

The trophic strategy of the European honey buzzard *Pernis apivorus* during breeding: extravagant specialization or genius solution?

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Abstract

The study of the diet of extreme specialist species can help to understand the selective pressures that modulate the trophic strategies of raptors. This article provides insight into the trophic strategy of a little-known top predator and allows for a better understanding of the selective pressures that shape its diet. We studied the diet of European honey-buzzards, a raptor specialized in the consumption of social wasp brood. The ratio of predator to prey biomasses is one of the highest among raptors. We studied some factors that affect the energy demand of pairs which influence the diet composition and the daily rate of prey delivery to the nest. We explore hypotheses about the role of native and exotic vespids in the diet and the influence of the number and age of nestlings on diet composition, daily rate of prey delivery, and size of combs delivered. We installed trail cameras in 24 honey-buzzards nests in north-western Spain in 2018-2021. We estimated the proportion and daily rate of delivery of native common-wasps (*Vespula vulgaris*), invasive Asian-hornets (*Vespa velutina*), reptiles, and birds and the honey-buzzard's preferences for vespid species. We performed LMMs, GLMMs, and MLRMs to analyse relationships between response variables and predictors. We identified 4611 prey. Honey-buzzards mainly consumed vespids (82% of prey). Common-wasps and Asian-hornets were almost the only two vespids consumed. The invasive hornet was the second most important prey consumed, but common-wasps were preferred. Vespids were more important as the age and number of nestlings increased. Our results suggest that the honey-buzzard's diet is the adaptive result of the conflict between being a median-sized insect-eating migratory nidicolous raptor and collecting enough morsels for the growth of its nestlings, supporting the prey size and ingestion rate hypothesis. We discuss implications of our findings for the management of the invasive wasp

1. Introduction

The diet of predators is influenced by strong selective pressures, as the diet has direct repercussion in the fitness (Johnson and Agrawal 2003). There is a wide range of types of diets in raptors, but they can be classified as generalists or specialists based on the range of prey consumed (Newton 1979). The study of the diet of extreme specialist species and the influence on the diet of some factors that affect the energy demand of individuals, such as the number and age of nestlings, may help to understand the selective pressures that modulate the trophic strategies. Furthermore, knowing the diet is important to understand the interactions between species in an ecosystem, which is necessary for better management of species, both prey and specialist predators, including conservation goals (Sergio *et al.* 2008).

The genus *Pernis* Cuvier, 1817 includes four species of raptors (known as honey-buzzards), widely distributed along Eurasia and the African continent. These species are highly specialised in the consumption of social Hymenoptera, mainly vespids (Gamauf and Haring 2004, van Manen *et al.* 2011, Ziesemer and Meyburg 2015, Purroy and Purroy 2016). In most ecosystems, Vespidae play important roles, mostly regulating other

populations of insects by predation but also providing ecosystem services like pollination or carrion recycling (Sumner *et al.* 2018). Therefore, the study of the interaction between raptors and vespid species is uncommon and interesting from an ecological and management perspective.

European honey-buzzards (*Pernis apivorus* L. 1758) (hereafter, honey-buzzards) locate underground colonies of eusocial vespids and digs out combs filled with brood (larvae and pupae) (Ziesemer and Meyburg 2015). During the breeding season, honey-buzzards carry these combs to the nest to feed the nestlings. This insectivorous diet represents an exceptional case for a medium-sized raptor that deserves investigation. Due to its relatively high body weight (600-800 g), a diet consisting of individual insects might not be effective in balancing the energy expenditure of hunting and transporting. The fact that honey-buzzards feed on eusocial insects would allow them to obtain a significant amount of biomass from each prey (piece of comb with brood) that it delivers to the nest.

Additionally, the recent inclusion of the invasive species Asian-hornet (*Vespa velutina* Lepeletier, 1836, var. *nigrithorax* du Buysson, 1905) in the diet of European honey-buzzards arouses special interest (Macià *et al.* 2019, Rebollo *et al.* 2019, Rebollo *et al.* 2023). Asian-hornets were introduced accidentally in Europe in 2004, but have now expanded to large areas of southwestern Europe (Arca *et al.* 2015). The European Union listed Asian-hornets as an invasive alien species of concern in 2014 (UE1143/2014). Its presence is causing significant impacts on local biodiversity and economic losses in agriculture and beekeeping (Laurino *et al.* 2019, Rojas-Nossa and Calviño-Cancela 2020). Hence, studying the response of a specialized raptor to the sudden appearance of an exotic prey species is of both ecological and management interest.

The available studies on the diet of honey-buzzards are limited in number and often based on small amounts of observations gathered by collecting prey remains at the nest or analysing faecal samples and stomach contents of hunted individuals (Itämies and Mikkola 1972, Roberts and Coleman 2001, van Manen *et al.* 2011, Ziesemer and Meyburg 2015, Purroy and Purroy 2016). The paucity of studies may be influenced by the fact that the honey-buzzards is a species with discrete habits. This species is migratory, with a brief stay in Europe between May and August and it prefers sparsely populated wooded habitats for both breeding and hunting. These factors make it challenging to study, resulting in its trophic biology and ecology being among the least investigated of European diurnal raptors (Hagemeijer and Blair 1997). Therefore, more information is needed about the trophic ecology, consumption preferences, and reproductive biology of honey-buzzards, especially with the recent addition of a new invasive exotic wasp to its diet.

The aim of the present study is to examine the trophic strategy of honey-buzzards in a population of the south-western Europe. We address the following specific objectives: (1) Assess the composition of the honey-buzzard's diet and the daily rate of delivery of prey items to the nest during the breeding season. We defined an "item" as any prey that adults delivered to the nest, whether intact (*e. g.*, a lizard) or not (*e. g.*, a comb of a vespid colony). (2) Determine the honey-buzzard's preferences for native and exotic eusocial vespids species in the ecosystem. (3) Investigate the changes in the diet throughout the breeding season, considering the age of the nestlings, number of nestlings, and study year. (4) Discuss the selective pressures that modulated the trophic strategy of honey-buzzards and potential implications of our findings on the management of the exotic Asian-hornet. We expect a preference for Asian-hornets due to their high abundance in the study area and larger larvae compared to native common-wasps (*Vespula vulgaris*) (Hypothesis 1, H1). We also expect some increase in the proportion of Asian-hornets in the diet along the years as honey-buzzards may learn how to take advantage of the high availability of this new trophic resource (Hypothesis 2, H2). The diet should vary throughout the breeding period due both to nestlings demands and to the phenology of prey species, especially vespids, with small colonies at early summer and high rates of production of workers at late summer. The proportion of vertebrates in the diet of honey-buzzards may be higher during the early stages of the breeding period, when the abundance and colony sizes of Vespidae species are still low (Hypothesis 3, H3). The rate of prey delivery to the nest is expected to increase with both the number and age of chicks (Hypothesis 4, H4). The size of the vespid combs delivered to the nest should increase with either the number or age of nestlings due to the higher energetic demands of the nestlings and throughout the summer as the wasp colonies grow (Hypothesis 5, H5).

2. Methods

2.1. Study area

The study area (about 670 km²) is in the north-western Spain (42° 20' N, 8° 47' W) (**Supplementary Figure S1**). It presents a mild humid-oceanic climate, with annual average precipitation of 1402 mm and annual average temperature of 14.2°C (Rodríguez-Lado *et al.* . 2018).

The landscape is mountainous with an average height of 213 m.s.n.m (0–646 m.s.n.m) and interspersed valleys and plains, all conforming a heterogeneous mosaic of forest patches and farms (Rebollo *et al.* . 2017). The 50.9% of all the study area is covered by patches of forest masses, mainly occupying the middle and upper parts of the slopes. These forest patches are dominated by non-native eucalyptus plantations (*Eucalyptus globulus* Labill., 1800) but also there are mixed patches with native species such as the oak (*Quercus robur* L.) or the maritime pine (*Pinus pinaster* Ait., 1789).

2.2. Study species

European honey-buzzards show the greatest distribution compared to other species of the genus *Pernis* , occupying most part of Europe and some parts of Asia during the breeding season (Gamauf and Haring 2004). Wintering areas are distributed throughout sub-Saharan Africa. Post-nuptial migration occurs from late August and pre-nuptial migration mainly from early May.

At the Iberian Peninsula, honey-buzzards breed at low densities populations, mainly at forest masses in the northern Spain and Portugal (Purroy and Purroy 2016). A census by SEO-Birdlife in 2009–2010 estimated a total of 1850 breeding pairs in Spain (Palomino Nantón and Valls 2011). Adults begin the construction of the nest at early May and the first eggs are laid on the second half of May (Rebollo *et al.* 2023). Usually, two eggs are laid in alternating days. Chicks hatch after 33-35 days of incubation. Once the nestlings are 35-40 days old, they start the firsts short flights, coming back for eating until its complete independence around 65 days old (van Manen *et al.* 2011, Ziesemer and Meyburg 2015).

At the study site, eleven species of eusocial Vespidae wasps can be found (Vega *et al.* . 2022), all of them show annual biological cycles. The surviving queens, which mated before hibernation, emerge at the end of the winter, and begin the cycle building new colonies (Archer 2012). The first generation of workers is raised by the queen/s until they complete their development, and the production of reproductive individuals (males and gynes) takes place at the beginning of autumn. After the mating season, males die and gynes take refuge for wintering (Archer 2012). Asian-hornets usually begin the cycle with a primary underground nest, but in mid-summer, when the colony grows and they need more space, they usually move to the tree canopy and build an aerial secondary nest (Diéguez-Antón *et al.* 2022).

2.3. Tracing honey-buzzard nests and installation of trail-cameras in the nests

The forest patches at the study area have been surveyed systematically for four years (2018-2021) to find all honey-buzzard nests (Rebollo *et al.* 2023). We installed trail-cameras in 24 nests of honey-buzzards: 5 in 2018, 4 in 2019, 6 in 2020 and 9 in 2021. The cameras (Browning SPEC OPS and SPEC OPS EDGE) were connected to an extra battery to ensure they could cover the whole breeding period. Cameras were placed in the surrounding branches at 1.5–2 m from the nest and programmed to take only one picture when triggered, with a delay of 20 seconds between pictures. Accessing to the nest and installation of trail-cameras was performed once the nestlings were 16 days old, moment in which they can thermoregulate by themselves.

At the time of trail-camera installation we estimated the breeding phenology from the age of nestlings, based on the length of the wing and body mass (Bijlsma 1997). Laying dates were estimated by subtracting the incubation time of a single egg (35 days) from the hatching date of the oldest nestling in each nest (Roberts *et al.* . 1999). Laying phenology was estimated in julian days, with January 1st defined as day 1.

2.4. Identification of wasp combs

The images taken by the trail cameras allowed us to differentiate whether the comb had large cells typical

of the genus *Vespa* and *Dolichovespula*, or small cells of the genus *Vespula* or *Polistes*. We were able to differentiate the vespidae subfamilies *Polistinae* from *Vespininae* based on the configuration of the combs (see details in Rebollo *et al.* 2023).

In order to check the identification carried out in the photographic register, the 24 honey-buzzard's nests were visited regularly each 7 or 14 days to collect the remains of the consumed wasp combs that had fallen to the ground. We also collected wasp combs directly in the honey-buzzard's nests during the installation (July) and deinstallation (September) of the cameras. The wasp combs were stored at -20 °C until laboratory analyses, in which we identified the combs using the morphology of the mandibles of the larval exuviae (see details in Rebollo *et al.* 2023).

2.5. Estimating the abundance of vespidae species in the field

During 2020 and 2021 we installed baited traps (Avispa'clac®) to estimate the abundance of vespidae species in the nesting territories of honey-buzzards. We surveyed 6 nesting territories in 2020 and 4 in 2021. Seven baited traps were installed per territory as follows: 1 trap at 0 m from the nest, 3 traps at 500 m from the nest, and 3 traps at 1000 m from the nest (**Supplementary Figure 2**). The traps were always restricted to forest patches as it is the main hunting habitat of honey-buzzards (van Manen *et al.* 2011). We used water, sugar and yeast (5 / 2 / 0.06 kg, respectively) as a bait. Traps remained active for 7 days in each survey. In 2020 we performed one survey in mid-July and one in mid-August. In 2021, we performed two surveys in July and two in August. Trapped insects were preserved in 70% ethanol until identification.

2.7. Estimation of the daily rate of prey delivery in the nests

We estimated the daily rate of delivery for each type of prey item between 16 and 34 days old. We did not consider prey consumed by nestlings older than 35 days because nestlings can move to the branches (Roberts *et al.* 1999, Purroy and Purroy 2016) and may consume some prey outside the nest. To minimise bias in the estimates, we only considered nests with at least five complete days of data available.

2.8. Statistical analyses

We studied the size of wasp combs delivered to the nest (recorded by the cameras) in terms of the number of cells, based on the number of cells of the largest diameter (D) and the smallest diameter (d), using the ellipse area formula:

$$N = D/2 \times d/2 \times \pi$$

We used Linear Mixed Models (LMM) to study the variations in size of common-wasp and Asian-hornet combs. Year, breeding phenology (julian date), vespidae species, number of nestlings, and age of the nestlings were predictors. Nesting territory was the random factor. To avoid overdispersion in the response variable, we calculated the mean values of cells of the wasp combs delivered each day to each nest.

To assess honey-buzzard prey preferences for vespidae species, we used Ivlev's selectivity index (E) to relate the proportion of prey delivered to nests to the proportion of the same prey available to the environment (Rebollo *et al.* 2017):

$$E = \frac{r - p}{r + p}$$

Where r was the proportion of cells of each wasp species delivered to the nest. This proportion was estimated with the total of comb items recorded by the cameras. The proportion of wasps available in the field (p) was estimated as the average percentage of workers of each wasp species captured within the 7 traps of each territory sampled. The E index ranges from -1 to + 1. Positive values indicate that honey-buzzards prey upon a species above its availability. We considered a "preferred prey" the species with an E index above zero (Rebollo *et al.* 2017).

We performed Cumulative Link Mixed Models (CLMM) to study the variations in the proportion of prey items delivered to the nests. We differentiated the 4 main types of prey items (common-wasp, Asian-hornet, reptiles, and birds) as response variables. CLMM models estimate the change in the proportion between the categories of the response variable directly from the number of observations. We explored the age of the nestlings, the study year, and the number of nestlings as predictors.

Finally, we analysed changes in the rate of prey delivery using GLMM with a Poisson error distribution and log link function. The response variable was the daily rate of prey delivery, measured as the account of prey items delivered to the nest each day. We explored the number of nestlings, the age of the nestlings, and the study year as predictors. The random effect was the nesting territory.

In all cases, Akaike’s (1987) information criterion (AIC) was calculated for each model for the model selection process; a smaller AIC indicates a better-fitting model as determined from the parsimony in the number of parameters. We used the cut-off of $\Delta\text{AIC} > 2$ units to differentiate models with better explanatory power (Burnham and Anderson 2002). When faced with models having comparable AIC values after the selection process, the model with the lowest AIC value was preferred, even if it was more complex. This decision aimed to enhance the clarity of result interpretation and discussion. In all statistical procedures we considered a level of significance of $p < 0.05$. All statistical analyses were performed with R software v. 4.2.1 (R Core Team 2022). LMM, CLRM and GLMM analysis were performed with packages stats (R Core Team 2022), lme4 (Bates *et al.* 2014), nlme (Pinheiro *et al.* 2022), nnet (Venables and Ripley 2002), ordinal (Christensen 2022) and MuMIn (Barton 2022).

3. Results

3.1 Honey-buzzard’s diet composition

A total of 2381 wasp comb fragments were collected in the 24 honey-buzzard’s nests and surroundings, accounting for 61533 large cells and 150847 small cells analysed. We identified combs from 6 wasp species: three with small cells (*Vespula vulgaris*, *Vespula germanica*, *Polistes sp.*) and three with large cells (*Vespa velutina*, *Vespa crabro*, *Dolichovespula media*). The two most abundant species were common-wasps (*Vespula vulgaris*) and Asian-hornets, accounting for the 99.2% of the small cells and the 99.0% of the large cells, respectively (**Table 1**). This allowed us to simplify our statistical analyses by assuming that all small cell combs could be associated to common-wasps and all large cell combs to be Asian-hornets with minimum error.

We obtained a total of 752678 pictures in the 24 nests from which 4611 prey items were recorded, accounting for 3909 vespids items, 607 vertebrate items, and 95 unidentifiable prey items. 81.9% of the prey items were vespids. Common-wasps were the most abundant species (57.0%), and Asian-hornets the second (24.2%) (**Table 2**).

The best-fitting model explaining comb size recorded by the cameras included the interaction between wasp species and number of nestlings (**Supplementary material Table 1**). Combs of common-wasps had more cells than those of Asian-hornets ($t = 16.26$; $p < 0.001$) and this difference was greater in nests with one nestling ($t = -3.49$; $p < 0.001$). There was not an isolated effect of the number of nestlings on comb size (**Figure 1**). Neither the year nor the nestling age influenced the size of the combs delivered to the nest, which means that the size of delivered combs remained stable during the study period.

Baited traps captured a total of 15803 wasps, 5709 in 2020 and 10094 in 2021. In both years, the most abundant species was Asian-hornets (68.1% of all vespids captured: 63.9% in 2020 and 74.3% in 2021). The second most abundant species was common-wasps (30.3%: 34.7% in 2020 and 23.5% in 2021). The other vespids species (*V. germanica*, *Vespa crabro*, *Dolichovespula media*, *D. sylvestris*, *Polistes dominula*, *P. nimpha*) represented the 1.6% (1.3% in 2020 and 2.1% in 2021). This resulted in a mean Ivlev’s selectivity index value (E) of -0.71 for Asian-hornets and 0.52 for common-wasps, which indicated a preference of honey-buzzards for the native species and a rejection for the exotic species (**Table 3**).

Vertebrates accounted for 16.7% of all prey items (**Table 2**). Reptile was the most important group of

vertebrates (9%). Lacertidae (8.3%) were predominant compared to Anguidae (0.3%). The images did not allow us to identify up to the species level all vertebrate items. However, it was remarkable the abundance of Iberian emerald lizard (*Lacerta schreiberi* Bedriaga 1878) accounting for the 56.9% of all reptiles. Birds were the second most important group of vertebrates (4.9%). Chicks without feathers (4.2%) were predominant respect to feathered birds (adults, fledglings, and older nestlings) that accounted for 0.7%. In the case of avian prey, the common wood pigeon (*Columba palumbus* L. 1758) was the most abundant species (50.5% of all avian prey). Amphibians (all frogs) and mammals (mainly voles) were rare in the diet accounting for 0.3% and 0.1% of all prey items, respectively.

The proportions of the four main types of prey (common-wasp, Asian-hornet, reptiles, and birds) changed significantly with the age of the nestlings and the number of nestlings, but not with the study year. The best-fitting model included the interaction between the age and the number of nestlings and the additive effect of the study year (**Supplementary material Table S1**). Our results show an increase in the mean proportion of vespids with the age of nestlings (from 70.8% at 16 days of age to 91.9% at 45 days) due to the increase of common-wasp (from 38.4% to 74.6%) while Asian-hornet proportions decreased (from 32.4% to 17.4%). This caused an important reduction in the mean proportions of vertebrates with the age of nestlings, which constituted the 29.2% of the diet at 16 days of age and 8.1% at 45 days, showing a drastic reduction of reptiles (from 17.7% to 5.4%) and avian prey (from 11.5% to 2.7%). The interaction of the number of nestlings and age also showed a significant effect over the proportions of prey groups delivered (Likelihood ratio = 47.63, df = 2, p < 0.001), wherein the proportion of common-wasps increased more intensely with the age of the nestlings in nests with two nestlings (**Figure 2**). We observed a non-significant effect of year over the mean proportion of each prey group (Likelihood ratio = 7.14, df = 3, p = 0.067, **Figure 3**).

3.2 Rates of prey delivery in the honey-buzzard's nests

Honey-buzzards delivered, on average, 7.13 prey items per day: 5.5 were vespids, 1.57 were vertebrates, and 0.1 were unidentified prey (**Table 4**). The best-fitting model to explain variations in the daily rate of prey delivery included the number and age of nestlings (**Supplementary material Table S1**) but just the number of nestlings showed a significant effect on the response variable ($z = 5.34$; p < 0.001). Nests with two nestlings received a mean of 2.57 prey items per day more than nests with only one nestling (**Figure 4**). The daily rate of prey delivery did not vary significantly neither with the age of nestlings nor year.

4. Discussion

This study analysed the trophic strategy of an unusual forest insect-eating medium-sized raptor specialised in consuming social hymenopterans. We studied 4611 prey items obtained in 4 years in a total of 24 honey-buzzard's nests. Our results suggest that the honey-buzzard's diet is the adaptive result of the conflict between being an insect-eating median-sized migratory nidicolous raptor and collecting enough number of morsels for the growth of their nestlings, supporting the prey size and ingestion rate hypotheses.

Diet composition and extreme specialization

Honey-buzzards behaved as an extreme specialist raptor that predate mainly upon underground nests of social wasps. More than 80% of the diet was comprised by this type of vespid and the first dominant (common-wasp) and the second dominant (Asian-hornet) accounted for 57.0% and 24.2% of prey items, respectively. Previous studies have also reported a high proportion of wasps with underground nests in the diet although with some variation in the composition of species depending on the study (Itämies and Mikkola 1972, Gamauf 1999, van Manen *et al.* 2011, Ziesemer and Meyburg 2015). Van Manen *et al.* (2011) found an even higher proportion of social wasps (92%) in The Netherlands, but they caution about the possibility of bias in their samples because they estimated the diet composition based only on remains collected at the nests. As far as we know, the present study and Rebollo *et al.* (2023) are the firsts to provide a reliable method (trail cameras installed in the nests) that allows to study a minimally biased diet during the breeding period.

Vertebrates comprised only 16.7% of the honey-buzzard's diet (**Table 2**): reptiles (9%), birds (4.9%), am-

phibians (0.3%), mammals (0.1%) and unidentifiable vertebrates (2.1%). Contrarily to other studies (Itäemies and Mikkola 1972, Gamauf 1999, Roberts and Coleman 2001), which declare amphibians (mainly frogs) playing an important role in the diet, in our study small reptiles and chicks of birds represented more than the 95% of the identified vertebrates. Differences may be due to the varying abundance of these vertebrate groups among different regions, as there are environmental differences between our study area and other European areas.

The specialization of *Pernis* species as predators of underground nesting social wasps can be confirmed by studying their anatomical adaptations. European honey-buzzards show scale-like feathers, beak, nostrils, tarsi, and nails specifically adapted for excavation of underground wasp nests (Vansteelant and Agostini 2021). See also Sievwright and Higuchi (2011 and 2016) for the Oriental Honey-buzzard, *Pernis ptilorhynchus*, a similar species to the European honey-buzzard.

Preferences towards native and exotic vespid species

In the study area, honey-buzzards mainly preyed upon colonies of common-wasps and Asian-hornets (**Table 2**). The proportion of other wasp species in the diet was negligible. This finding was in line with the abundance of wasp species in the study area, where common-wasps and Asian-hornets were by far the most abundant species (more than 97.5%, **Table 3**). Other authors (Roberts *et al.* 1999 and Roberts and Coleman 2001) also found in Britain that, despite the variety of wasp species in the area, the diet of honey-buzzards was constituted mainly by only two species while others were poorly represented. Ziesemer and Meyburg (2015) suggested that not all species of wasps have the same strategy or phenology, so honey-buzzards would be choosing to prey on those species that offer more resources for hunting effort.

Honey-buzzards showed strong preference towards common-wasps and rejected Asian-hornets. The high abundance of Asian-hornets in our study area and its larger brood led us to hypothesize (H1) that honey-buzzards would preferentially use this new trophic resource to feed their nestlings. This rejection could be due to the relocation of secondary nests in Asian-hornet, making these colonies less accessible by honey-buzzards. Gamauf (1999) also found that large underground colonies of *Vespa* spp. were preferred over their abundance whereas big European-hornets (similar in size to Asian-hornets) were rejected. This could be explained because European-hornets construct nests in tree cavities, making them practically impregnable for honey-buzzards (Nadolski 2012).

It is remarkable how fast an invasive exotic species has become the second most abundant prey species in the diet of this raptor. This result was shown in Rebollo *et al.* (2023), where Asian-hornet was consumed by all pairs of honey-buzzards and even became the main trophic resource in terms of biomass in one of the two years studied. Carlsson *et al.* (2009) discussed how the genetic diversity of natural populations of native predators, as well as their phenotypic plasticity, enhance their adaptation and learning capacity to include an exotic invasive species as prey in a rapid manner. This can only happen if the exotic prey species is within the feeding capabilities of the native predator population. In this sense, we expected an increase in the proportion of Asian-hornets in the honey-buzzard's diet within the four-year study period (H2) but results did not show it. The time that honey-buzzards and Asian-hornets have been in coexistence in Europe is very short. If the incorporation of this prey into the honey-buzzard's diet is providing some ecological advantage, it is expected that these preferences will change adaptively and, therefore, the importance of Asian-hornet in honey-buzzard's diet will change in the future as well.

Changes in diet composition and rate of prey delivery with the age and number of nestlings

Proportions of each type of prey in the diet as the breeding season and the age of the nestlings progressed showed significant differences attributable to the phenology of each group of prey. As expected (H3), the daily rate of vertebrate delivery to the nest and the proportion of them in the diet decreased as the breeding season and the age of the nestlings progressed. This was probably due to the increase in detectability of wasp colonies throughout the summer, which increased the daily rate of comb delivery and the proportion of comb items in the diet over time. As other authors suggested (Kostrzewa 1998, Roberts and Coleman 2001), the role of vertebrates on the diet could be even higher immediately after prenuptial migration and prior to egg

laying when it is important to replenish their fat reserves. Thus, our findings suggests that honey-buzzards consume vertebrates to complement the diet when wasp colonies are not abundant, although we cannot discard that a higher consume of vertebrates at the beginning of the nestling phase responds to nutritional needs of nestlings in the initial stages of their growth (maybe calcium or phosphorus), an option that deserves future research.

There was an unexpected decrease in the daily rate of Asian-hornet comb delivery and in the proportion of this species in the diet as the breeding season and the age of the nestlings progressed. This reduction could be explained because the relocation of underground colonies to the tree canopy during mid-summer (Diéguez-Antón *et al.* 2022) avoiding honey-buzzards attacks.

There was an increase in the proportion of common-wasps in the diet as breeding season and age of nestlings progressed, a pattern previously observed by other authors (Itämies and Mikkola 1972, van Manen *et al.* 2011, Ziesemer and Meyburg 2015). The increase in the proportion of common-wasps was more pronounced in nests with two nestlings than nests with one nestling (as we expected in H4). Thus, honey-buzzards became more specialized in consuming its preferred prey as energy demands increased (*i. e.* the number of nestlings increased). This suggests that common-wasp provides the highest energy return relative to the effort of searching for and processing the wasp nests and provides a more effective strategy for feeding honey-buzzard´s nestlings.

Contrary to expectations (H5), the size of wasp comb items delivered to the nest (number of cells) did not change with either the number and age of nestlings. The increase in comb size over age of nestlings was expected due to wasp colony growing during the summer. This result could indicate that honey-buzzards exert some selection on the sizes of colonies it preys upon, avoiding the small colonies. It is likely that at the beginning of the breeding season, only the most developed colonies are detectable by honey-buzzards, which appear to locate colonies by following the movement of foraging wasp workers (Birkhead 1974). It is also important to consider the flight burden that honey-buzzards can sustain during a trip back to the nest. Wasp colonies can contain a high brood biomass, but honey-buzzards fragment the combs and transports them to the nest in multiple trips (van Manen *et al.* 2011, Ziesemer and Meyburg 2015). The average comb items of Asian-hornets and common-wasps contained 141 and 345 cells, respectively. Assuming that all items are fully loaded with brood and considering that the average weight of a *V. velutina* larva is 413 mg and a *V. vulgaris* larva is 65 mg (Rebollo *et al.* 2023), we found that for each comb item, a honey buzzard would carry at most 58.2 g of Asian-hornet brood and 22.4 g of common-wasp brood. The weight of the inedible paper paste was not considered in these calculations, but the weight of the comb item does not appear to be a limiting factor for the choice of comb size provided in each item.

Selective pressures that modulated the trophic strategy of honey-buzzards: extravagant specialization or genius solution?

In seasonal environments, nidicolous and migratory birds must efficiently manage the limited time available for breeding. Raptors usually feed on prey relatively large compared to the bite size that nestlings consume. It has been suggested that raptors have been under strong evolutionary pressure to manage this conflict between collecting and processing food for nestlings, *i. e.* , the prey size and ingestion rate hypotheses (Slagsvold and Sonerud 2007). Larger prey items provide more bites but require more time to collect and process, which may result in a relatively low ingestion rate compares to smaller prey. Raptors have limitations in feeding on individual insects during the breeding season despite insects being small-sized prey easy to process. The energy yield of insects is low if the raptor carries a single prey and must move long distances many times between the capture site of insects and the nest. Hence, such a non-social insect-based diet is unlikely in raptors (Sonerud *et al.* 2014).

Honey-buzzard´s diet would be the result of the evolutionary pressure to manage the conflict between collecting and processing food for nestlings. They found a genius solution; to feed on a small-sized prey easy to process (comb with brood) which rends a high nutritional value and a high amount of edible biomass per delivery for an insect-eating raptor. The ratio between the size of raptor (between 600 and 800 g) and the

size of prey (less than 1 g) is possibly one of the highest among the raptors in the world. Larvae and pupae are individualized in the cells of combs and their size allows nestling to swallow them in a few seconds. Thus, provisioning for nestlings does not need to prepare prey items into pieces of suitable morsels. Nestlings would start feeding unassisted at a younger age (van Manen *et al.* 2011, Ziesemer and Meyburg 2015) allowing the female to resume hunting at an earlier stage of nestlings. The vertebrates consumed by honey-buzzards also support this interpretation because they are mainly small reptiles with short appendices and easy to swallow in one bite. In the case of birds, they are mainly immature individuals without feathers and easy to process.

*Implications for the management of the exotic *Vespa velutina**

The European Union listed Asian-hornets as an invasive alien species of concern in 2014 (UE1143/2014). Our results agree with Rebollo *et al.* (2023) regarding the predation pressure of honey-buzzards on this species, which could be of interest for the management of the exotic wasp, at least on a small scale in the proximity of honey-buzzards' nests. Four years after colonization, the Asian hornet became the second most important prey of honey-buzzards in the study area. Our findings allow us to identify two aspects of the Asian-hornet honey-buzzard interaction that could limit the magnitude of honey-buzzards' effects on the exotic wasp. On one hand, honey-buzzards did not appear to show a preference for Asian-hornets compared to the native common-wasps, likely because the annual life cycle of Asian-hornet colonies is not entirely underground, and this predator has specific adaptations to primarily target upon underground nests. It would be expected that in those years in which the phenology of Asian-hornets is delayed due to weather conditions, honey-buzzards would include a higher proportion of the exotic wasp in their diet. On the other hand, the degree of specialization exhibited by honey-buzzards on common-wasps may make them particularly vulnerable to invasion by Asian-hornets. Since its arrival, Asian-hornets have become the most abundant social wasps in the study area, and their presence may have a direct impact on the populations of common-wasps, both through direct predation and competition for resources. We observed Asian-hornets preying on common-wasp workers at the entrance of their nest, especially after a honey-buzzard attack on common-wasp colony, which could have a demographic effect on common-wasps. If the exotic hornet manages to significantly reduce the populations of common-wasps, honey-buzzard's populations could decrease unless they adapt their trophic preferences and hunting behaviour to compensate for the decrease in its staple prey. There are examples where an invasive species affects the staple prey of a raptor, leading to its local extinction (Spencer *et al.* 1991). Future long-term research should study the evolution of honey-buzzards' preferences for Asian-hornets. Additionally, the effects of this species on ecosystem services provided by European native wasps and on the density of predators specialized in the consumption of native wasps, such as honey-buzzards, should be considered.

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Figure and table captions

Table 1: Abundance of vespid species in the comb remains collected in honey-buzzard nests and surroundings. The abundance was estimated as a percentage of cells of each species relative to the total of large and small cells collected. The annual data for the period 2018-2021 and total are shown.

Table 2: Percentages of prey items in honey-buzzard’s diet. Large cell combs were considered “Asian-hornet” and small cell combs “common-wasp” (see **Table 1**). For vertebrates, we distinguished Lacertidae and Anguinae for reptile items, and feathered (adults, fledglings, and older nestlings) and chicks (without feathers) for avian items. The annual data for the period 2018-2021 and total are shown.

Table 3: Relative abundance of vespid species in the diet of the studied nests of honey-buzzards estimated from the number of cells consumed, and relative abundances of vespids species in the nesting territories estimated by baited traps. Ivlev selectivity index (E) was calculated for Asian-hornet and common-wasp in 2020 and 2021.

Table 4: Daily rate of prey items delivered to honey-buzzard’s nests. Large cell combs were considered “Asian-hornet” and small cell combs “common-wasp” (see **Table 1**). For vertebrates, we distinguished Lacertidae and Anguinae for reptile items, and feathered (adults, fledglings, and older nestlings) and chicks (without feathers) for avian items. The annual data for the period 2018-2021 and total are shown.

Figure 1: Interaction effect of vespid species and number of nestlings over the number of cells of the combs delivered to honey-buzzard’s nests. Common-wasps show more cells per comb than Asian-hornets and this difference is greater in nests of one nestling ($a - a' / b' - b$). The isolated effect of the number of nestlings was not significant.

Figure 2: Interaction effect of the age and number of nestlings in the proportions of the four main types of prey delivered to the honey-buzzard nests: common-wasp (light grey), Asian-hornet (median grey), reptile (dark grey), and birds (black). Proportions are shown stacked. A significant effect was observed in the interaction of age and number of nestlings.

Figure 3: Effect of the year in the proportions of the four main types of prey delivered to the honey-buzzard nests: common-wasp (light grey), Asian-hornet (median grey), reptile (dark grey), and birds (black). Proportions are shown stacked. Note that the proportions are slightly different from **Table 2** as here the model weighs the random effect of the nest.

Figure 4: Effect of the number and the age of nestlings over the number of prey delivered daily to honey-buzzard nests. Age did not show a significant effect in the rate of prey delivered, only the number of nestlings. The decrease in the rate of prey delivered to the nests with the age was not significant.

Table 1:

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image1.emf available at <https://authorea.com/users/665373/articles/666594-the-trophic-strategy-of-the-european-honey-buzzard-vernis-apivorus-during-breeding-extravagant-specialization-or-genius-solution>

Table 2

Prey group	2018		2019		2020		2021		All Years	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Vespidae Items	83.38	2.96	73.93	7.31	85.43	1.01	84.72	1.59	81.87	2.68
Large cells items (mainly <i>Vespa velutina</i>)	48.28	6.79	13.41	4.5	17.57	2.56	22.66	3.7	24.23	6.63
Small cell items (mainly <i>Vespa vulgaris</i>)	40.11	7.52	60.52	6.2	65.59	2.61	61.99	5.02	57.04	5.75
Unidentified Vespidae Items	0	0	0	0	2.27	0.81	0.14	0.09	0.6	0.56
Vertebrate Items	15.53	2.81	26.07	7.31	12.1	1.29	13.2	1.53	16.73	3.2
Reptile Items	6.48	2.89	17.5	3.6	5.06	0.97	7.07	1.38	9.03	2.86
Lacertidae Items	6.13	2.93	17.5	3.6	4.82	1	6.48	1.28	8.73	2.94
Anguillidae Items	0.35	0.35	0	0	0.25	0.11	0.69	0.27	0.32	0.14
Unidentified Reptile Items	0	0	0	0	0	0	0	0	0	0
Avian Items	4.17	2.02	5.16	4.82	5.47	1.13	4.88	1.51	4.92	0.28
Feathered Items	1.47	0.88	0.98	0.98	0.16	0.16	0.27	0.17	0.72	0.31
Chick Items	2.7	1.56	4.18	3.85	5.31	1.1	4.51	1.48	4.18	0.55
Unidentified Bird Items	0	0	0	0	0	0	0	0	0	0
Amphibian Items	0.74	0.74	0.8	0.52	0	0	0.8	0.32	0.58	0.2
Mammal Items	0.22	0.22	0	0	0.08	0.08	0.1	0.1	0.1	0.05
Unidentified Vertebrate Items	3.93	1.73	2.61	1.26	1.48	0.27	0.36	0.26	2.1	0.76
Unidentified Food Items	1.09	0.61	0	0	2.47	0.67	2.08	0.58	1.41	0.55

Table 3

Nest	Year	Abundance of cells of vespid items consumed			Estimation of the available abundance of vespids species				N/LEV value (E)	
		<i>V. velutina</i> (%)	<i>V. vulgaris</i> (%)	Total cells accounted	<i>V. velutina</i> (%)	<i>V. vulgaris</i> (%)	Other species* (%)	All vespids captured	<i>V. velutina</i>	<i>V. vulgaris</i>
A Grela	2020	10.3	89.7	57788	60.5	38.3	1.2	749	-0.71	0.40
Matadero		6.6	93.4	60540	58.2	37.9	3.9	900	-0.80	0.42
Navalejo		9.5	90.5	68238	47.3	52.3	0.3	881	-0.67	0.27
Pedregande		16.9	83.1	78528	44.7	54.5	0.8	1037	-0.45	0.21
Picon Bajo		16.1	83.9	43339	71.4	26.1	2.5	1175	-0.63	0.53
San Cosme		7.9	92.1	47987	70.4	28.4	1.1	967	-0.80	0.53
Carballo		15.2	84.8	72125	80.7	18.2	1.1	2597	-0.68	0.65
Embudo	2021	21.5	78.5	48448	92.2	7.3	0.5	2772	-0.62	0.83
Rio Truchas		3.6	96.4	35875	88.5	8.1	3.4	2322	-0.92	0.84
Tanora		6.2	93.8	90369	66.8	31.6	1.5	2403	-0.83	0.50

*Here we include *V. germanica*, *Dolichovespula* spp., *Polybia* spp. and *Vespa crabro*

Table 4

Prey group	2018		2019		2020		2021		All Years	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Vespidae Items	5.13	0.66	5.53	0.6	5.68	0.62	5.44	0.79	5.46	0.1
Large cells items (mainly <i>Vespa velutina</i>)	2.88	0.49	0.85	0.33	1.36	0.2	1.66	0.28	1.69	0.43
Sm all cell items (mainly <i>Vespa vulgaris</i>)	2.3	0.43	4.67	0.64	4.13	0.55	3.78	0.75	3.72	0.51
Unidentified Vespidae Items	0	0	0	0	0.19	0.1	0	0	0.05	0.05
Vertebrate Items	1.3	0.24	2.6	0.93	1	0.06	1.4	0.1	1.57	0.35
Reptile Items	0.52	0.29	1.73	0.35	0.48	0.11	0.82	0.17	0.89	0.29
Lacertidae Items	0.5	0.3	1.73	0.35	0.45	0.11	0.75	0.15	0.86	0.3
Anguillidae Items	0.03	0.03	0	0	0.03	0.01	0.08	0.03	0.04	0.02
Unidentified Reptile Items	0	0	0	0	0	0	0	0	0	0
Avian Items	0.36	0.19	0.53	0.49	0.36	0.1	0.48	0.15	0.43	0.04
Feathered Items	0.19	0.14	0.17	0.17	0.01	0.02	0.01	0.01	0.1	0.05
Chick Items	0.17	0.1	0.36	0.32	0.34	0.1	0.45	0.14	0.33	0.06
Unidentified Bird Items	0	0	0	0	0	0	0	0	0	0
Amphibian Items	0.07	0.07	0.07	0.04	0	0	0.05	0.03	0.05	0.02
Mammal Items	0.02	0.02	0	0	0.01	0.01	0.01	0.01	0.01	0
Unidentified Vertebrate Items	0.33	0.15	0.29	0.15	0.16	0.05	0.03	0.02	0.2	0.07
Unidentified Food Items	0.05	0.03	0	0	0.19	0.06	0.16	0.05	0.1	0.04
All Food Items	6.53	0.87	8.13	1.1	6.87	0.67	6.99	0.85	7.13	0.35

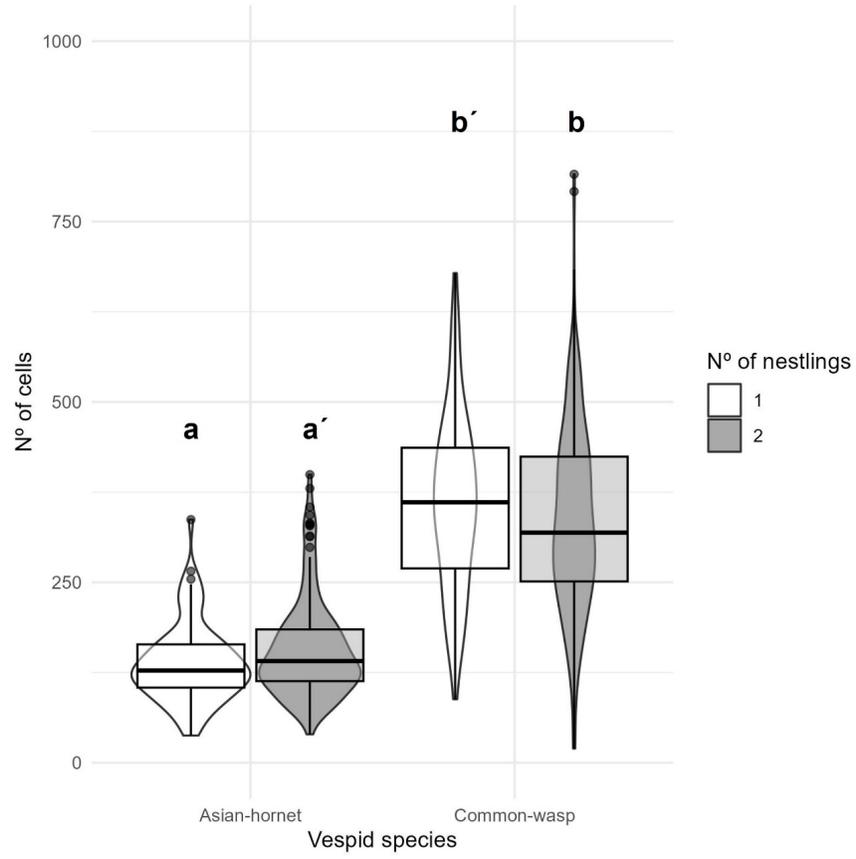


Figure 1

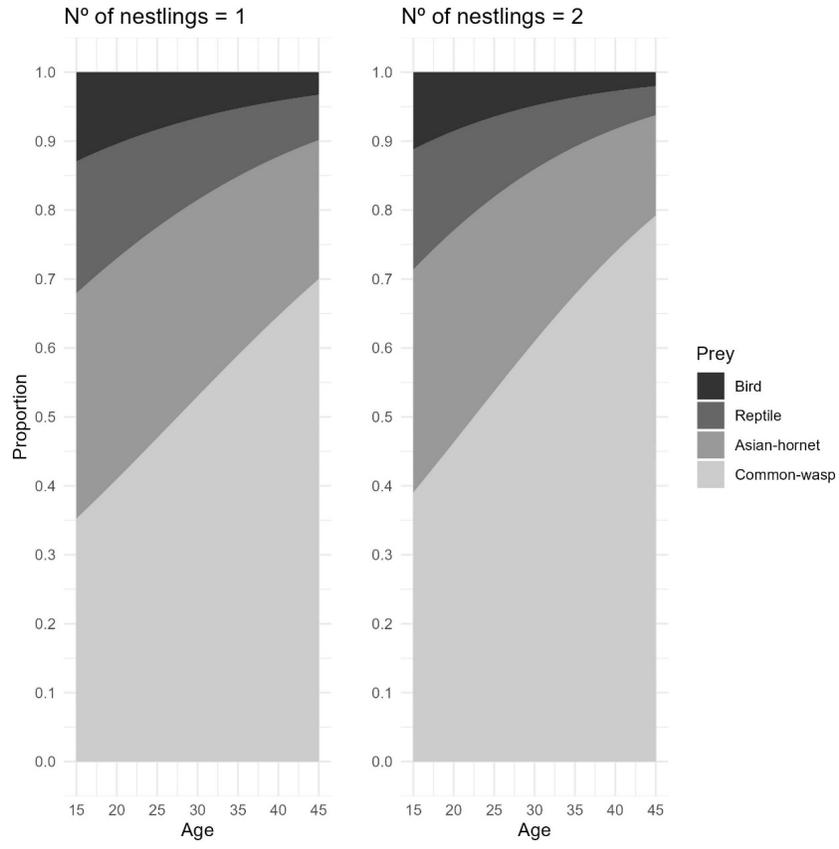


Figure 2

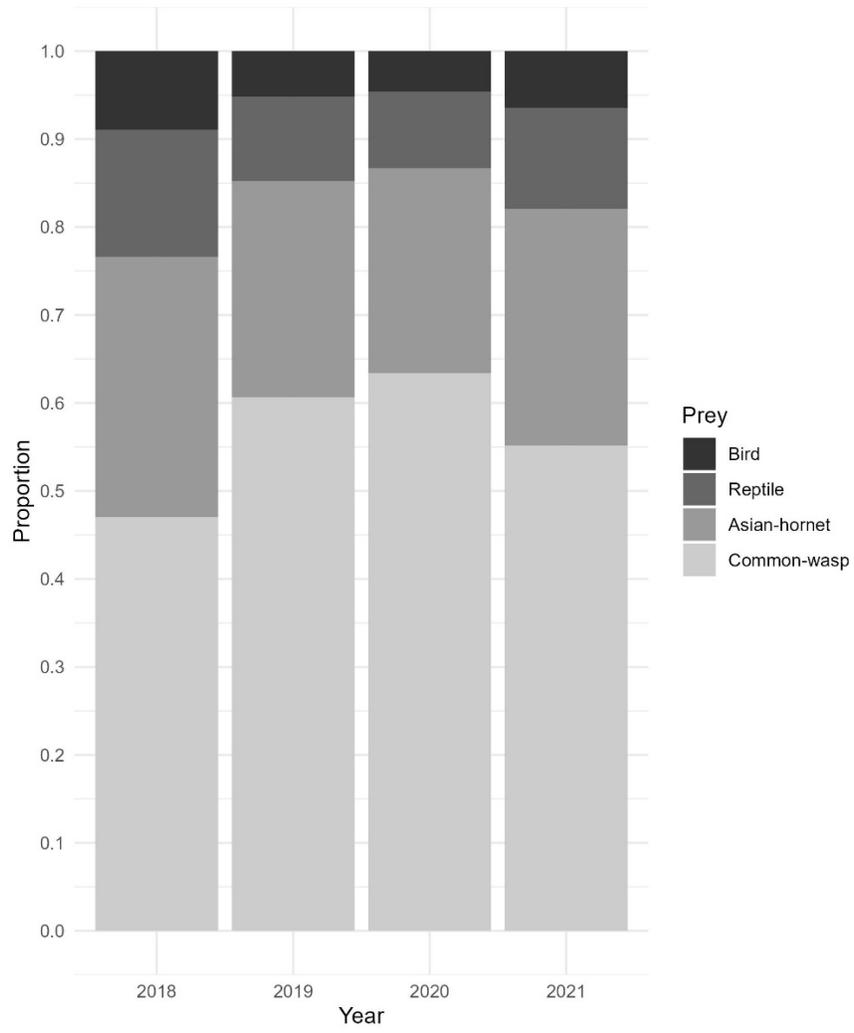


Figure 3

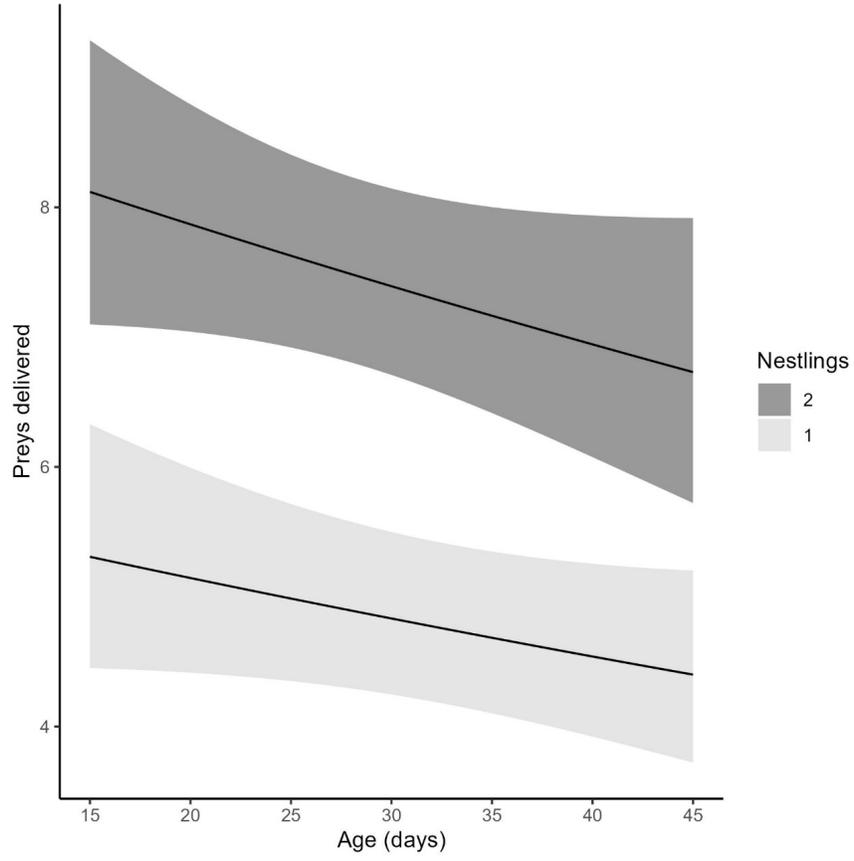


Figure 4