. At nestling stage 2 (NS2 hereafter), at day 16, both females and males are involved in searching for food outside the nest (Martín-Vivaldi et al., 1999), although males still offer prey to the females. Depending on the nestling stage, adults were provided with different prey representing differences in food quality in terms of digestibility and/or size. Small prey, pupae and larvae of the flies *Calliphora* and *Sarcophaga*, were used in both NS1 and NS2 stages, while large prey, adult crickets, *Gryllus bimaculatus*, and late-stage silkworm larvae, *Bombyx mori*, were used only in the NS2 stage.

We considered pupae to be lower quality prey than larvae because their hard chitinous covering reduces their digestible biomass (Ruppert et al., 1994). Chitin is difficult or impossible for birds to digest (Duke, 1997; Jackson et al., 1992; Karasov, 1990), so hoopoes usually regurgitate it as pellets (Cramp, 1998; M. Martín-Vivaldi & L. Arco, personal observations). Of the large prey (NS2), crickets have a higher proportion of indigestible chitin than silkworms (Chae et al., 2018; Hahn et al., 2020) and thus were lower quality prey. In addition, we considered size as a proxy of prey quality since its mass and length are directly proportional to its energy content (Sinervo, 2012).



Figure 1. (a) General layout of the cage showing (1) the position of the nestbox and (2) the aluminium roof that protected the food from the weather. (b) Detailed picture of the provisioning equipment showing (1) the wooden panel that hid the researcher, (2) the carpet, (3) the PVC pipe and (4) the plastic feeder.

The experiment was performed with 10 hoopoe pairs but, due to adverse weather conditions or failures in the recording equipment, some sessions could not be completed in two nests and the final number of pairs with available information was eight. Since our experimental design involved two food availability treatments and was repeated in two stages of the nestling period, we had complete information for 32 trials.

Brood size in our experimental cages (fledglings in NS2: $N = 8$, average 4.5) was higher than the natural variation found in our study area ($N = 60$, average 3.02; [Martín-Vivaldi et al., 1999](#)).

Control Session

To identify the amount of food required to simulate 'abundance' for each nest in the experimental treatment, we conducted two ad libitum feeding trials (one in the morning, one in the afternoon), on the day before each experimental session. Half an hour before starting, we cleaned the cage of food remains. We then started feeding larvae and pupae (for both NS1 and NS2), one by one, through the PVC pipe until the birds habituated to it and took food without paying attention to the apparatus. From that point, we provided prey continuously for 1 h, recording the total number consumed. We then provided prey ad libitum in their normal feeding tray for 1 h, and recorded the number eaten, adding this to the number eaten from the pipe. We then used average number consumed across the morning and afternoon sessions as the level to be used for each nest 'abundance' treatment. This approach specifically tailored the amount of supplementary feeding to each nest, appropriate to the brood size.

The order of food presentation in control sessions (first PVC pipe and then filled tray or vice versa) was changed between morning and afternoon observations and between consecutive nests. The order of providing each type of prey through the PVC pipe was made following a random number series for each observation and nest (obtained from the software STATISTICA 12, Statsoft Inc., Tulsa, OK, U.S.A.).

Experimental Session

At each nestling stage, we performed two treatments (abundant/scarce food) on the same day, one in the morning and the other in the afternoon, alternating this order in consecutive nests. Each treatment lasted 2 h, always providing prey one by one through the PVC pipe. The morning control and experimental sessions started half an hour after sunrise and the afternoon sessions started 3 h before sunset. Between trials and after the afternoon treatment, food was provided ad libitum allowing the parents to feed the nestlings during the last hour of the day.

In the abundant food treatment at NS1, we provided the same number of prey items as during the control session with food ad libitum. This number of prey was distributed as 50% larvae and 50% pupae. The interval between prey additions was adjusted according to the previous control session (120 min/number of prey consumed in the control session = minutes to provide each prey in the experimental session).

Similarly, for NS2, the number of prey items used for the abundant food treatment was estimated during the control session, in this case with the four types of prey. For this calculation, we conservatively assumed that a large prey was equivalent to two small ones. The amount of food to provide in the abundant food treatment was calculated as number of prey of the four types, larvae 33.3%, pupae 33.3%, silkworms 16.7% and crickets 16.7%, so each type was equivalent to about 25% of the total amount of food calculated. The interval between prey additions was adjusted according to the control session (120 min/number of prey resulting

from the previous biomass calculation = minutes to provide each prey during the experimental session). If one prey was not consumed in 10 min, it was considered rejected and the trial continued with the next prey. To generate the scarce food treatment for each nest, we multiplied the abundant food value by 0.6. The decision to reduce food by 0.6 was made because we considered that this was an appropriate reduction to obtain a clear situation of food scarcity without compromising nestling survival.

To estimate the biomass of prey, 20 individuals of each type of prey were dried in an oven for 24 h at 70 °C. Afterwards, average biomass (g dry weight \pm SE) was calculated (larvae: 0.014 ± 0.0015 ; pupae: 0.028 ± 0.0008 ; silkworms: 0.180 ± 0.0120 ; crickets: 0.159 ± 0.0080).

Ethical Note

We performed the experiment in accordance with relevant Spanish national guidelines (Real Decreto 1201/2005, de 10 de octubre) and under the permission of Junta de Andalucía (Dirección General de Gestión del Medio Natural). This administration authorized the establishment and maintenance of the captive breeding population (Resolución de 14 de abril de 2008) and granted the permits (Ref: SGYB/FOA/AFR) required to perform the present research according to Spanish regulations (Resoluciones de 14 de abril de 2008 and 23 de marzo de 2010). The scarce food treatment did not adversely affect nestlings and parental body condition, since we always provided food ad libitum immediately after the experimental sessions. Adults fed nestlings normally after the experiment and no chick died within 2 days after the experiment (we checked the nest every day).

Statistical Analyses

Descriptive estimators for groups are presented as average \pm SE from the raw data.

Confirmatory analyses

We used generalized linear mixed models (GLMMs) to analyse whether our experimental treatment produced different conditions of food availability. Number of prey collected from the tray by males in NS1 or by both parents in NS2 were included as a Poisson-distributed response variable with log link function, treatment (abundant/scarce food) as fixed factor and nest ID (eight nests) as random factor. In this model, for both NS1 and NS2, the total number of units of replication is 16 (two treatments \times eight nests). In NS1, the number of prey collected from the tray by males differed significantly between the two treatments ([Table A1](#); abundant food: 69.9 ± 16.6 ; scarce food: 58.4 ± 6.8). In NS2, the experimental treatment significantly reduced the number of prey collected by both adults in the scarce food treatment ([Table A1](#); abundant food: 80.3 ± 14.6 ; scarce food: 46.1 ± 8.8). Therefore, our experimental treatment had a significant food reduction effect.

From here on, in models for NS1, the total number of units of replication is 32 (two prey types \times two treatments \times eight nests), while in NS2 the total number of units of replication is 64 (four prey types \times two treatments \times eight nests).

We also analysed whether males in NS1 or both parents in NS2 rejected any specific type of prey (not used for their own consumption or for the nestlings) from prey offered in the tray. We used binomial GLMMs with logit link functions, fitting number of prey rejected/number of prey offered as the response variable, type of prey (larvae/pupae in NS1; larvae/pupae/silkworms/crickets in NS2) and treatment (abundant/scarce food) as fixed effects and nest ID (eight nests) as a random effect. In NS1, males were more likely to reject pupae from the prey offered in the tray ([Tables A2,](#)

A3). Males rejected a smaller proportion of prey in the scarce food treatment (Table A2; abundant food: 0.075 ± 0.040 ; scarce food: 0.018 ± 0.010). In NS2, parents rejected a higher proportion of pupae than any other type of prey, while they rejected a similar proportion of crickets, silkworms and larvae (Tables A2, A3 and A4).

Experimental analyses

In a first set of models, we used binomial GLMMs with logit link functions to determine the effects of treatment and type of prey on prey consumption by each family member (male, female and nestlings in different models) in NS1. Type of prey (larvae/pupae) and treatment (abundant/scarce food) were included as fixed effects, nest ID (eight nests) as a random effect and the proportion of prey consumed as the response variable. As males provided and therefore handled all prey consumed by family members, the response variable for males was number of prey consumed/number of prey they handled (GLMM 1.1). Females distributed the prey provided by males between themselves and their nestlings, so that their decisions were limited to the subset of prey offered by males. Therefore, the response variable for females was number of prey consumed by females/number of prey offered by males (GLMM 1.2). Finally, the response variable for nestlings was number of prey consumed/number of prey handled by males (GLMM 1.3). For GLMM 1.2, the unit of replication ($N = 29$) differed with respect to GLMM 1.1 and GLMM 1.3 ($N = 32$), since males consumed all pupae or larvae in three trials, leaving females without the opportunity to use this type of prey.

In a second set of models, we used binomial GLMMs with logit link functions to determine the effects of treatment and type of prey on prey consumption by each family member (male, female and nestlings in different models) in NS2. Treatment (abundant/scarce food) and type of prey (larvae/pupae/silkworms/crickets) were included as fixed effects, nest ID (eight nests) as a random effect and the proportion of prey consumed as the response variable. In this stage, both parents collected prey and fed the nestlings, but males also offered prey to females. For males, the response variable was number of prey consumed/number of prey handled by males (GLMM 2.1) and for females it was number of prey consumed/number of prey handled by females (prey captured by themselves + prey offered by males; GLMM 2.2). Finally, the response variable for nestlings was number of prey consumed/number of prey handled by males and females (GLMM 2.3). Males did not handle any pupae (either to eat or to offer) in three trials, females did not handle larvae or pupae in six trials and the nestlings did not receive pupae from their parents in three trials. Therefore, the unit of replication was 61 for GLMM 2.1 and GLMM 2.3 and 58 for GLMM 2.2.

In a third set of models, we performed GLMMs with Gaussian distribution and log link functions to explore the effects of treatment and type of prey on the biomass of prey consumed by each family member (male, female and nestlings) in NS1 and NS2. Treatment (abundant/scarce food) and type of prey (larvae/pupae in NS1; larvae/pupae/silkworms/crickets in NS2) were included as fixed effects, nest ID (eight nests) as a random factor and biomass consumption as the response variable. Biomass consumption was log transformed to fit parametric assumptions. Log-transformed biomass models explored these effects separately for males, females and nestlings in NS1 (GLMM 3.1, 3.2 and 3.3, respectively) and NS2 (GLMM 3.4, 3.5 and 3.6, respectively). Residuals followed a Gaussian distribution (Kolmogorov–Smirnov normality test: $P > 0.15$).

In a final set of models, we used binomial GLMMs with logit link functions to explore prey delivery decisions by males and females in NS2. For male decisions, we investigated prey offered by males to females, fitting number of prey offered to females/number of prey offered to females and nestlings as the response variable, treatment

(abundant/scarce food) and prey type (larvae/pupae/silkworms/crickets) as fixed effect and nest ID (eight nests) as a random factor (GLMM 4.1). In this model, there were 11 trials where the males did not offer prey to either the females or the nestlings, so the unit of replication was reduced to 53.

We also investigated female provisioning decisions, fitting the response variable as number of prey offered by females to nestlings but previously received from males/number of prey offered by females to nestlings (prey directly captured by females + prey previously received from males). Treatment (abundant/scarce food) and type of prey (larvae/pupae/silkworms/crickets) were included as fixed effects and nest ID (eight nests; GLMM 4.2). In this model, there were 13 trials where females did not offer any prey to nestlings, so the unit of replication was reduced to 51.

The P values of each explanatory variable were calculated by chi-square comparison between the complete model and the reduced model of the variable of interest.

Statistical analyses were performed with R v 4.0.3 (R Core Team, 2013), using function `glmmTMB` implemented in the package `GLMMTMB` (Magnusson et al., 2017).

RESULTS

Food Distribution and Consumption in NS1

In NS1, males were more likely to consume pupae than larvae (GLMM 1.1, Table 1, Fig. 2a). Males ate a similar proportion of prey in the abundant food treatment (0.57 ± 0.07) and in the scarce food treatment (0.49 ± 0.06 ; GLMM 1.1, Table 1, Fig. 2a) from the prey they handled, offering the rest of the prey to the females. Males obtained significantly more biomass from pupae than from larvae, although this biomass consumption did not differ between treatments (GLMM 3.1, Table 1).

Females were more likely to consume pupae than larvae (GLMM 1.2, Table 1, Fig. 2b) in both treatments. Females ate a lower proportion of prey in the scarce food treatment (0.18 ± 0.05) than in the abundant food treatment (0.25 ± 0.06 ; GLMM 1.2, Table 1, Fig. 2b) from the prey offered by males, delivering the remaining prey to the nestlings. Females obtained significantly more biomass from pupae than from larvae, although this biomass consumption did not differ between treatments (GLMM 3.2, Table 1).

Nestlings were more likely to be fed larvae than pupae (GLMM 1.3, Table 1, Fig. 2c). The nestlings were fed a similar proportion of prey in the abundant food treatment (0.31 ± 0.05) and in the scarce food treatment (0.41 ± 0.06) from the prey handled by males (GLMM 1.3, Table 1, Fig. 2c). Biomass obtained by nestlings differed neither by type of prey nor by treatment (GLMM 3.3, Table 1).

Food Distribution and Consumption in NS2

Males

In NS2, the probability of males consuming each type of prey differed significantly (GLMM 2.1, Table 1) in the following order: pupae > larvae > silkworms > crickets (Fisher LSD post hoc tests: $P < 0.008$; Fig. 3a). Males ate a similar proportion of prey in the abundant food treatment (0.44 ± 0.07) and in the scarce food treatment (0.48 ± 0.07 ; GLMM 2.1, Table 1, Fig. 3a) from the prey they handled.

Males obtained a similar amount of biomass in both treatments (GLMM 3.4, Table 1, Fig. 4a). However, the consumed biomass differed significantly between each type of prey. Males obtained significantly more biomass from silkworms and pupae than from crickets (Fisher LSD post hoc test: $P < 0.001$; Fig. 4a), while they obtained similar biomass from pupae, larvae and silkworms (Fisher LSD post hoc test: $P > 0.091$; Fig. 4a).

Table 1
Summary of the results of generalized linear mixed models showing the effects of treatment and prey type on the proportion and biomass of prey consumed by males, females and nestlings

	Dependent variable	Factors	Estimate (±SE)	Factor type	df	χ ²	P
Nestling stage 1 (NS1)							
GLMM 1.1	Proportion of prey handled by males that they consumed	Type of prey	0.88 (±0.13)	Fixed	1,28	46.11	<0.001
		Treatment	0.09 (±0.14)	Fixed	1,28	0.46	0.495
		Nest		Random	8,28	9.83	0.002
GLMM 1.2	Proportion of prey offered by males that females consumed	Type of prey	0.72 (±0.22)	Fixed	1,25	10.91	<0.001
		Treatment	−0.47 (±0.23)	Fixed	1,25	4.24	0.039
		Nest		Random	8,25	30.79	<0.001
GLMM 1.3	Proportion of prey handled by males that nestlings consumed	Type of prey	−1.09 (±0.13)	Fixed	1,28	66.13	<0.001
		Treatment	0.16 (±0.14)	Fixed	1,28	1.37	0.242
		Nest		Random	8,28	32.58	<0.001
GLMM 3.1	Biomass consumption of males	Type of prey	0.11 (±0.02)	Fixed	1,28	25.35	<0.001
		Treatment	−0.003 (±0.02)	Fixed	1,28	0.03	0.868
		Nest		Random	8,28	2.58	0.108
GLMM 3.2	Biomass consumption of females	Type of prey	0.03 (±0.01)	Fixed	1,28	5.30	0.021
		Treatment	−0.02 (±0.01)	Fixed	1,28	2.79	0.095
		Nest		Random	8,28	6.54	0.010
GLMM 3.3	Biomass consumption of nestlings	Type of prey	−0.001 (±0.01)	Fixed	1,28	0.005	0.939
		Treatment	−0.007 (±0.01)	Fixed	1,28	0.22	0.636
		Nest		Random	8,28	12.44	<0.001
Nestling stage 2 (NS2)							
GLMM 2.1	Proportion of prey handled by males that they consumed	Type of prey	C-P: 5.01(±0.51) C-L: 4.38(±0.49) C-S: 1.73(±0.51)	Fixed	3,55	374.70	<0.001
		Treatment	0.33 (±0.20)	Fixed	1,55	2.58	0.108
		Nest		Random	8,55	2.79	0.094
GLMM 2.2	Proportion of prey handled by females that they consumed	Type of prey	C-P: 4.05(±0.50) C-L: 4.67(±0.51) C-S: 1.87(±0.52)	Fixed	3,52	224.52	<0.001
		Treatment	0.74 (±0.24)	Fixed	1,52	9.68	0.002
		Nest		Random	8,52	1.15	0.283
GLMM 2.3	Proportion of prey handled by parents that nestlings consumed	Type of prey	C-P: −4.56(±0.37) C-L: −4.92(±0.38) C-S: −1.92(±0.37)	Fixed	3,55	521.28	<0.001
		Treatment	−0.75 (±0.19)	Fixed	1,55	15.38	<0.001
		Nest		Random	8,55	6.43	0.011
GLMM 3.4	Biomass consumption of males	Type of prey	C-P: 0.08(±0.02) C-L: 0.04(±0.02) C-S: 0.08(±0.02)	Fixed	3,58	14.51	0.002
		Treatment	−0.01 (±0.01)	Fixed	1,58	0.70	0.402
		Nest		Random	8,58	1.64	0.200
GLMM 3.5	Biomass consumption of females	Type of prey	C-P: 0.08(±0.02) C-L: 0.02(±0.02) C-S: 0.07(±0.02)	Fixed	3,58	13.64	0.003
		Treatment	−0.01 (±0.01)	Fixed	1,58	0.57	0.447
		Nest		Random	8,58	4.90	0.027
GLMM 3.6	Biomass consumption of nestlings	Type of prey	C-P: −0.37(±0.03) C-L: −0.39(±0.03) C-S: −0.06(±0.03)	Fixed	3,58	91.95	<0.001
		Treatment	−0.08 (±0.02)	Fixed	1,58	12.17	<0.001
		Nest		Random	8,58	16.33	<0.001

Generalized linear mixed models exploring the effects of treatment (abundant/scarce food) and type of prey (larvae/pupae in NS1; larvae/pupae/silkworms/crickets in NS2) on the proportion of prey consumed by the male, female and nestlings in NS1 (day 4 after hatching of the first egg, GLMM 1) and NS2 (day 16 after hatching of the first egg, GLMM 2) (models were fitted with binomial distributions and logit link functions), and the \log_{10} -transformed biomass consumed by the male, female and nestlings in NS1 and NS2 (GLMM 3; models fitted with a Gaussian distribution and log link functions). *P* values were calculated by chi-square comparison between the complete model and the reduced model of the variable of interest. Significant *P* values are shown in bold. In NS2, type of prey had four levels, so 'crickets' was set as baseline for the calculation of the estimates (C: crickets; L: larvae; P: pupae; S: silkworms).

Females

Females also were selective in the type of prey consumed (GLMM 2.2, Table 1), following a different order of preferences than males: larvae > pupae > silkworms > crickets (Fisher LSD post hoc tests: $P < 0.032$; Fig. 3b). Females ate a higher proportion of prey in the scarce food treatment (0.38 ± 0.07) than in the abundant food treatment (0.34 ± 0.06) from the prey they handled (prey captured by themselves plus prey offered by the male; GLMM 2.2, Table 1, Fig. 3b) delivering the remaining to nestlings.

Females consumed a similar amount of biomass in both treatments (GLMM 3.5, Table 1, Fig. 4b). They obtained significantly

more biomass from silkworms and pupae than from crickets (Fisher LSD post hoc test: $P < 0.030$; Fig. 4b) and more from silkworms than from larvae (Fisher LSD post hoc test: $P = 0.010$; Fig. 4b).

Nestlings

Nestlings were more likely to be fed crickets than any other prey type (GLMM 2.3, Table 1; Fisher LSD post hoc test: $P < 0.001$; Fig. 3c). Nestlings were also fed a higher proportion of silkworms than larvae or pupae (Fisher LSD post hoc test: $P < 0.001$; Fig. 3c). Finally, nestlings consumed a similar proportion of larvae and pupae (Fisher LSD post hoc test: $P = 0.109$;

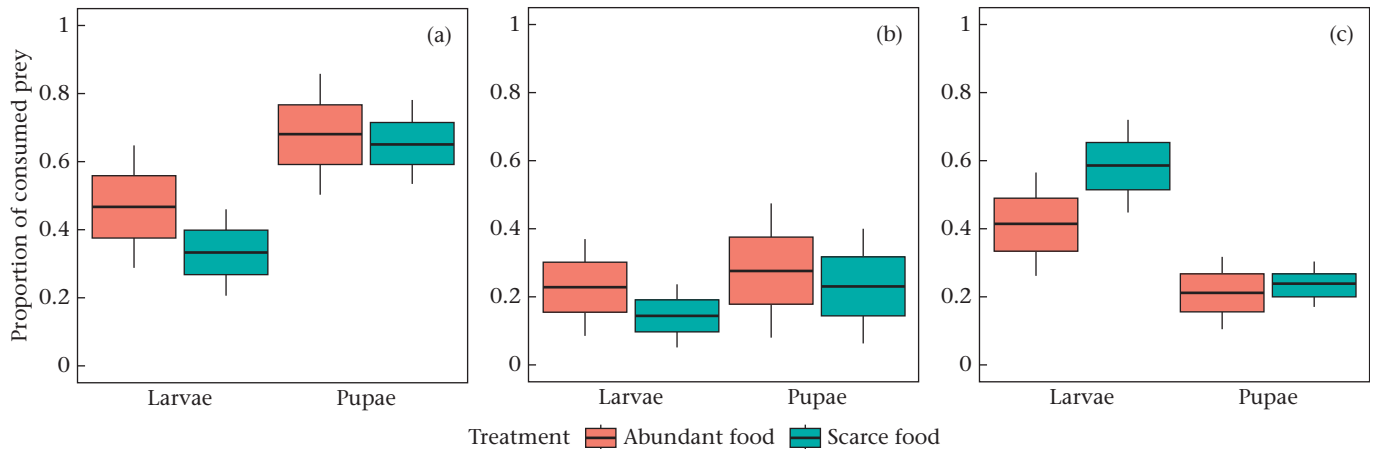


Figure 2. Proportion of larvae and pupae consumed by (a) males, (b) females and (c) nestlings in abundant and scarce food treatments at nestling stage 1 (day 4 after hatching of the first egg). At this stage all prey were brought to the nest by males. Bold lines, boxes and whiskers show mean, standard error and its 95% confidence interval from raw data, respectively.

Fig. 3c). Nestlings were fed a higher proportion of prey in the abundant food treatment (0.50 ± 0.07) than in the scarce food treatment (0.46 ± 0.07 ; GLMM 2.3, Table 1, Fig. 3c) from prey handled by both parents.

Nestlings obtained significantly less biomass in the scarce food treatment than in the abundant food treatment (GLMM 3.6, Table 1, Fig. 4c). Crickets and silkworms provided nestlings with significantly more biomass than larvae and pupae (Fisher LSD post hoc test: $P < 0.001$; Fig. 4c). Biomass consumption did not differ between crickets and silkworms or between larvae and pupae (Fisher LSD post hoc test: $P > 0.052$; Fig. 4c).

Delivery decisions

In NS2, males offered females a higher proportion of prey in the scarce food treatment (0.90 ± 0.04) than in the abundant food treatment (0.76 ± 0.07 ; GLMM 4.1, Table 2), and the rest was offered to the nestlings. Males provided a similar proportion of crickets and silkworms and of larvae and pupae to females (Fisher LSD post hoc test: $P > 0.094$), although they provided a higher proportion of crickets and silkworms than larvae and pupae (Fisher LSD post hoc test: $P < 0.020$).

Of the prey offered by females to nestlings but previously received from males, a similar proportion was offered in the abundant food treatment (0.78 ± 0.07) and in the scarce food treatment (0.79 ± 0.06 ; GLMM 4.2, Table 2, Fig. 5); the rest of the prey offered were captured by females. Of prey provided by males, females offered a similar proportion of larvae, crickets and silkworms (Fisher LSD post hoc tests: $P > 0.372$) and a significantly lower proportion of pupae (Fisher LSD post hoc tests: $P < 0.032$).

DISCUSSION

In line with central-place foraging theory (Kacelnik & Cuthill, 1990; Orrians & Pearson, 1979; Ydenberg, 1994), we predicted that hoopoes should deliver high-quality prey to nestlings but eat low-quality ones themselves (Prediction 1). Given that the hoopoe is a short-lived species, we also predicted that, in situations of scarcity, parents would not reduce the amount of biomass provided to their nestlings (Prediction 2), maintaining their selective provisioning strategy (Prediction 3). Finally, we predicted that the reduction in prey consumption would be more marked in females than in males, since females suffer survival costs in harsh years

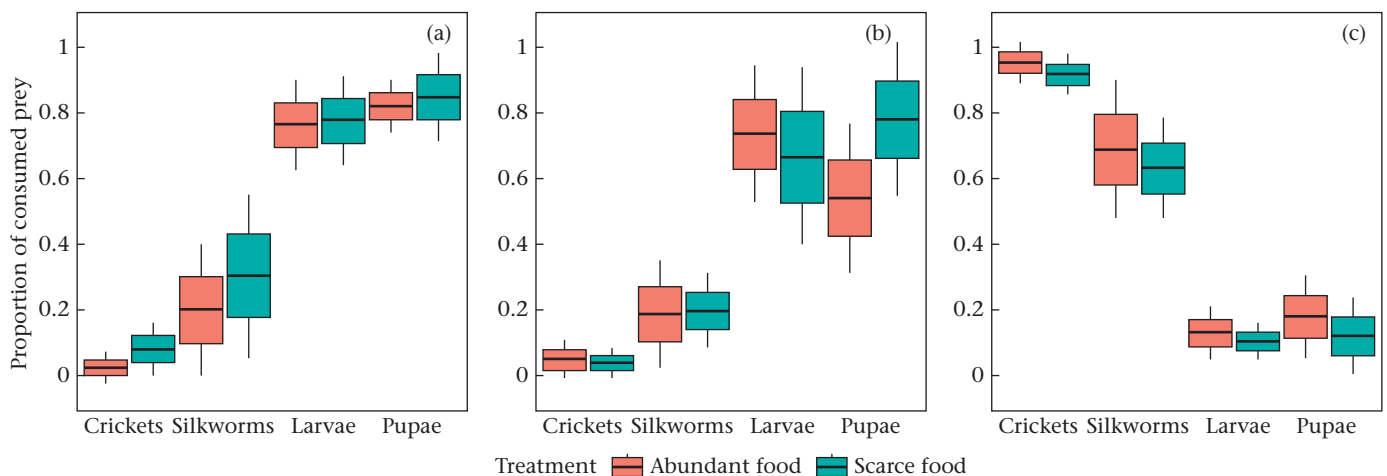


Figure 3. Proportion of each type of prey (crickets, silkworms, larvae and pupae) consumed by (a) males, (b) females and (c) nestlings in abundant and scarce food treatments at nestling stage 2 (day 16 after hatching of the first egg). At this stage both parents brought prey to the nest. Bold lines, boxes and whiskers show mean, standard error and its 95% confidence interval from raw data, respectively.

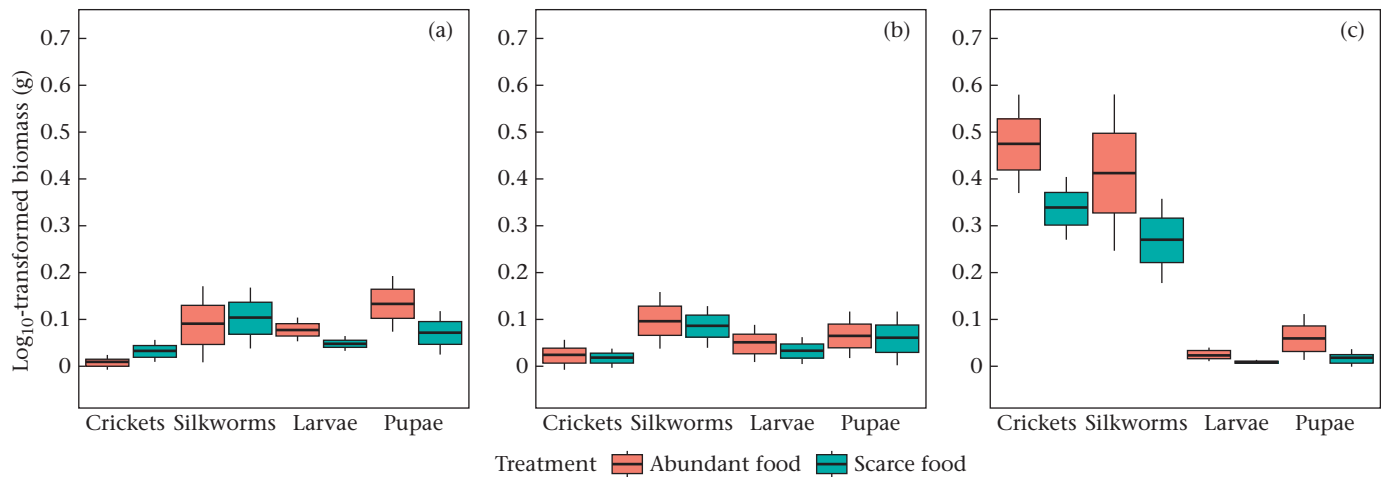


Figure 4. Biomass (g, after \log_{10} transformation) of each type of prey (crickets, silkworms, larvae and pupae) consumed by (a) males, (b) females and (c) nestlings in abundant and scarce food treatments at nestling stage 2 (day 16 after hatching of the first egg). Bold lines, boxes and whiskers show mean, standard error and its 95% confidence interval from raw data, respectively.

Table 2
Summary of the results of generalized linear mixed models showing the effects of treatment and prey type on the proportion of prey offered by males and females in nestling stage 2 (NS2)

	Dependent variable	Factors	Estimate (\pm SE)	Factor type	df	χ^2	P
GLMM 4.1	Proportion of prey offered by males to females	Type of prey	C-P: $-1.56(\pm 0.65)$ C-L: $-1.83(\pm 0.67)$ C-S: $0.79(\pm 0.46)$	Fixed	3,47	20.41	<0.001
		Treatment	2.25 (± 0.47)	Fixed	1,47	29.34	<0.001
		Nest		Random	8,47	191.33	<0.001
GLMM 4.2	Proportion of prey received from males that females offered to nestlings	Type of prey	C-P: $-1.42(\pm 0.64)$ C-L: $0.77(\pm 0.86)$ C-S: $0.46(\pm 0.52)$	Fixed	3,45	8.89	0.030
		Treatment	0.50 (± 0.48)	Fixed	1,45	1.11	0.291
		Nest		Random	8,45	119.9	<0.001

Generalized linear mixed-effects models with binomial distribution and logit link functions exploring the effects of treatment (abundant/scarce food) and type of prey (larvae/pupae/silkworms/crickets) during NS2 (day 16 after hatching of the first egg) on the proportion of prey offered by males to females (GLMM 4.1) and the proportion of prey received from males but offered by females to nestlings (GLMM 4.2). *P* values were calculated by chi-square comparison between the complete model and the reduced model of the variable of interest. Significant *P* values are shown in bold. In NS2, type of prey had four levels, so 'crickets' was set as baseline for the calculation of the estimates (C: crickets; L: larvae; P: pupae; S: silkworms).

(Prediction 4; Plard et al., 2018). In general terms, we found that parents delivered more digestible prey to nestlings at the early nestling stage (NS1) and larger prey at the late nestling stage (NS2), while eating the less profitable prey themselves. In the scarce food treatment, parents reduced the amount of biomass offered to their nestlings in NS2 but did not change the provisioning strategy of feeding the nestlings with the most profitable prey items in either NS1 or NS2. Finally, neither parent reduced their biomass consumption in the scarce food treatment, but females responded by decreasing (NS1) or increasing (NS2) their proportion of prey eaten, while males did not. Below we discuss in detail possible scenarios that would explain these parental decisions.

Food Distribution Patterns in NS1 and NS2

In NS1, we provided two prey types with different chitin content and, therefore, of different quality (Ruppert et al., 1994): fly pupae and larvae. Males ate a higher proportion of pupae and half of the prey they collected, offering the rest to the females. We may speculate that this high consumption of chitinized prey but with a large biomass, would guarantee the self-maintenance of the male. In this stage, males collect all food for the family (Martín-Vivaldi et al., 1999) and bear all the foraging costs (Bryant, 1997). A good

physical condition of males may ensure the survival of the female and the brood and, therefore, the success of the breeding attempt (Barrionuevo et al., 2018; Tveraa et al., 1998; Wendeln & Becker, 1999). At this stage, females do not leave the nest (Martín-Vivaldi et al., 1999), so must decide how to allocate the prey provided by males between offspring and themselves. Our results show that females ate a higher proportion of pupae than larvae and few prey overall (a quarter of the total provided by males). This low consumption may be due to females saving energy related to searching, prey handling time and provisioning trips, expensive tasks that males must perform (Post & Gotmark, 2006). The combined decisions of both parents (males when collecting and females when allocating) result in a better-quality diet for their offspring, with a higher proportion of digestible larvae, supporting Prediction 1. This selective pattern of hoopoes has been observed in other studies on insectivorous birds, such as the bluethroat, *Luscinia svecica* (Orłowski et al., 2014). These authors found that the nestlings were fed more profitable prey (soft-bodied and heavier prey items), and the parents adjusted their own diet by consuming less profitable prey (more chitinized and smaller). This pattern has also been found in acorn woodpeckers, *Melanerpes formicivorus* (Koenig et al., 2008), Cory's shearwaters, *Calonectris borealis* (Alonso et al., 2012) and grey-headed albatrosses, *Thalassarche chrysostoma* (Richoux et al., 2010).

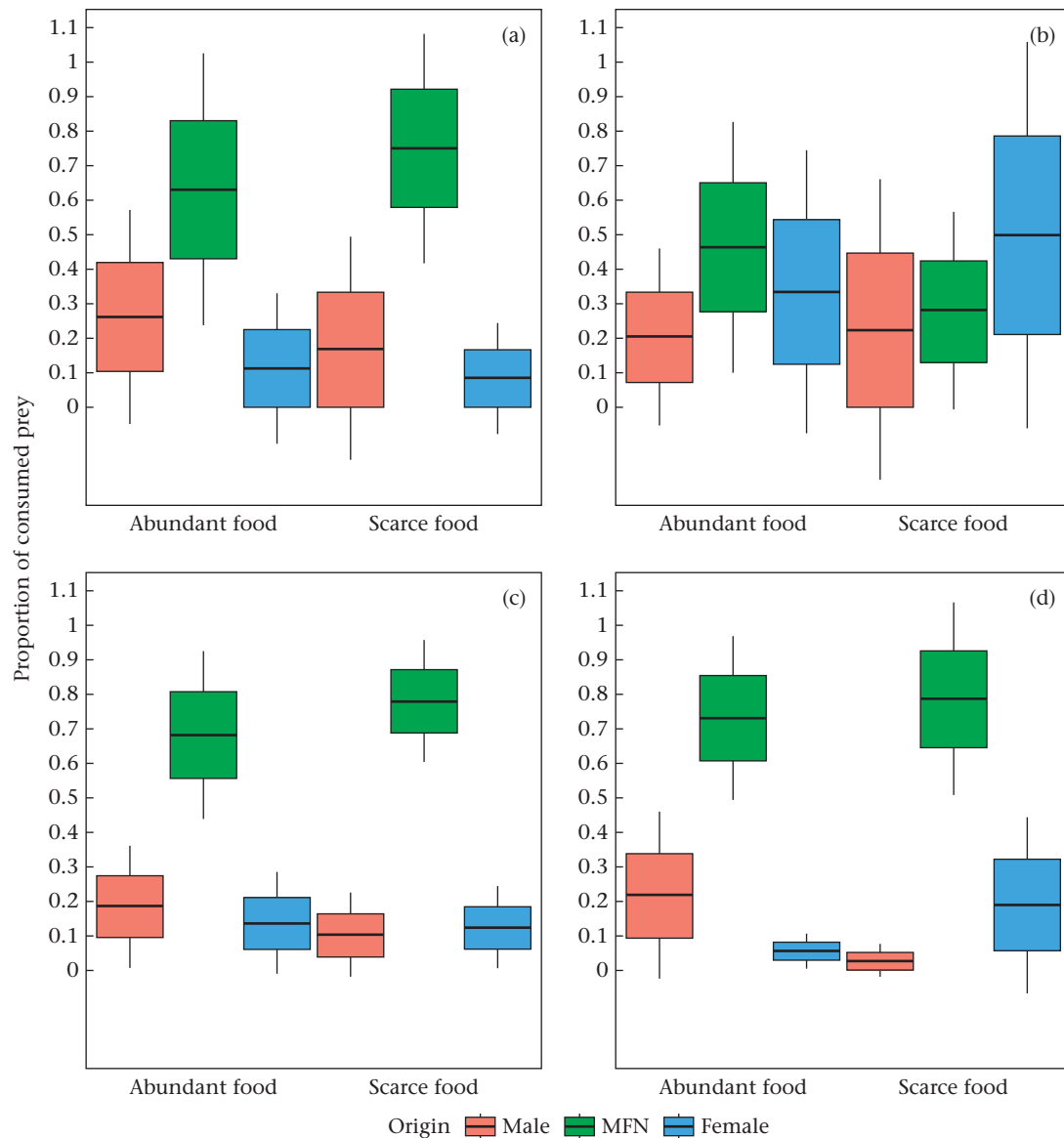


Figure 5. Proportion of (a) larvae, (b) pupae, (c) crickets and (d) silkworms consumed by nestlings in abundant and scarce food treatments at nestling stage 2 (day 16 after hatching of the first egg) and according to the origin of the prey (MFN: sequence male-female-nestling). Bold lines, boxes and whiskers show mean, standard error and its 95% confidence interval from raw data, respectively.

In NS2, we offered four types of prey with different chitin content and different sizes (fly pupae and larvae, crickets and silkworm). Both parents ate a higher proportion of larvae and pupae than silkworms and crickets. The decisions of both parents resulted in a nestling diet with higher energy content, that is, a higher proportion of crickets and silkworms than larvae and pupae, supporting Prediction 1. Parental decisions at this stage to provide larger prey to nestlings are in accordance with previous findings of food provisioning in a Swiss hoopoe population (Arlettaz et al., 2010; Fournier & Arlettaz, 2001). In this population, the dominant large prey in the nestling diet is the mole cricket, *Gryllotalpa gryllotalpa*. A reduction in the proportion taken was associated with a significant decrease in the survival of nestlings and in the reproductive success of parents (Arlettaz et al., 2010; Fournier & Arlettaz, 2001; Guillo et al., 2016).

Furthermore, the hoopoe is a ground-foraging bird (Cramp, 1998) so the searching time for prey depends on both the abundance and the accessibility of underground-dwelling prey

(Tagmann-Joset et al., 2012). Therefore, the best strategy is to maximize provisioning effort per unit of time spent foraging. In this sense, adult hoopoes ate the small prey right after finding it to satisfy their own energy requirements while selecting larger prey to feed their nestlings and make the trip to the nest more profitable (Kacelnik & Cuthill, 1990). Direct observations have shown that parents in several seabirds consumed the smaller and less profitable prey in situ, but carried larger and high-quality ones to their nestlings (Danhardt et al., 2011; Davoren & Burger, 1999; Wilson et al., 2004). Similar results have been obtained with other terrestrial species such as raptors (Catry et al., 2016) and passerines (Beaulieu & Sockman, 2014).

Regarding large prey, we found an opposite pattern to what was expected. Both parents ate more silkworms than crickets and offered the most chitinized prey to nestlings. We offer here some plausible speculations to this parental choice. First, adult hoopoes may be more familiar with crickets than silkworms. We supplied crickets daily during the breeding season and silkworms were only

supplied during the experimental treatment (Martínez-García et al., 2016). Moreover, mole crickets in Switzerland (Fournier & Arlettaz, 2001) and adult field crickets, *Gryllus campestris* (Barbaro et al., 2008) in southwestern France are the main prey in the diet of nestling hoopoes, more similar to our crickets, *G. bimaculatus*, than silkworms. Second, the silkworms seem more difficult for parents to handle as they usually take longer to kill than crickets (L. Arco, personal observation). This behaviour of killing silkworms is similar to how hoopoes kill pine processionary moth caterpillars, *Thaumetopoea pityocampa* (M. Martín-Vivaldi & J. M. Peralta-Sánchez, personal observations), one of the main prey of hoopoes in Mediterranean environments (Barbaro et al., 2008; Battisti et al., 2000). This extra time spent handling silkworms can reduce their profitability (Banbura et al., 1999; Cansse et al., 2020); thus, it makes sense for parents to select for their nestlings those prey requiring less handling time. Finally, as the nestlings grow, their ability to digest more chitinized prey may increase as has been observed in other species (Orłowski et al., 2015). This improvement in digestibility would help parents to evaluate the profitability of the prey based on other characteristics, such as handling time or prey accessibility (Cansse et al., 2020).

In NS2, females decided the destination of most prey items since males offered a high proportion of prey (> 0.70) to females and the rest to nestlings. This result implies that males delegate most provisioning decisions to females. One possible explanation for this pattern is that females may maximize food allocation because they spend more time in the nest and may gather more reliable information about the nutritional status of the nestlings (Gottlander, 1987; Nuhlickova et al., 2021; Ryser et al., 2016). Hoopoe eggs hatch asynchronously and hence broods comprise nestlings of different ages and sizes (Martín-Vivaldi et al., 1999). Ryser et al. (2016) found that hoopoe males showed a preference for nestlings that were closer to the nestbox entrance, favouring larger nestlings. Females, feeding inside the nest, can allocate food more evenly among nestlings, benefiting younger ones, which could increase the number of fledglings (Ryser et al., 2016). This mate-feeding behaviour can also be explained as a display of male quality or as a reinforcement of pair bonds (Costanzo et al., 2020; Korpimäki, 1989). Indeed, species where males feed their females are also those where males invest more in feeding their offspring (Møller & Cuervo, 2000) as occurs in the hoopoe. In addition, mate feeding may maintain females in good body condition, which can positively affect the fitness of both parents (Galván & Sanz, 2011). Both strategies could increase the male's opportunity to lay a second clutch with the same female, which is common in this species (Hoffmann et al., 2015; Martín-Vivaldi et al., 1999).

Effect of Food Scarcity in NS1 and NS2

Adults of short-lived species facing food limitation are expected to increase their current breeding effort even at the cost of their survival, according to life history theory (Boutin, 1990; Martin, 1987). This hypothesis was supported in NS1, when the scarce food treatment did not affect either the total biomass offered (Prediction 2) or the delivery of the most profitable prey (Prediction 3) to the nestlings. In addition, females responded by eating a lower proportion of prey in the scarce food treatment, although this effect did not translate into a change in ingested biomass between the two treatments. Pupae have a higher dry weight than larvae, so a larger difference between pupae consumed in the abundant and scarce food treatments is likely to be needed to produce changes in ingested biomass. These results indicate that parents (females in our case) invest in current reproduction over their own maintenance (Grieco, 2001; Markman, 2014; Markman et al., 2002) as in other short-lived species.

In NS2 (16 days after hatching), the nestlings' energy demand and thus provisioning activity are higher than in NS1 (Arlettaz et al., 2010; Ryser et al., 2016). In this stage, hoopoe parents maintained their biomass consumption in the scarce food treatment but the nestlings suffered the consequences. They consumed significantly less biomass and a lower proportion of prey in the scarce food treatment. Despite these results contradicting our Prediction 2, parents still provided nestlings with the most profitable prey in the scarce food treatment (Prediction 3). However, this provisioning strategy did not fully compensate for the reduced availability of food. This result contrasts with previous studies with short-lived species and central-place foragers where parents increased provisioning rates and therefore their feeding effort in enlarged broods (reviewed by Gow & Wiebe, 2014) and in food supplementation experiments (Markman et al., 2002). A study conducted by Gow and Wiebe (2014) found that the northern flicker, *Colaptes auratus*, a short-lived woodpecker and central-place forager, did not respond by increasing provisioning rate in an enlarged brood experiment in the short term (24 h). These authors hypothesized that the lack of response could be due to energetic limitations of this species which has large home ranges and a prolonged nestling period. Therefore, their ability to respond to increased offspring demands could be limited. In the same study, Gow and Wiebe (2014) found that five of six species that did not respond to increased brood demands had large home ranges (> 25 ha), and that flickers have longer nestling periods (25–29 days) than the 80% of 15 species (mostly small passerines) that responded to enlarged brood manipulations. These findings are in line with some characteristics of hoopoes. Home range size of hoopoes varied between 4.4 and 72.2 ha in Switzerland (mean \pm SD = 39.6 ± 25.4 ha, Tagmann-Ioset et al., 2012), between 7.41 and 30.76 ha in France (mean \pm SD = 12.78 ± 5.96 ha, Barbaro et al., 2008) and between 5.8 and 42.9 ha in Croatia (Podletnik & Denac, 2015). Moreover, the hoopoe nestling period lasts 27.1 ± 2.0 days (Martín-Vivaldi et al., 1999) similar to that of northern flickers. The same research group showed that northern flicker parents do respond to enlarged broods in the long term: they increased their provisioning rate but raised nestlings in poorer condition (Musgrove & Wiebe, 2014). These characteristics of hoopoes shared with northern flickers may support the hypothesis proposed by Gow and Wiebe (2014), where some birds may experience an atypical response for short-lived species, at least in the short term.

Our results do not support Prediction 4 that females reduced self-maintenance more than males in the scarce food treatment. Conversely, females ate a higher proportion of prey in the scarce food treatment in NS2. Plard et al. (2018) found that females experienced poorer reproductive success and survival after intense breeding efforts (raising second broods) in harsh years. Moreover, one-third of hoopoe females are double-breeders while only one-fifth of the males try for a second brood (Hoffmann et al., 2015). Our finding that females maintained the level of biomass consumed and even increased their proportion of consumed prey in the scarce food treatment might be explained by a high proportion of them leaving their brood before the nestlings fledge to start a second clutch (Arlettaz et al., 2010; Hoffmann et al., 2015). Thus, in our study, females could be evaluating food availability from the point of view of raising a second brood successfully. For males, their reproductive effort in the first brood in harsh years negatively affected the success of the second brood in the same breeding season (Plard et al., 2018). These intraseasonal costs may limit the males' investment in the reproductive season. Furthermore, males extend their parental care until the postfledgling period (Arlettaz et al., 2010) and may therefore be more reluctant to change their prey consumption pattern. Our results support this idea, as males did not change the biomass or the proportion of prey they ate in

NS2 during the scarce food treatment. Males may be conserving resources to care for the fledglings until their independence, an idea proposed by Musgrove and Wiebe (2014). While males followed a fixed investment strategy during the nestling period, females responded more flexibly to changes in food availability in both stages (Low et al., 2012; Markman et al., 2002). This differential response may be the result of different parental investment when nestlings are close to fledging, since they show different life-history strategies (Plard et al., 2018). This pattern has also been observed in other short-lived nonpasserine species, such as the American kestrel, *Falco sparverius*, where males responded more weakly than females to food supplementation (Dawson & Bortolotti, 2002).

In summary, hoopoes followed a central-place foraging strategy, providing the most profitable prey to nestlings while eating the poorest quality, regardless of food availability and nestling stage. In the late stage, when the energy demands of the nestlings and the provisioning activity of the parents increased, the scarcity of food affected the nestlings but not the parents. Traits that limit the energetic capacity of the parents, such as a large home range and prolonged nestling period, could explain this atypical response, as proposed by Gow and Wiebe (2014). In turn, although both parents continued to ingest the same amount of biomass in both stages, females were more responsive to changes in food availability, perhaps due to different investment at the end of the breeding stage. We suggest that future work on sex differences in reproductive allocation should investigate whether parents adjust their responses to changes in the contribution of their partner or to changes in offspring behaviour.

Author Contributions

Laura Arco: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Visualization; Roles/Writing – original draft; review & editing. **Manuel Martín-Vivaldi:** Conceptualization; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Writing – review & editing. **Juan Manuel Peralta-Sánchez:** Data curation; Formal analysis; Validation; Visualization; Writing – review & editing. **Natalia Juárez-García-Pelayo:** Investigation; Writing – review & editing. **Manuel Soler:** Conceptualization; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Writing – review & editing.

Acknowledgments

We are grateful to Jonathan Romero Masegosa, Manuel Soto, Jorge Doña, Alicia Astasio, Elisa García, Rosa María Morales of University of Granada for help in caring for captive hoopoes. We thank Francisco Castillo for his help and advice in proofreading the English. Support by funding was provided by the Spanish Ministry of Science and Innovation, European funds (FEDER) (CGL2007-61940/BOS, CGL2010-19233-C03-03) and the Junta de Andalucía (P09-RNM-4557). L.A. received a contract of technical support staff from the Spanish Ministry of Science and Innovation (Subprogram PTA-MICINN) (Ref. PTA2010-4298-I). We thank funding for open access charge to University of Granada/CBUA. We thank two anonymous referees and, especially, editor Matt Bell for their recommendations and suggestions that have undoubtedly improved the manuscript.

References

Alonso-Álvarez, C., & Velando, A. (2012). Benefits and costs of parental care. In N. J. Royle, P. T. Smiseth, & M. Kolliker (Eds.), *Evolution of parental care* (pp.

- 40–61). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199692576.001.0001>
- Alonso, H., Granadeiro, J. P., Paiva, V. H., Dias, A. S., Ramos, J. A., & Catry, P. (2012). Parent-offspring dietary segregation of Cory's shearwaters breeding in contrasting environments. *Marine Biology*, 159(6), 1197–1207. <https://doi.org/10.1007/s00227-012-1900-2>
- Arlettaz, R., Schaad, M., Reichlin, T. S., & Schaub, M. (2010). Impact of weather and climate variation on Hoopoe reproductive ecology and population growth. *Journal of Ornithology*, 151(4), 889–899. <https://doi.org/10.1007/s10336-010-0527-7>
- Ballard, G., Dugger, K. M., Nur, N., & Ainley, D. G. (2010). Foraging strategies of Adelie penguins: Adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series*, 405, 287–302. <https://doi.org/10.3354/meps08514>
- Banbura, J., Banbura, M., Gladalski, M., Kalinski, A., Markowski, M., Michalski, M., Nadolski, J., Skwarska, J., & Zielinski, P. (2011). Body condition parameters of nestling Great Tits *Parus major* in relation to experimental food supplementation. *Acta Ornithologica*, 46(2), 207–212. <https://doi.org/10.3161/000164511x625991>
- Banbura, J., Lambrechts, M. M., Blondel, J., Perret, P., & Cartan-Son, M. (1999). Food handling time of Blue Tit chicks: Constraints and adaptation to different prey types. *Journal of Avian Biology*, 30(3), 263–270. <https://doi.org/10.2307/3677352>
- Barbaro, L., Couzi, L., Bretagnolle, V., Nezan, J., & Vetillard, F. (2008). Multi-scale habitat selection and foraging ecology of the Eurasian Hoopoe (*Upupa epops*) in pine plantations. *Biodiversity and Conservation*, 17(5), 1073–1087. <https://doi.org/10.1007/s10531-007-9241-z>
- Barriónuevo, M., Ciancio, J., Marchisio, N., & Frere, E. (2018). Parental body condition and high energy value of fish determine nestling success in Magellanic Penguin (*Spheniscus magellanicus*). *Marine Biology*, 165(6), 16. <https://doi.org/10.1007/s00227-018-3358-3>
- Battisti, A., Bernardi, M., & Ghirardo, C. (2000). Predation by the Hoopoe (*Upupa epops*) on pupae of *Thaumetopoea pityocampa* and the likely influence on other natural enemies. *Biocontrol*, 45(3), 311–323. <https://doi.org/10.1023/a:1009992321465>
- Beaulieu, M., & Sockman, K. W. (2014). Comparison of optimal foraging versus life-history decisions during nestling care in Lincoln's Sparrows *Melospiza lincolni* through stable isotope analysis. *Ibis*, 156(2), 424–432. <https://doi.org/10.1111/ibi.12146>
- Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates—patterns, problems, and the future. *Canadian Journal of Zoology*, 68(2), 203–220. <https://doi.org/10.1139/z90-031>
- Bryant, D. M. (1997). Energy expenditure in wild birds. *Proceedings of the Nutrition Society*, 56(3), 1025–1039. <https://doi.org/10.1079/pns19970107>
- Burke, C. M., & Montevecchi, W. A. (2009). The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology*, 278(4), 354–361. <https://doi.org/10.1111/j.1469-7998.2009.00584.x>
- Cansse, T., Fauchet, L., Wells, M. R., & Arnould, J. P. Y. (2020). Factors influencing prey capture success and profitability in Australasian Gannets (*Morus serrator*). *Biology Open*, 9(1), 9. <https://doi.org/10.1242/bio.047514>
- Catry, I., Catry, T., Alho, M., Franco, A. M. A., & Moreira, F. (2016). Sexual and parent-offspring dietary segregation in a colonial raptor as revealed by stable isotopes. *Journal of Zoology*, 299(1), 58–67. <https://doi.org/10.1111/jzo.12324>
- Chae, K. S., Shin, C. S., & Shin, W. S. (2018). Characteristics of cricket (*Gryllus bimaculatus*) chitosan and chitosan-based nanoparticles. *Food Science and Biotechnology*, 27(3), 631–639. <https://doi.org/10.1007/s10068-018-0314-4>
- Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton University Press. <https://doi.org/10.2307/j.ctvs325j>
- Costanzo, A., Tommasi, N., Galimberti, A., Scesa, G. C., Ambrosini, R., Griggio, M., Cecere, J. G., & Rubolini, D. (2020). Extra food provisioning reduces extra-pair paternity in the Lesser Kestrel *Falco naumanni*. *Journal of Avian Biology*, 51(9), 7. <https://doi.org/10.1111/jav.02535>
- Cramp, S. (1998). *The complete birds of the Western Palearctic on CD-ROM*.
- Danhardt, A., Freseman, T., & Becker, P. H. (2011). To eat or to feed? Prey utilization of Common Terns *Sterna hirundo* in the Wadden Sea. *Journal of Ornithology*, 152(2), 347–357. <https://doi.org/10.1007/s10336-010-0590-0>
- Davoren, G. K., & Burger, A. E. (1999). Differences in prey selection and behaviour during self-feeding and chick provisioning in Rhinoceros Auklets. *Animal Behaviour*, 58, 853–863. <https://doi.org/10.1006/anbe.1999.1209>
- Dawson, R. D., & Bortolotti, G. R. (2002). Experimental evidence for food limitation and sex-specific strategies of American Kestrels (*Falco sparverius*) provisioning offspring. *Behavioral Ecology and Sociobiology*, 52(1), 43–52. <https://doi.org/10.1007/s00265-002-0486-y>
- Drent, R. H., & Daan, S. (1980). The prudent parent - Energetic adjustments in avian breeding. *Ardea*, 68(1–4), 225–252.
- Duke, G. E. (1997). Gastrointestinal physiology and nutrition in wild birds. *Proceedings of the Nutrition Society*, 56(3), 1049–1056. <https://doi.org/10.1079/pns19970109>
- Eldegard, K., & Sønnerud, G. A. (2010). Experimental increase in food supply influences the outcome of within-family conflicts in Tengmalm's Owl. *Behavioral Ecology and Sociobiology*, 64(5), 815–826. <https://doi.org/10.1007/s00265-009-0898-z>
- Fournier, J., & Arlettaz, R. (2001). Food provision to nestlings in the Hoopoe *Upupa epops*: Implications for the conservation of a small endangered population in the Swiss Alps. *Ibis*, 143(1), 2–10. <https://doi.org/10.1111/j.1474-919X.2001.tb04163.x>
- Galván, I., & Sanz, J. J. (2011). Mate-feeding has evolved as a compensatory energetic strategy that affects breeding success in birds. *Behavioral Ecology*, 22(5), 1088–1095. <https://doi.org/10.1093/beheco/arr094>

- Ghalambor, C. K., & Martin, T. E. (2001). Fecundity-survival trade-offs and parental risk-taking in birds. *Science*, 292(5516), 494–497. <https://doi.org/10.1126/science.1059379>
- González, L., Margalida, A., Sánchez, R., & Oria, J. (2006). Supplementary feeding as an effective tool for improving breeding success in the Spanish Imperial Eagle (*Aquila adalberti*). *Biological Conservation*, 129(4), 477–486. <https://doi.org/10.1016/j.bioccon.2005.11.014>
- Gottlander, K. (1987). Parental feeding-behaviour and sibling competition in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica*, 18(4), 269–276. <https://doi.org/10.2307/3676895>
- Gow, E. A., & Wiebe, K. L. (2014). Responses by central-place foragers to manipulations of brood size: Parent flickers respond to proximate cues but do not increase work rate. *Ethology*, 120(9), 881–892. <https://doi.org/10.1111/eth.12259>
- Granbom, M., & Smith, H. G. (2006). Food limitation during breeding in a heterogeneous landscape. *Auk*, 123(1), 97–107. [https://doi.org/10.1642/0004-8038\(2006\)123\[0097:fldbia\]2.0.Co;2](https://doi.org/10.1642/0004-8038(2006)123[0097:fldbia]2.0.Co;2)
- Grieco, F. (2001). Short-term regulation of food-provisioning rate and effect on prey size in Blue Tits, *Parus caeruleus*. *Animal Behaviour*, 62, 107–116. <https://doi.org/10.1006/anbe.2001.1736>
- Grieco, F. (2002). Time constraint on food choice in provisioning Blue Tits, *Parus caeruleus*: The relationship between feeding rate and prey size. *Animal Behaviour*, 64, 517–526. <https://doi.org/10.1006/anbe.2002.3073>
- Guilod, N., Arlettaz, R., & Jacot, A. (2016). Impact of spatial variation of a crucial prey, the Molecricket, on Hoopoe territory occupancy and reproduction. *Journal of Avian Biology*, 47(5), 697–705. <https://doi.org/10.1111/jav.00990>
- Hahn, T., Tafi, E., Paul, A., Salvia, R., Falabella, P., & Zibek, S. (2020). Current state of chitin purification and chitosan production from insects. *Journal of Chemical Technology and Biotechnology*, 95(11), 2775–2795. <https://doi.org/10.1002/jctb.6533>
- Hamel, S., Gaillard, J. M., Yoccoz, N. G., Loison, A., Bonenfant, C., & Descamps, S. (2010). Fitness costs of reproduction depend on life speed: Empirical evidence from mammalian populations. *Ecology Letters*, 13(7), 915–935. <https://doi.org/10.1111/j.1461-0248.2010.01478.x>
- Harrison, F., Barta, Z., Cuthill, I., & Szekely, T. (2009). How is sexual conflict over parental care resolved? A meta-analysis. *Journal of Evolutionary Biology*, 22(9), 1800–1812. <https://doi.org/10.1111/j.1420-9101.2009.01792.x>
- Hernández-Piiego, J., Rodríguez, C., & Bustamante, J. (2017). A few long versus many short foraging trips: Different foraging strategies of Lesser Kestrel sexes during breeding. *Movement Ecology*, 5, 16. <https://doi.org/10.1186/s40462-017-0100-6>
- Hinde, C. A., & Kilner, R. M. (2007). Negotiations within the family over the supply of parental care. *Proceedings of the Royal Society B: Biological Sciences*, 274(1606), 53–60. <https://doi.org/10.1098/rspb.2006.3692>
- Hoffmann, J., Postma, E., & Schaub, M. (2015). Factors influencing double brooding in Eurasian Hoopoes *Upupa epops*. *Ibis*, 157(1), 17–30. <https://doi.org/10.1111/ibi.12188>
- Houston, A. I., & Davies, N. B. (1985). The evolution of cooperation and life history in the dunnoek, *Prunella modularis*. In R. Sibly, & R. Smith (Eds.), *Behavioural ecology: the ecological consequences of adaptive behaviour* (pp. 471–487). Blackwell.
- Houston, A. I., Szekely, T., & McNamara, J. M. (2005). Conflict between parents over care. *Trends in Ecology & Evolution*, 20(1), 33–38. <https://doi.org/10.1016/j.tree.2004.10.008>
- Iserby, A., Griffioen, M., Ens, M., & Muller, W. (2019). Enduring rules of care within pairs how blue tit parents resume provisioning behaviour after experimental disturbance. *Scientific Reports*, 9. <https://doi.org/10.1038/s41598-019-39139-9>
- Jackson, S., Place, A. R., & Seiderer, L. J. (1992). Chitin digestion and assimilation by seabirds. *Auk*, 109(4), 758–770.
- Johnstone, R. A., & Hinde, C. A. (2006). Negotiation over offspring care - how should parents respond to each other's efforts? *Behavioral Ecology*, 17(5), 818–827. <https://doi.org/10.1093/beheco/arl009>
- Kacelnik, A. (1984). Central place foraging in Starlings (*Sturnus vulgaris*). I. Patch residence time. *Journal of Animal Ecology*, 53(1), 283–299. <https://doi.org/10.2307/4357>
- Kacelnik, A., & Cuthill, I. (1990). Central place foraging in Starlings (*Sturnus vulgaris*). 2. Food allocation to chicks. *Journal of Animal Ecology*, 59(2), 655–674. <https://doi.org/10.2307/4887>
- Karasov, W. H. (1990). Digestion in birds: Chemical and physiological determinants and ecological implications. *Studies in Avian Biology*, 13, 391–415.
- Koenig, W. D., Schaefer, D. J., Mambelli, S., & Dawson, T. E. (2008). Acorns, insects, and the diet of adult versus nestling Acorn Woodpeckers. *Journal of Field Ornithology*, 79(3), 280–285. <https://doi.org/10.1111/j.1557-9263.2008.00174.x>
- Koenig, W. D., & Walters, E. L. (2012). An experimental study of chick provisioning in the cooperatively breeding Acorn Woodpecker. *Ethology*, 118(6), 566–574. <https://doi.org/10.1111/j.1439-0310.2012.02043.x>
- Korpimäki, E. (1989). Mating system and mate choice of Tengmalm Owls *Aegolius funereus*. *Ibis*, 131(1), 41–50. <https://doi.org/10.1111/j.1474-919X.1989.tb02742.x>
- Krause, E. T., Kruger, O., & Pogany, A. (2017). Zebra finch nestlings, rather than parents, suffer from raising broods under low nutritional conditions. *Behavioral Ecology and Sociobiology*, 71(10), 12. <https://doi.org/10.1007/s00265-017-2382-5>
- Lessells, C. M. (1999). Sexual conflict in animals. In L. Keller (Ed.), *Levels of selection in evolution* (pp. 75–99). Princeton University Press.
- Lessells, C. M., & McNamara, J. M. (2012). Sexual conflict over parental investment in repeated bouts: Negotiation reduces overall care. *Proceedings of the Royal Society B: Biological Sciences*, 279(1733), 1506–1514. <https://doi.org/10.1098/rspb.2011.1690>
- Low, M., Makan, T., & Castro, I. (2012). Food availability and offspring demand influence sex-specific patterns and repeatability of parental provisioning. *Behavioral Ecology*, 23(1), 25–34. <https://doi.org/10.1093/beheco/arr145>
- Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., Van Benthem, K., Bolker, B., Brooks, M., & Brooks, M. M. (2017). *Package 'glmmTMB'*. <https://journal.r-project.org/archive/2017/RJ-2017-066/index.html>
- Markman, S. (2014). Parental self-feeding effects on parental care levels and time allocation in Palestine sunbirds. *PLoS One*, 9(12), Article e113890. <https://doi.org/10.1371/journal.pone.0113890>
- Markman, S., Pinshow, B., & Wright, J. (2002). The manipulation of food resources reveals sex-specific trade-offs between parental self-feeding and offspring care. *Proceedings of the Royal Society B: Biological Sciences*, 269(1503), 1931–1938. <https://doi.org/10.1098/rspb.2002.2118>
- Martin, T. E. (1987). Food as a limit on breeding birds: A life-history perspective. *Annual Review of Ecology and Systematics*, 18(1), 453–487. <https://doi.org/10.1146/annurev.es.18.110187.002321>
- Martín-Vivaldi, M., Palomino, J. J., Soler, M., & Soler, J. J. (1999). Determinants of reproductive success in the Hoopoe *Upupa epops*, a hole-nesting non-passerine bird with asynchronous hatching. *Bird Study*, 46, 205–216. <https://doi.org/10.1080/000636599090461132>
- Martín-Vivaldi, M., Soler, J. J., Peralta-Sánchez, J. M., Arco, L., Martín-Platero, A. M., Martínez-Bueno, M., Ruiz-Rodríguez, M., & Valdivia, E. (2014). Special structures of Hoopoe eggshells enhance the adhesion of symbiont-carrying uropygial secretion that increase hatching success. *Journal of Animal Ecology*, 83(6), 1289–1301. <https://doi.org/10.1111/1365-2656.12243>
- Martínez-García, A., Martín-Vivaldi, M., Ruiz-Rodríguez, M., Martínez-Bueno, M., Arco, L., Rodríguez-Ruano, S., Peralta-Sánchez, J. M., & Soler, J. J. (2016). The microbiome of the uropygial secretion in hoopoes is shaped along the nesting phase. *Microbial Ecology*, 72(1), 252–261. <https://doi.org/10.1007/s00248-016-0765-1>
- McNamara, J. M., Gasson, C. E., & Houston, A. I. (1999). Incorporating rules for responding into evolutionary games. *Nature*, 401(6751), 368–371. <https://doi.org/10.1038/43869>
- Moller, A. P., & Cuervo, J. J. (2000). The evolution of paternity and paternal care in birds. *Behavioral Ecology*, 11(5), 472–485. <https://doi.org/10.1093/beheco/11.5.472>
- Mullers, R. H. E., Navarro, R. A., Daan, S., Tinbergen, J. M., & Meijer, H. A. J. (2009). Energetic costs of foraging in breeding Cape Gannets *Morus capensis*. *Marine Ecology Progress Series*, 393, 161–171. <https://doi.org/10.3354/meps08250>
- Musgrove, A. B., & Wiebe, K. L. (2014). Northern Flickers increase provisioning rates to raise more but poorer quality offspring when given experimentally enlarged broods. *Auk*, 131(4), 571–582. <https://doi.org/10.1642/auk-14-51.1>
- Nakagawa, S., Gillespie, D. O. S., Hatchwell, B. J., & Burke, T. (2007). Predictable males and unpredictable females: Sex difference in repeatability of parental care in a wild bird population. *Journal of Evolutionary Biology*, 20(5), 1674–1681. <https://doi.org/10.1111/j.1420-9101.2007.01403.x>
- Nuhlickova, S., Svetlik, J., Eckenfellner, M., Knauer, F., & Hoi, H. (2021). Interaction between nestling behaviour and nest-space use. *Ethology Ecology & Evolution*, 33(5), 496–514. <https://doi.org/10.1080/03949370.2020.1858173>
- Orians, G. H., & Pearson, N. E. (1979). On the theory of central place foraging. In D. J. Horn, R. D. Mitchell, & G. R. Stair (Eds.), *Analysis of ecological systems* (pp. 155–177). Ohio State University Press.
- Orłowski, G., Rusiecki, S., & Karg, J. (2014). Partial dietary segregation between adult and nestling Bluethroats *Luscinia svecica*. *Acta Ornithologica*, 49(1), 107–118. <https://doi.org/10.3161/000164514x682931>
- Orłowski, G., Wuczynski, A., & Karg, J. (2015). Effect of brood age on nestling diet and prey composition in a hedgerow specialist bird, the barred warbler *Sylvia nisoria*. *PLoS One*, 10(6), 16. <https://doi.org/10.1371/journal.pone.0131100>
- Plard, F., Arlettaz, R., & Schaub, M. (2018). Hoopoe males experience intra-seasonal while females experience inter-seasonal reproductive costs. *Oecologia*, 186(3), 665–675. <https://doi.org/10.1007/s00442-017-4028-8>
- Podletnik, M., & Denac, D. (2015). Selection of foraging habitat and diet of the Hoopoe *Upupa epops* in the mosaic-like cultural landscape of Goricko (NE Slovenia). *Acrocephalus*, 36(166–67), 109–132. <https://doi.org/10.1515/acro-2015-0008>
- Post, P., & Gotmark, F. (2006). Predation by Sparrow Hawks *Accipiter nisus* on male and female Pied Flycatchers *Ficedula hypoleuca* in relation to their breeding behaviour and foraging. *Journal of Avian Biology*, 37(2), 158–168. <https://doi.org/10.1111/j.0908-8857.2006.03338.x>
- R Core Team. (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rauter, C. M., & Moore, A. J. (2004). Time constraints and trade-offs among parental care behaviours: Effects of brood size, sex and loss of mate. *Animal Behaviour*, 68, 695–702. <https://doi.org/10.1016/j.anbehav.2003.09.018>
- Richoux, N. B., Jaquemet, S., Bonnevie, B. T., Cherel, Y., & McQuaid, C. D. (2010). Trophic ecology of Grey-headed Albatrosses from Marion Island, Southern Ocean: Insights from stomach contents and diet tracers. *Marine Biology*, 157(8), 1755–1766. <https://doi.org/10.1007/s00227-010-1448-y>
- Robinson, B. G., Franke, A., & Derocher, A. E. (2015). Estimating nestling diet with cameras: Quantifying uncertainty from unidentified food items. *Wildlife Biology*, 21(5), 277–282. <https://doi.org/10.2981/wlb.00114>
- Royle, N. J., Smiseth, P. T., & Kölliker, M. (2012). *The evolution of parental care*. Oxford University Press.
- Ruffino, L., Salo, P., Koivisto, E., Banks, P. B., & Korpimäki, E. (2014). Reproductive responses of birds to experimental food supplementation: A meta-analysis. *Frontiers in Zoology*, 11. <https://doi.org/10.1186/s12983-014-0080-y>

- Ruppert, E. E., Fox, R. S., & Barnes, R. D. (1994). *Invertebrate zoology* (6th ed.). Saunders College Publishing, Harcourt Brace.
- Ryser, S., Guillo, N., Bottini, C., Arlettaz, R., & Jacot, A. (2016). Sex-specific food provisioning patterns by parents in the asynchronously hatching European Hoopoe. *Animal Behaviour*, 117, 15–20. <https://doi.org/10.1016/j.anbehav.2016.04.015>
- Sanz, J. J., Kranenbarg, S., & Tinbergen, J. M. (2000). Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). *Journal of Animal Ecology*, 69(1), 74–84. <https://doi.org/10.1046/j.1365-2656.2000.00373.x>
- Schaub, M., Reichlin, T. S., Abadi, F., Kery, M., Jenni, L., & Arlettaz, R. (2012). The demographic drivers of local population dynamics in two rare migratory birds. *Oecologia*, 168(1), 97–108. <https://doi.org/10.1007/s00442-011-2070-5>
- Schoener, T. W. (1979). Generality of the size-distance relation in models of optimal feeding. *American Naturalist*, 114(6), 902–914. <https://doi.org/10.1086/283537>
- Sinervo, B. (2012). Optimal foraging theory: Constraints and cognitive processes. In *Behavioral genetics to evolution* (pp. 105–130). Tophatmonocle Corp. Retrieved from http://bio.research.ucsc.edu/~barrylab/classes/animal_behavior/BEHAVIOR.HTM.
- Sonerud, G. A. (1989). Allocation of prey between self-consumption and transport in 2 different-sized central place foragers. *Ornis Scandinavica*, 20(1), 69–71. <https://doi.org/10.2307/3676711>
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press. <https://doi.org/10.1046/j.1420-9101.1993.6020304>
- Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory: 1*. Princeton University Press. <https://doi.org/10.1515/9780691206790>
- Tagmann-Isoet, A., Schaub, M., Reichlin, T. S., Weisshaupt, N., & Arlettaz, R. (2012). Bare ground as a crucial habitat feature for a rare terrestrially foraging farmland bird of Central Europe. *Acta Oecologica*, 39, 25–32. <https://doi.org/10.1016/j.actao.2011.11.003>
- Tveraa, T., Saether, B. E., Aanes, R., & Erikstad, K. E. (1998). Regulation of food provisioning in the Antarctic Petrel; the importance of parental body condition and chick body mass. *Journal of Animal Ecology*, 67(5), 699–704. <https://doi.org/10.1046/j.1365-2656.1998.00234.x>
- Wendeln, H., & Becker, P. H. (1999). Effects of parental quality and effort on the reproduction of common terns. *Journal of Animal Ecology*, 68(1), 205–214. <https://doi.org/10.1046/j.1365-2656.1999.00276.x>
- Wilson, L. J., Daunt, F., & Wanless, S. (2004). Self-feeding and chick provisioning diet differ in the Common Guillemot *Uria aalge*. *Ardea*, 92(2), 197–207.
- Ydenberg, R. C. (1994). The behavioral ecology of provisioning in birds. *Écoscience*, 1(1), 1–14.

Appendix

Table A1

Confirmatory analyses to test whether the experimental treatment had an effect

Nestling stage	Dependent variable	Factors	Estimate (\pm SE)	Factor type	df	χ^2	P
NS1	No. of prey collected by males	Treatment	−0.18 (\pm 0.06)	Fixed	1,13	8.26	0.004
		Nest		Random	8,13	174.04	<0.001
NS2	No. of prey collected by both adults	Treatment	−0.55 (\pm 0.07)	Fixed	1,13	74.64	<0.001
		Nest		Random	8,13	226.03	<0.001

Generalized linear mixed models exploring the effects of treatment (abundant/scarcely food) on the number of prey collected from the tray by males in NS1 (GLMM 1.1) and by both adults in NS2 (GLMM 1.2) (models were fitted with a Poisson distribution and log link functions). In NS1 (day 4 after hatching of the first egg), males collected all prey items consumed by the whole family. In NS2 (day 16 after hatching of the first egg), both males and females collected prey and females also received prey from males. *P* values were calculated by chi-square comparison between the complete model and the reduced model of the variable of interest. Significant *P* values are shown in bold.

Table A2

Confirmatory analyses to test whether parents rejected specific prey

Nestling stage	Dependent variable	Factors	Estimate (\pm SE)	Factor type	df	χ^2	P
NS1	Proportion of prey rejected by males	Type of prey	1.35 (\pm 0.57)	Fixed	3,28	25.38	<0.001
		Treatment	−3.37 (\pm 1.04)	Fixed	1,28	6.57	0.010
		Nest		Random	8,28	48.04	<0.001
NS2	Proportion of prey rejected by both adults		C-P: −3.41 (\pm 1.08)				
		Type of prey	C-L: −1.17 (\pm 1.13)	Fixed	3,58	44.63	<0.001
			C-S: −0.05 (\pm 1.45)				
		Treatment	−0.84 (\pm 0.40)	Fixed	1,58	4.54	0.033
		Nest		Random	8,58	45.77	<0.001

Generalized linear mixed models exploring the effects of treatment (abundant/scarcely food) and type of prey (larvae/pupae in NS1; larvae/pupae/silkworms/crickets in NS2) on the proportion rejected by males in NS1 (GLMM 2.1) and by both adults in NS2 (GLMM 2.2) (models were fitted with binomial distributions and logit link functions). In NS1 (day 4 after hatching of the first egg), males collected all prey items consumed by the whole family. In NS2 (day 16 after hatching of the first egg), both males and females collected prey and females also received prey from males. *P* values were calculated by chi-square comparison between the complete model and the reduced model of the variable of interest. Significant *P* values are shown in bold. In NS2, type of prey had four levels, so ‘crickets’ was set as baseline for the calculation of the estimates (C: crickets; L: larvae; P: pupae; S: silkworms).

Table A3

Mean (\pm SE) proportion of prey rejected by males in NS1 (day 4 after hatching of the first egg) and by both parents in NS2 (day 16 after hatching of the first egg)

Nestling stage	Larvae	Pupae	Silkworms	Crickets
NS1	0.006 (\pm 0.006)	0.087 (\pm 0.040)	—	—
NS2	0.009 (\pm 0.005)	0.211 (\pm 0.098)	0.009 (\pm 0.009)	0.004 (\pm 0.004)

Nonrejected prey were consumed by parents or offspring.

Table A4

Fisher LSD post hoc test showing differences in the proportion of each type of prey rejected by hoopoe parents in NS2 (day 16 after hatching of the first egg)

	Larvae	Pupae	Silkworms	Crickets
Larvae	—			
Pupae	<0.001	—		
Silkworms	0.329	0.003	—	
Crickets	0.308	0.002	0.974	—

Significant *P* values are shown in bold.