Inversión parental en la abubilla, (*Upupa epops*), escenarios de conflicto y cooperación

Laura Arco González

Tesis Doctoral, Granada 2023

Programa de Doctorado de Biología Fundamental y de Sistemas
Director De Tesis: Manuel Martín-Vivaldi Martínez

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Memoria presentada por Laura Arco González para optar al Título de Doctor por la Universidad de Granada, dentro del Programa de Doctorado en Biología Fundamental y de Sistemas.

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En Granada a 20 de noviembre de 2023

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A Diego

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RESUMEN GENERAL

Los pollos de las aves altriciales necesitan cuidados parentales desde la misma eclosión, ya que su estado de desarrollo impide que puedan valerse por sí mismos. La reproducción en estas aves es un evento en el que el nido juega un papel central. En él se localizan huevos y pollos y ambos padres deben de cooperar e invertir en los consiguientes cuidados parentales. La provisión de alimento por parte de los progenitores es crucial para la supervivencia y crecimiento de sus pollos en el nido y constituye una parte sustancial de los costes del cuidado parental. Además, los padres deben equilibrar la asignación de alimentos entre ellos y su descendencia para maximizar su éxito reproductivo a lo largo de la vida. Esto lleva a un compromiso entre la inversión en el aprovisionamiento de la descendencia frente al mantenimiento propio y la reproducción futura. En este escenario de inversión y de costes y beneficios, donde los cuidados son biparentales, se producen conflictos relativos a cuánto invierte cada progenitor (el conflicto sexual), entre los intereses de la descendencia y el de los padres (el conflicto paterno-filial), y la competencia entre los mismos pollos por acaparar la atención, cuidados y alimentos de los padres (el conflicto entre hermanos).

En esta tesis se explora estos conflictos evolutivos en una población de abubillas (*Upupa epops*) mantenidas en cautividad desde 2008. Una configuración experimental en cautividad y la abubilla como especie modelo tienen numerosas ventajas. La abubilla es un modelo excelente para probar hipótesis sobre estos conflictos y sus decisiones en el reparto de alimento por varios motivos. Es una especie que se comporta como forrajeador de un lugar central y, además, solo puede cargar una presa en el pico por viaje. Para maximizar la ganancia neta de energía por viaje al nido, los padres deberán de ser selectivos con las presas que lleva al nido y con las presas que utiliza para su propio mantenimiento. Por lo tanto, los padres pueden tener que seleccionar presas grandes o más digeribles para sus pollos, mientras reservan presas más pequeñas o menos digeribles para ellos mismos. Ambos progenitores tienen además diferentes papeles durante la reproducción, ya que difieren en tareas, costes reproductivos y estrategias de forrajeo. Por lo tanto, el valor de cada presa para cada sexo puede cambiar a lo largo del período de cuidado de los pollos e influenciar en las decisiones de si esa presa se utiliza para autoalimentarse, para entregar a la descendencia y, en último lugar, en cómo asignar esta presa entre sus pollos. Son especies con una marcada asincronía de eclosión, es decir, con pollos de diferentes edades y tamaños donde la asignación de alimento está sesgada hacia

los pollos de mayor tamaño. Cuando las condiciones ambientales no son las idóneas, la petición de los pollos más pequeños es ignorada y se suele seguir la estrategia de la reducción de nidada, muriendo los pollos más pequeños de inanición. Por tanto, la asignación de presas dentro de la nidada estará influenciada por esta jerarquía de tamaños y sobre todo por la disponibilidad de alimento en el nido. Es una especie de vida relativamente corta que se reproduce varias veces en y entre temporadas de cría. En estas especies el valor de la nidada actual es alto, por lo que tienden a preservar la inversión en la reproducción a expensas de su propia condición, así que también influirá en como reparten las presas, especialmente cuando el alimento escasea. Y, por último, la abubilla se reproduce con éxito en cautividad. Esta circunstancia nos permite que podamos manipular de forma precisa la cantidad y calidad de alimento que recibe la familia creando condiciones de escasez y abundancia. Y permite seguir el destino final de cada una de las presas que los padres manipulan, registrando todas las decisiones parentales.

En este contexto experimental, la hipótesis general es que las condiciones del nido y la disponibilidad de alimento afectarán a las decisiones de aprovisionamiento de forma diferencial a cada progenitor.

En esta tesis, realizamos un primer experimento donde alimentamos a la familia de abubillas *ad libitum* (abundancia) o reduciendo la alimentación de cada familia a un 60% (escasez). El experimento lo realizamos en dos fases del periodo de pollos (fase temprana y fase tardía de pollos) y aportamos presas que varían en calidad y tamaño.

Con respecto a las decisiones parentales de reparto de alimento entre ellos y la descendencia, los resultados mostraron que, en las dos fases de pollos, ambos progenitores suministraron presas de mayor calidad a los pollos, ingiriendo ellos las de menor digestibilidad o tamaño, dependiendo de la fase. Estos resultados apoyan las expectativas de los forrajeadores de un lugar central, ya que los adultos suministraron las mejores presas a los pollos. Sin embargo, cuando la disponibilidad de alimento fue limitada, los progenitores en ambas fases no redujeron la cantidad de biomasa que ellos consumían. En cambio, los pollos sí experimentaron una reducción en la biomasa consumida, pero solo en la fase tardía de pollos. En este caso, las abubillas no siguieron una estrategia típica de una especie de vida corta, ya que ambos se aseguraron su alimentación en condiciones de escasez en detrimento de sus pollos. Esta repuesta atípica puede deberse a las limitaciones energéticas de esta especie, que tiene grandes áreas de forrajeo y un período prolongado de estancia de los pollos en el nido. Por otro lado, las hembras mostraron una respuesta más flexible que los machos a los cambios en la disponibilidad de alimento. Mientras los machos no cambiaron su patrón de consumo de presas, las hembras consumieron una mayor proporción de presas al final del periodo reproductor. Estas respuestas dependientes del sexo podrían estar relacionadas con la diferente inversión en cuidados parentales en esta fase, en la que los machos cuidan de los volantones hasta su independencia y las hembras se preparan para una segunda nidada.

Con respecto a la asignación de presas por parte de la hembra en la fase temprana de pollos, el rango de los pollos (pista de tamaño) y los componentes de la petición relacionados con el tamaño explicaron la asignación de las cebas en los nidos de abubilla. La intensidad del comportamiento petitorio fue igual para todos los pollos y no influyó en las decisiones de reparto, reflejando señales de hambre. Las hembras alimentaron preferentemente a los pollos grandes ignorando a los más pequeños, independientemente del tratamiento de abundancia o escasez, aunque esta tendencia aumentó en condiciones de escasez de alimento. Igualmente, la probabilidad de que un pollo sea alimentado en condiciones de escasez aumentaba cuando ningún pollo más grande pedía. El que no haya un cambio en la asignación de presas según la disponibilidad de alimento puede deberse a dos razones. La primera es que, en esta fase temprana de pollos, el experimento se realizó con presas pequeñas por lo que los padres podrían no haber conseguido saciar a los pollos grandes, estando todos los pollos hambrientos y pidiendo con la misma intensidad. En este caso la hembra alimenta según la pista del tamaño. Por otra parte, los pollos pequeños podrían estar destinados a morir, aunque hubiera suficiente comida, incluso sirviendo de comida a los hermanos mayores, como se ha visto en trabajos anteriores. Estos resultados sugieren que transportar presas grandes capaces de saciar temporalmente a los pollos grandes, podría aumentar las perspectivas de supervivencia de los pollos más pequeños y, por lo tanto, aumentar el éxito del volantón.

El parasitismo de cría no solo supone un coste reproductivo por criar a un pollo de otra especie, sino que además cambia las condiciones y el contexto social del nido. El pollo parásito, para obtener cuidado parental del hospedador, debe explotar los sistemas de comunicación entre padres e hijos, sintonizando sus llamadas de petición con la de sus hermanos adoptivos, para así poder competir por el alimento dentro de la nidada. Por su parte, los padres pueden haber desarrollado defensas tales como el reconocimiento del pollo parásito. El críalo (*Clamator glandarius*) es un parásito de cría cuyo hospedador principal es la urraca (*Pica pica*), pero también puede usar hospedadores que anidan en agujeros de tamaño mediano, como grajillas (*Corvus monedula*) y chovas (*Pyrrhocorax pyrrhocorax*). La abubilla anida en cavidades y sigue una estrategia de reducción de nidada, como lo hacen los hospedadores del críalo, y alimenta a sus pollos con insectos, una dieta adecuada para este parásito de cría. En un segundo experimento, comprobamos si la abubilla, siendo un potencial hospedador del críalo, presenta defensas después de la fase de huevo, ya que la abubilla no expulsa huevos foráneos del nido. Para ello, en los nidos de abubilla en cautividad, añadimos pollos de críalo, creando nidos con sólo críalos y nidos mixtos con abubillas y críalos. Mientras los pollos de críalo estuvieron dentro del nido, las abubillas los alimentaron de forma similar a como lo hacían con sus propios pollos. Sin embargo, en la fase de volantones, ya fuera del nido, las abubillas de nidos mixtos alimentaron con menor frecuencia a los volantones de críalos que a los de abubilla, y los adultos se acercaron más a menudo a alimentar a los volantones de abubilla que a los de críalo. Además, la supervivencia de los volantones de críalo, tanto en las nidadas mixtas como en las de sólo críalos, fue significativamente menor que la de los volantones de abubilla. Estos resultados sugieren que las abubillas discriminarían a los volantones de críalo, con o sin comparación directa con sus propios volantones. Sin embargo, la supervivencia de algunos críalos sugiere que las abubillas no han alcanzado defensas altamente eficientes. Por tanto, otros rasgos de la estrategia vital que dificultan el parasitismo de los críalos (dificultad de encontrar nidos por el parásito y/o dificultad de acceso al nido para poner el huevo) podrían explicar las bajas tasas de parasitismo y los bajos niveles de defensas de esta especie potencialmente hospedadora.

GENERAL ABSTRACT

Nestlings of altricial birds require parental care from hatching due to their developmental stage, which prevents them from self-feeding. Reproduction in these birds focus around the nest, where eggs and nestlings are situated. Both parents must collaborate and invest in subsequent parental care. Food provision by parents is critical for the survival and growth of nestlings, constituting a substantial portion of parental care costs. Additionally, parents must balance food allocation between themselves and their offspring to maximize lifetime reproductive success. This results in a trade-off between investing in offspring provisioning versus self-maintenance and future reproduction. In this biparental care context, conflicts arise regarding each parent's investment (sexual conflict), the interests of offspring versus parents (parent-offspring conflict), and competition among nestlings for parental attention, care, and food (sibling competition).

This thesis explores these evolutionary conflicts in a captive population of hoopoes (*Upupa epops*) since 2008. An experimental setup in captivity, with the hoopoe as a model species, offers several advantages. The hoopoe is an excellent model for testing hypotheses about these conflicts and their food allocation decisions for several reasons. The hoopoe is a central place forager, capable of carrying only one prey item per trip. To maximize net energy gain per trip to the nest, parents must be selective in the prey they bring to the nest for their nestlings and for their own consumption. Therefore, parents should choose larger or more digestible prey for their nestlings, while reserving smaller or less digestible prey for themselves. Furthermore, both parents have different roles during reproduction, differing in tasks, reproductive costs, and foraging strategies. Hence, the value of each prey item for each sex may change throughout the nestling period, influencing decisions on whether the prey is used for self-feeding, delivery to offspring, and ultimately, how to allocate this prey among their nestlings.

Additionally, the hoopoe presents a marked hatching asynchrony with nestlings of different ages and sizes, where food allocation is biased towards the larger nestlings. In harsh environmental conditions, begging by smaller nestlings is often ignored, and hence, parents follow a brood reduction strategy and smaller nestlings die by starvation. Therefore, prey allocation within the brood is influenced by this size hierarchy and, especially, by the food availability. The hoopoe is also a relatively short-lived species that breeds multiple times within and between breeding seasons. In this species, the current brood holds high value, leading hoopoes to preserve investment in this breeding attempt at the expense of their own condition, influencing how they distribute prey, especially in times of scarcity. Finally, hoopoes breed successfully in captivity, enabling precise manipulation of the quantity and quality of food received by the family, creating conditions of both scarcity and abundance. This experimental setup allows tracking the final destiny of each prey that parents manipulate, recording every parental decision from capture to consumption of each prey.

In this experimental context, the general hypothesis is that nest conditions and food availability differentially affect provisioning decisions of each parent.

In this thesis, we conducted a first experiment where we provided the hoopoe family with food *ad libitum* (abundance) or reduced each family's food to 60% (scarcity). The experiment took place in two stages of the nestling period (early and late nestling stage), and we provided prey varying in quality and size.

Regarding parental decisions on food allocation between parents and nestlings, both parents supplied the highest quality prey to the nestlings in both nestling stages, while ingesting those of lower digestibility or size, depending on the phase. These results confirm the expectations for a central-place forager, as adults provided the best prey to the nestlings. However, when food availability was limited, parents in both stages did not reduced the amount of biomass they consumed. In contrast, nestlings experienced a reduction in consumed biomass, but only in the late nestling stage. In this stage, hoopoes did not follow the typical strategy of a short-lived species, as both parents ensured food for self-consumption under scarce conditions, to the detriment of their nestlings. This atypical response may be due to the energetic limitations of this species, which has large home ranges and a prolonged nestling period. Females exhibited a more flexible response to changes in food availability than males. While males did not alter their prey consumption pattern, females consumed a higher proportion of prey at the end of the reproductive period. These sex-dependent responses could be related to different investments in parental care at this stage, with males caring for fledglings until independence and females preparing for a second brood.

Regarding female decisions in prey allocation at the early nestling stage, nestling rank (size cue) and size-related components of begging explained food allocation in hoopoe nests. The intensity of begging behavior was similar for all nestlings and did not influence allocation decisions, reflecting hunger signals. Females preferentially fed larger nestlings while ignoring smaller ones, regardless of abundance or scarcity treatment, although this tendency significantly increased under scarcity conditions. Similarly, the probability of a nestling being fed in scarcity increases when a larger nestling did not beg for food. The lack of change in prey allocation according to food availability may be due to two reasons. First, at the early nestling stage, the experiment was performed with small prey, preventing parents from satiating larger nestlings, and hence, all nestlings were hungry and demanding at the same intensity. In this case, hoopoe females fed according to size cues. On the other hand, the smaller nestlings could be destined to die, even with enough food, or they might serve as food for the larger siblings, as shown in previous works. These results suggest that carrying large prey that temporarily satiates larger nestlings could increase the survival prospects of smaller ones, thereby enhancing fledging success.

Brood parasitism not only incurs reproductive costs of rearing a nestling of another species but also results in changes in the conditions and social context of the brood. The parasitic nestling, to receive parental care from its host, must exploit parent-offspring communication systems, tuning its calls to its hosting siblings for successful competition for food within the brood. Host parents may evolve defenses such as recognition of the parasitic nestling. The great spotted cuckoo (*Clamator glandarius*) is a brood parasite whose primary host is the magpie (*Pica pica*). Still, it parasitizes other medium-sized hole-nesting hosts such as jackdaws (*Corvus monedula*) and choughs (*Pyrrhocorax pyrrhocorax*). Hoopoes, nesting in cavities and employing a brood-reduction strategy similar to other hosts, feed their nestlings with insects, making them suitable hosts for this brood parasite.

In a second experiment, we tested whether the hoopoe, a potential host of the great spotted cuckoo, showed defenses after the egg stage since the hoopoe does not reject foreign eggs from the nest. For this purpose, we introduced great spotted cuckoo nestlings into hoopoe nests in captivity, creating broods with only cuckoo nestlings and mixed broods with both hoopoes and cuckoo nestlings. While the cuckoo nestlings were inside the nest, the hoopoes fed them similarly to their own nestlings. However, in the fledgling stage, already outside the nest, hoopoes from mixed broods fed cuckoo fledglings less frequently than hoopoe fledglings, and adults came more often to feed hoopoe fledglings than cuckoo ones. Moreover, the survival of cuckoo fledglings in both mixed and only cuckoo broods was significantly lower than that of hoopoe fledglings. These results suggest that hoopoes could discriminate against cuckoo fledglings, with or without a direct comparison to their own fledglings. However, the survival of some cuckoo fledglings suggests that hoopoes have not evolved highly efficient defenses. Therefore, other life history traits hindering cuckoo parasitism (difficulty in finding nests by the parasite and/or difficulty in accessing the nest to lay the egg) could explain the low parasitism rates and low levels of defenses in this potential host species.

INTRODUCCIÓN

1. Cuidado parental. Diversidad. Beneficios y costes

El cuidado parental puede ser definido como “cualquier forma de comportamiento de los padres que pueda aumentar la eficacia biológica de su descendencia” (Clutton-Brock 1991), o “cualquier rasgo parental que mejore la eficacia biológica de su descendencia, y que es probable que se haya originado y/o se mantenga actualmente para esta función” (Royle et al. 2012). El cuidado parental es beneficioso para los padres si aumenta la supervivencia, el crecimiento, la calidad y el éxito reproductivo de la descendencia a lo largo de la vida (Clutton-Brock 1991; Alonso-Álvarez and Velando 2012; Klug and Bonsall 2014). Estas definiciones engloban tanto rasgos comportamentales, por ejemplo, la distribución de alimento a las crías o su defensa frente a los depredadores y parásitos, como rasgos no comportamentales, tales como la viviparidad o el aporte extra de nutrientes a los huevos para que se produzca un mayor éxito en la fertilización (Smiseth et al. 2012). Sin embargo, según la definición de Royle et al. (2012), para que se consideren como una forma de cuidado parental, estos rasgos deben haber surgido y/o mantenerse actualmente para aumentar la eficacia biológica de la descendencia. Es decir, comportamientos que puedan favorecer a la descendencia pero no se hayan seleccionado por ese motivo, no serían en realidad cuidados parentales. Un ejemplo sería la defensa por parte de los machos de los mejores territorios de reproducción, cuya función principal sería tener éxito atrayendo a la hembras, aunque, de forma accidental, pueden causar un aumento en la supervivencia de las crías al ser territorios con mejores recursos (Smiseth et al. 2012). Otros investigadores prefieren utilizar el término “cuidado parental” para referirse únicamente a períodos específicos del desarrollo de la descendencia, ya sea después de la fecundación o después de la eclosión o el nacimiento (Blumer 1979; Crump 1995; Klug et al. 2012; Klug and Bonsall 2014). Esta definición es más específica y apropiada para discutir el origen y la presencia o ausencia de cuidado parental entre especies o sexos (Klug et al. 2012; Smiseth et al. 2012).

El cuidado parental es muy diverso dentro y entre grupos taxonómicos en cuanto a su forma, nivel y duración, así como en el grado en que lo proporciona el macho, la hembra o ambos progenitores (Clutton-Brock 1991; Smiseth et al. 2012; Wong et al. 2013). En el sentido más amplio del concepto de cuidado parental, las formas de cuidado que los padres proporcionan a sus crías pueden abarcar desde la nutrición del embrión en desarrollo a través de una placenta o en forma de yema hasta el cuidado de las crías ya maduras (Smiseth et al. 2012). La duración de estos cuidados puede variar desde unos minutos hasta varios años y, además, los cuidados pueden aportar desde un ligero beneficio a la descendencia hasta ser totalmente imprescindibles para la supervivencia de las crías (Balshine 2012; Smiseth et al. 2012; Trumbo 2012). También existe una gran disparidad entre los taxones en cuanto a la presencia/ausencia de cuidado parental (Clutton-Brock 1991; Reynolds et al. 2002; Royle et al. 2012). Por una parte, mientras el cuidado parental es universal en aves y mamíferos, la mayoría de reptiles, peces, anuros e invertebrados no proporcionan ningún cuidado parental posterior a la fecundación (Clutton-Brock 1991; Reynolds et al. 2002; Royle et al. 2012), abandonando sus huevos después de la puesta (Balshine 2012). De manera general y teniendo en cuenta que dentro de los grupos hay excepciones a estos patrones, el cuidado biparental es común en las aves (90-95%) y el materno es la norma en los mamíferos así como en los invertebrados que presentan cuidados parentales (Cockburn 2006; Balshine 2012; Trumbo 2012). En peces, la mayoría de las veces el cuidado es uniparental (Reynolds et al. 2002), siendo más común el cuidado paterno. En los anfibios, los patrones de cuidado de los padres son variados, incluyendo el cuidado uniparental por parte de los machos, de las hembras y el cuidado biparental (Crump 1996). En los reptiles, solo se ha observado cuidado parental por parte de las hembras en el 1% y 3% de las especies de lagartijas y serpientes ovíparas, respectivamente (While et al. 2009; Sherbrooke 2017).

Beneficios del cuidado parental

Los beneficios de los cuidados parentales se pueden clasificar en: supervivencia a corto plazo, mejora de la calidad de la descendencia, optimización de la tasa de desarrollo o ayudas en la etapa adulta y subadulta (Clutton-Brock 1991; Alonso-Álvarez and Velando 2012).

En primer lugar, los padres pueden aumentar la supervivencia a corto plazo de sus hijos durante la etapa en la que ambos están físicamente asociados (Klug and Bonsall 2014), a través de mecanismo tales como: la protección de la descendencia frente a entornos adversos (depredadores, congéneres, parásitos, infecciones) (Soler et al. 1999b; Croshaw and Scott 2005; Hamel and Cote 2009; Damron et al. 2021); el suministro de alimentos directamente o mediante la lactancia (Barba et al. 1996; Yip and Rayor 2014); la eliminación de los desechos del nido (Hurd et al. 1991; Ibáñez-Álamo et al. 2013); la reducción de los riesgos de deshidratación de huevos o desecación de la descendencia

(Rasa 1998; Stahlschmidt et al. 2008); aumentando la oxigenación de los huevos (mediante la aireación o bombeo a la progenie) (Järvi-Laturi et al. 2008; Munguia-Steyer et al. 2008; y revisado en Alonso-Álvarez and Velando (2012) y en Klug and Bonsall (2014)). Por ejemplo, en un sistema parásito de cría – hospedador, las urracas (*Pica pica*) reconocen a los críalos (*Clamator glandarius*) como enemigos y los atacan cuando los detectan cerca de sus nidos (Soler et al. 1999b). Los padres de algunas especies de anfibios llevan los huevos y los renacuajos en la espalda, en sus patas traseras, en bolsas dorsales, sacos vocales e incluso en el estómago (Tyler et al. 1983; Vagi et al. 2019; Schulte et al. 2020) hasta que se desarrollan como adultos o para transportarlos y alimentarlos en lugares libres de depredadores (Crump 1995; Balshine 2012; Wells 2019). Los escarabajos enterradores (*Nicrophorus vespilloides*) defienden los cadáveres y regurgitan alimento para sus larvas, aumentando así sus probabilidades de supervivencia (Eggert et al. 1998).

En segundo lugar, el cuidado de los padres puede mejorar algún aspecto de la calidad de la descendencia que tiene como consecuencia un aumento posterior en la supervivencia de la descendencia y/o el éxito reproductivo cuando los padres y la descendencia ya no están vinculados (revisado en Clutton-Brock 1991; Alonso-Álvarez and Velando 2012; Klug and Bonsall 2014). Por ejemplo, en el herrerillo común (*Cyanistes caeruleus*), la presencia paterna en el nido aumenta la respuesta inmunitaria de las crías y por tanto la probabilidad de cría durante el año siguiente (Tinne et al. 2005).

En tercer lugar, los padres podrían aumentar la supervivencia o el éxito reproductivo de la descendencia, manipulando la tasa de desarrollo de la descendencia (Klug and Bonsall 2014). Por un lado, los padres disminuyen la cantidad de tiempo que los hijos pasan en etapas que son peligrosas para su supervivencia y aumentan el tiempo que pasan en las etapas más seguras. Por ejemplo, las hembras de la araña escupidora (*Scytodes pallida*) ajustan el tiempo de eclosión de los huevos en respuesta a la amenaza de depredación (Li 2002). Por otro lado, los padres pueden aumentar la tasa de maduración de la descendencia, como por ejemplo hacen las hembras del diamante de Gould (*Erythrura gouldiae*) aumentando el aprovisionamiento a las crías y haciendo que éstas emplumen antes (Pryke and Griffith 2010).

Por último, los padres pueden aumentar directamente el éxito reproductor de sus hijos cuando ambos permanecen en estrecho contacto hasta la edad adulta, ya sea ayudando a sus hijos en el apareamiento, en la reproducción o proporcionando recursos a sus nietos (Smiseth et al. 2012; Klug and Bonsall 2014). Esta forma de cuidado parental hacía crías maduras es raro y se da solo en algunos vertebrados sociales longevos (Clutton-Brock 1991). Por ejemplo, las machos de los bonobos (*Pan paniscus*), mejoran sus interacciones competitivas con otros machos, su estatus social y su éxito de apareamiento en presencia de sus madres (Surbeck et al. 2011).

Costes del cuidado parental

Los beneficios de los cuidados parentales tiene costes asociados en términos de tiempo, energía y/o riesgos al cuidar de su descendencia, perjudicando la eficacia biológica de los padres tanto disminuyendo su supervivencia como las oportunidades de apareamiento y/o su éxito reproductor futuro (Clutton-Brock 1991). Se habla de “inversión parental” cuando se hace referencia a estos costes reproductivos, y se define como “cualquier inversión del padre en un descendiente que aumente su supervivencia y éxito reproductivo a costa de la capacidad del padre de invertir en otra descendencia actual o futura” (Trivers 1974; Smiseth et al. 2012). Su cuantificación es complicada ya que se requiere la demostración de la reducción en eficacia biológica futura (Mock and Parker 1997). Por eso se suele recurrir al término “gasto parental” definido como “cualquier gasto de recursos parentales (incluidos tiempo y energía) en el cuidado parental de una o más crías” (Clutton-Brock and Godfray 1991; Smiseth et al. 2012).

Según la revisión de Alonso-Álvarez and Velando (2012), los costes del cuidado parental se pueden dividir en costes no fisiológicos y fisiológicos.

Los costes no fisiológicos se producen principalmente al obtener los padres recursos en el medio ambiente, ya que están expuestos a infecciones, rivales, depredadores, parásitos de cría conespecíficos o interespecíficos y, además, se reduce el tiempo disponible para futuros apareamientos y para el automantenimiento (Alonso-Álvarez and Velando 2012). Con respecto al riesgo de infección en aves, niveles altos de parásitos sanguíneos están correlacionados con un elevado esfuerzo parental (Nordling et al. 1998; Stjernman et al. 2004; Knowles et al. 2009; Christe et al. 2012; Leivesley et al. 2019), definiendo este esfuerzo parental como “los costes combinados en la eficacia biológica en los que incurre el padre debido a la producción y el cuidado de toda la descendencia en un determinado período biológicamente relevante, como un intento de reproducción” (Clutton-Brock 1991). El cuidado parental también aumenta el riesgo de depredación y, por tanto, disminuye la supervivencia. Las especies que cargan a su descendencia después de su puesta (huevos) o eclosión/nacimiento (crías) poseen una mayor tasa de depredación (Li and Jackson 2003; Suzuki and Futami 2018). Estas especies pueden ver restringida su locomoción por la masa y el volumen de la carga (huevos y/o crías) disminuyendo su capacidad de escape (Ercit et al. 2014; Argaez and Munguía-Steyer 2023). Por último, el tiempo que dedican los padres al cuidado de su descendencia reduce sus oportunidades de apareamiento, la realización de nuevos eventos reproductivos y el automantenimiento (Nilsson and Svensson 1996; Alonso-Álvarez and Velando 2012).

Los costes fisiológicos están relacionados principalmente con la asignación de recursos y surgen cuando los recursos dirigidos al cuidado parental no pueden utilizarse para las funciones somáticas que contribuyen al automantenimiento o al apareamiento de los padres (Daan et al. 1996; Zera and Harshman 2001; Cox et al. 2010; Alonso-Álvarez and Velando 2012). Los costes fisiológicos se han basado principalmente en estudiar las pérdidas de energía o recursos limitantes durante la reproducción (Fowler and Williams 2017). Este gasto de energía se ha estimado a través de medidas de consumo de oxígeno, tasas metabólicas, etc. (Dijkstra et al. 1990; Deerenberg et al. 1995; Speakman 2001), aunque la mayoría de los estudios se han centrado en medir el gasto de energía como pérdidas en la masa corporal total o retraso en las tasas de crecimiento (Török et al. 2004; Rughetti and Ferloni 202; y revisado por Alonso-Álvarez and Velando 2012). Otros mecanismos subyacentes a estos costes y que están despertando un gran interés en los últimos años son el estrés oxidativo, la función inmune, los micronutrientes (carotenoides, calcio, etc.), el estrés fisiológico y el sistema hormonal, los cuales se han sugerido que pueden ser limitaciones clave en la evolución de las estrategias vitales, incluido el cuidado parental (Alonso-Álvarez and Velando 2012; Fowler and Williams 2017).

Parasitismo de cría para evitar costes

Existen especies que han conseguido evadir los costes del cuidado parental mediante una estrategia reproductiva llamada parasitismo de cría. En esta estrategia, los parásitos consiguen que los hospedadores se encarguen de los cuidados parentales de sus crías parásitas (Rothstein 1990; Davies 2000). Esta estrategia ha evolucionado sobre todo en aves e insectos, aunque también se ha encontrado en peces y ranas (Brown et al. 2009; Kilner and Langmore 2011; Lhomme and Hines 2019). El parasitismo de cría puede ser intra-específico, cuando el parásito y el hospedador son de la misma especie, o inter-específico, cuando son de especies diferentes. Adopta dos formas principales: parasitismo obligado, cuando el parásito depende completamente del cuidado parental de otra especie, o parasitismo facultativo, en los casos en que el parásito puede reproducirse de forma independiente siendo una estrategia que complementa la propia reproducción (Spottiswoode et al. 2012). Los parásitos de cría aviares desvían los costes del cuidado parental a los hospedadores obteniendo una serie de ventajas para ellos mismos, tales como tiempo y energía para adquirir recursos, evitar depredadores y tener más descendencia (Payne 1977; Rothstein 1990; Spottiswoode et al. 2012). En cambio, el parasitismo impone desventajas reproductivas a los padres hospedadores ya que éstos se enfrentan a la tarea de alimentar más pollos, desviando recursos de sus propios pollos y de ellos mismos, sobrecargados por un mayor esfuerzo parental (Soler and Soler 1991). Además, algunos de estos pollos parásitos matan a los del hospedador para monopolizar toda la comida, disminuyendo el éxito reproductivo de la especie hospedadora a cero (Kilner and Langmore 2011; Feeney et al. 2014). Estos costes drásticos para la eficacia biológica del hospedador son los que a menudo conducen a la evolución de defensas para evitar ser parasitado, como la capacidad de discriminar huevos o crías parásitas (Soler 2019). A su vez, la selección natural favorece contra-adaptaciones en los parásitos, como el desarrollo de rasgos difíciles de detectar por el hospedador, como por ejemplo una apariencia mimética de sus huevos con el color de los huevos del hospedador (Rothstein 1990; Soler 2019). Este marco básico de especies de parásitos y hospedadores que evolucionan desarrollando adaptaciones y contra-adaptaciones es lo que se conoce como "carrera de armamentos coevolutiva" (Feeney et al. 2012).

2. Decisiones de los padres cuando reparten alimento

Automantenimiento frente a alimentación de descendencia

Uno de los cuidados parentales más costosos desde el punto de vista energético es la alimentación de la descendencia (Drent and Daan 1980). En aves (nuestro modelo de estudio en esta tesis), los padres tienen que tomar muchas decisiones distintas a la hora de alimentar a los pollos, desde el mismo momento que capturan a las presas (Ydenberg 1994; Davoren and Burger 1999; Ydenberg 2007). En una primera instancia, los padres deben decidir si las presas capturadas son para su propia alimentación o, en cambio, son para entregárselas a la descendencia (Davoren and Burger 1999; Ydenberg 2007; Sonerud et al. 2013). Además, deben de decidir qué presas utilizarán según su calidad y tamaño, para su propia alimentación y cuáles destinarán a su descendencia (Sonerud 1989; Mcnamara and Houston 1997; Davoren and Burger 1999; Sonerud et al. 2013). Y finalmente, cómo repartir estas presas entre sus pollos (Clutton-Brock 1991). Estas decisiones llevan implícitos costes, ya que pueden reducir la probabilidad de supervivencia de los padres y su futuro éxito reproductivo (Clutton-Brock 1991; Alonso-Álvarez and Velando 2012). La teoría de las estrategias vitales predice que los padres deben realizar el balance adecuado en la distribución de alimentos entre ellos y su descendencia para maximizar el éxito reproductivo a lo largo de su vida. Por tanto, las decisiones parentales de distribución de alimento van a depender del compromiso entre la inversión en el aprovisionamiento de la descendencia frente al automantenimiento y la reproducción futura (Stearns 1992).

Forrajeadores de un lugar central (Central place foragers)

Los costes de la búsqueda de alimento pueden influir en las decisiones de los padres acerca de la cantidad y el tipo de presas que utilizan para alimentarse ellos y para distribuir entre los pollos (Ydenberg et al. 1994; Burke and Montevecchi 2009). En aves precociales (aves que nacen con los ojos abiertos, con plumón y capacidad de desplazarse), los pollos requieren cuidado parental limitado y son relativamente maduros, pudiendo seguir a sus padres después de la eclosión (Starck and Ricklefs 1998; Botelho and Faunes 2015; Scheiber et al. 2017). Los padres llevan a sus pollos a lugares de alimentación donde comen principalmente de forma autosuficiente, así que los padres tienen costes reducidos relacionados con la búsqueda de alimento. En cambio, en las aves altriciales (aves que nacen con los ojos cerrados, con nada o poco plumón y son incapaces de moverse por sí solos), los pollos requieren un cuidado parental intenso y extenso, como es el suministro de alimentos (Starck and Ricklefs 1998; Scheiber et al. 2017). Las aves altriciales son un claro ejemplo de forrajeador de un lugar central, las cuales recolectan alimentos de un área de campeo a cierta distancia y luego regresan con ellos a un lugar central, normalmente el nido o la colonia (Orians and Pearson 1979; Kacelnik 1984). Los costes de energía y tiempo que supone para los padres viajar a determinadas zonas, capturar, cargar y luego entregar ese alimento a sus pollos desde diferentes lugares y distancias del nido, influyen en el comportamiento de búsqueda de alimento y en la selección de las presas usadas para sí mismos y para la descendencia (Krebs et al. 1978). La teoría del forrajeo de un lugar central predice que los padres deberán maximizar la ganancia neta de energía por viaje al nido, o bien minimizando el tiempo de búsqueda de alimento, o bien seleccionando presas con mayor eficiencia energética para los pollos (Orians and Pearson 1979; Kacelnik 1984; Stephens and Krebs 1986; Burke and Montevecchi 2009). Esta teoría clásica distingue entre aves que solo pueden llevar al nido una presa en el pico (cargadores de una presa, *single prey loaders*), y aquellas que pueden llevar varias (cargadores múltiples, *multiple prey loaders*) (Orians and Pearson 1979). Para que la estrategia de búsqueda de alimento sea óptima para los cargadores múltiples, el tamaño de la carga (número de presas) que llevan al nido deberá aumentar con la distancia (promedio) a los parches de alimentación. En estas especies, la tasa de captura de las presas irá disminuyendo a medida que pasa tiempo en el parche buscando comida, ya que, por un lado, las presas se pueden agotar y, por otro lado, al mantener presas previamente capturadas, se puede reducir la eficiencia en la captura de otras presas (Orians and Pearson 1979; Houston 1985; Stephens and Krebs 1986). Para cargadores de una única presa, el tamaño de la presa transportada al nido tiende a aumentar con la distancia de forrajeo (Orians and Pearson 1979; Stephens and Krebs 1986). En estas especies, que sólo pueden ajustar el tamaño de la presa y no el número, se espera que los padres se vuelvan más selectivos a la hora de capturar presas para transportar al nido, destinando a ello las de mayor eficiencia energética, es decir, con un mayor contenido de energía por tiempo de manejo (Krebs et al. 1978). Los datos empíricos sobre el tamaño de las presas transportadas por forrajeadores de un lugar central a veces no suelen encajar con el óptimo predicho por esta teoría clásica en la búsqueda de alimento. Factores como el riesgo de depredación (Olsson et al. 2008), los costes de transporte (Schmid-Hempel et al. 1985) e incluso el viento (Alma et al. 2017) pueden explicar estos resultados contradictorios. La teoría del forrajeo óptimo (*optimal foraging theory*) predice que, para maximizar su inversión energética, los adultos consumirán presas con menor valor energético que las que entregarán a sus crías (Orians and Pearson 1979; Lessells and Stephens 1983; Carlson 1985; Ydenberg et al. 1994). Esta diferencia en la selección de presas para la autoalimentación y el aprovisionamiento a la descendencia se ha observado principalmente en estudios realizados en aves marinas (Davoren and Burger 1999; Wilson et al. 2004; McLeay et al. 2009; Danhardt et al. 2011; Alonso et al. 2012; Gwiazda and Ledwon 2016).

Limitaciones de las aproximaciones disponibles en la optimización del aprovisionamiento

Los estudios sobre las decisiones que toman los adultos respecto al uso que dan a los distintos tipos de presas son principalmente descriptivos y están basados en escaneos visuales y cuantificación de presas mediante análisis de contenidos estomacales individuales, excrementos fecales y egagrópilas, aunque pueden estar sesgados por sobreestimación, subestimación e incluso por falta de identificación de las presas (Karnovsky et al. 2012; Robinson et al. 2015). En las aves forrajeadoras de un lugar central, rastrear el comportamiento de los padres fuera del nido mediante observación directa es complicado (Hernandez-Pliego et al. 2017). El uso de análisis bioquímicos que incluyen análisis de isótopos estables (SIA), análisis de lípidos y de ADN proporciona una imagen más completa de la distribución de alimentos entre padres y pollos (Koenig et al. 2008; Karnovsky et al. 2012; Beaulieu and Sockman 2014; Orlowski et al. 2014; Catry et al. 2016; McInnes et al. 2016). Mediante el análisis de isótopos estables se puede caracterizar y determinar cómo varía la dieta midiendo los valores plasmáticos de $\delta^{15}N$ y $\delta^{13}C$ en de padres y pollos (Beaulieu and Sockman 2014). Su limitación metodológica es que no permite discriminar el destino final de cada presa y, por ende, la decisión de los padres al encontrarse una presa durante el aprovisionamiento.

Condicionantes de las estrategias vitales

Los rasgos de las estrategias vitales (es decir, longevidad, el tamaño al nacer, el número y la proporción de sexos de la descendencia, etc.) influyen en cómo los padres asignan los recursos para el crecimiento, la supervivencia y la reproducción (Stearns 1992; Capdevila et al. 2020). "Las estrategias vitales de los animales están representadas en un continuo que va desde estrategias de vida lentas caracterizadas por baja fecundidad, desarrollo lento y alta supervivencia, hasta estrategias de vida rápidas con alta fecundidad, desarrollo rápido y baja supervivencia" (Covas and Griesser 2007). En las especies de vida corta, que tienen una baja esperanza de vida y altas tasas de mortalidad, el valor de la eficacia biológica de la nidada actual es alto, ya que la probabilidad de sobrevivir de los padres para volver a reproducirse en el futuro es baja. Por esta razón, estas especies tienden a priorizar la inversión en la reproducción actual a expensas de su propia condición física o de su supervivencia (Stearns 1989; 1992; Covas and Griesser 2007; Klug et al. 2012). Por el contrario, las especies longevas suelen tener una fecundidad baja y aumentan su éxito reproductivo a lo largo de su vida maximizando el número de eventos reproductivos (Stearns 1976; Stearns 1992; Martin 2002; Klug et al. 2012). Por tanto, para los padres, el valor de la eficacia biológica de la descendencia actual es menor ya que tienen más probabilidades de reproducirse en el futuro, por lo que tienden a preservar su propia supervivencia y/o asegurar una reproducción futura a costa de su descendencia actual (Stearns 1992; Ghalambor and Martin 2001). Para probar estas predicciones sobre las especies de vida corta y de vida larga acerca de la inversión sobre la descendencia, se han realizado, por una parte, experimentos que modifican el esfuerzo parental con la manipulación del tamaño de nidada, y por otra, experimentos de suplementación de comida al nido. Los resultados han sido mixtos, con especies de vida corta que invierten más en su descendencia que en ellos mismos (e.g. Markman et al. 2002; McDermott et al. 2023), especies de vida larga que invierten más en su supervivencia y reproducción futura (e.g. Eldegard and Sonerud 2010) y especies tanto de vida corta como de vida larga que no siguen el patrón esperado (e.g. Gonzalez et al. 2006; Krause et al. 2017).

Conflicto paterno-filial

Las decisiones parentales sobre la distribución de alimento entre ellos y la descendencia también pueden verse afectadas por los conflictos que surgen entre los miembros de la familia y los niveles óptimos de inversión parental (Trivers 1972; Mock and Parker 1997; Parker et al. 2002). El conflicto familiar surge cuando los recursos son generalmente limitados y por una asimetría en las relaciones entre los miembros de la familia (Trivers 1972; 1974). La asimetría de parentesco es una aproximación a la fracción de genes propios que se comparten con un pariente (Hamilton 1964) y está determinada por el coeficiente de parentesco entre ellos ($0 \leq r \leq 1$). Los dos padres están igualmente emparentados con toda su descendencia (0.5), mientras que una cría está más emparentada consigo misma (1.0) que con sus hermanos (0.5) (Hamilton 1964; Trivers 1974). Cuando se utiliza este coeficiente para calcular en qué medida difieren los niveles óptimos de inversión entre los miembros de una familia, se manifiestan tres formas de conflicto evolutivo: 1) conflicto entre padres e hijos; (2) competencia entre hermanos; y (3) conflicto sexual (Hamilton 1964; Trivers 1974; Macnair and Parker 1979; Parker et al. 2002).

El conflicto paterno-filial surge cuando el óptimo de inversión parental entre padres e hijos no coincide, ya que los hijos demandarán más recursos a los padres de los que los padres están dispuestos a proporcionar (Trivers 1974). Dentro del conflicto paterno-filial se distingue dos posibilidades. En el conflicto paterno-filial inter-nido, la descendencia actual intenta obtener la inversión que los padres preferirán invertir en eventos reproductores futuros (Trivers 1972; 1974). Y en el conflicto paterno-filial intra-nido, la descendencia actual busca obtener una inversión que los padres intentarán proporcionar a otros miembros de la nidada actual (Macnair and Parker 1979), solapándose éste último conflicto con la competencia entre hermanos (Mock and Parker 1997). La región entre el óptimo parental y el óptimo de la descendencia es lo que se conoce como "campo de batalla" (*battleground*) y es dónde se desarrollará el conflicto paterno-filial (Godfray 1995a). Los modelos de campo de batalla han sido útiles para explorar cómo este conflicto está influenciado por el grado de parentescos, por el grado de promiscuidad (que afecta a la paternidad dentro de la nidada), por las asimetrías en el valor reproductivo de las crías, y por si los hijos son cuidados por uno o por los dos padres (Macnair and Parker 1978; Parker 1985; Godfray 1995a; Mock and Parker 1997; Parker et al. 2002). Sin embargo, estos modelos no hacen predicciones sobre el resultado del conflicto entre padres e hijos (Godfray 1995a), además de que es difícil a través de estudios conductuales demostrar el conflicto genético (Mock and Forbes 1992; Kilner and Hinde 2008) y cuantificar los niveles de inversión óptima de padres e hijos (Smiseth et al. 2012). Para abordar la pregunta de cómo se resuelve el conflicto paterno-filial han surgido diferentes modelos teóricos de resolución de conflictos. En estos modelos, se sugiere que las señales de petición de los pollos reflejan su estado nutricional o condición, y que estas señales son costosas y pueden servir como un mecanismo de resolución del conflicto entre padres e hijos sobre la cantidad y distribución de los recursos alimentarios (Godfray 1991; 1995b; Parker et al. 2002). Estos modelos a su vez se pueden clasificar en modelos de competencia por acaparamiento (*scramble competition models*) y modelos de señalización honesta (*honest signalling models*). En los modelos de competencia por acaparamiento entre hermanos, se asume que los pollos tienen el control sobre la distribución de la comida, la petición actúa como una forma de competencia entre hermanos y los padres proporcionan pasivamente alimento a los hijos que poseen la señal más fuerte (Macnair and Parker 1979; Godfray and Parker 1992; Parker et al. 2002). Por el contrario, los modelos de señalización honesta proponen que la petición es una señal honesta de necesidad, calidad o hambre, y los padres deciden activamente a qué pollos alimentar basándose en esas señales (Godfray 1991; 1995b; Kilner and Johnstone 1997; Godfray and Johnstone 2000). Este último modelo de señalización honesta lo veremos más desarrollado en el apartado 3 de la introducción.

Reparto entre los descendientes

Señales de petición

Los padres utilizan las señales de petición de sus pollos para tomar decisiones a la hora de asignar el alimento entre ellos (Kilner and Johnstone 1997; Royle et al. 2002; Wright et al. 2002). Para evitar el engaño y la ruptura de la comunicación entre padres e hijos, los modelos teóricos para la resolución de conflictos predicen que estas señales son honestas si son costosas de producir (Zahavi 1975; Grafen 1990; Godfray 1991; Maynard Smith and Harper 2003; Searcy and Nowicki 2010; Bradbury and Vehrencamp 2011). De esta forma, la petición sería evolutivamente estable, ya que el coste de la petición penaliza a los hijos que mienten sobre su condición, y los padres se benefician de obtener señales que contienen información honesta sobre su estado (Godfray 1991). Cuando son los padres quienes activamente controlan la distribución de los alimentos, la petición de los pollos les puede revelar tres tipos de información críptica sobre su estado/condición, pudiendo ser esta señal de necesidad, calidad o hambre (Godfray 1991; Royle et al. 2002; Wright et al. 2002; Mock et al. 2011). Según la hipótesis de la señal de necesidad (*Signal of Need hypothesis*) propuesta por Godfray (1991), la señal de necesidad transmite información sobre el aumento en la eficacia biológica de un pollo al recibir una unidad de alimento (Godfray 1991; Johnstone and Godfray 2002). En este modelo, los pollos más necesitados (es decir, en peores condiciones) invierten más en petición ya que una misma cantidad de alimento significa para ellos un mayor aumento en la eficacia biológica que para sus hermanos con mejor condición. De acuerdo con esta hipótesis, los pollos con mayor necesidad pedirán más fuerte o intensamente y serán alimentados preferentemente por sus padres (Godfray 1991; Kilner and Johnstone 1997; Johnstone and Godfray 2002). Esta hipótesis ha encontrado un gran apoyo teórico y empírico (Godfray 1995b; Price et al. 1996; Kilner and Johnstone 1997; Saino et al. 2000b; Johnstone and Godfray 2002; Redpath et al. 2017; Davis et al. 2019), sobre todo en especies sincrónicas (Caro et al. 2016; Mock 2016). En estas especies, todos los huevos eclosionan en unas pocas horas por lo que las jerarquias competitivas se reducen al tener todos los pollos aproximadamente la misma edad y tamaño, favoreciendo así una asignación de alimento más equitativa. En este escenario, alimentar a los pollos más necesitados aumenta la probabilidad de que toda la nidada sobreviva (Soler 2001; Caro et al. 2016; Fresneau and Muller 2016).

La hipótesis de la señal de calidad (*Signal of Quality hypothesis*) establece que la señal de calidad proporciona información sobre la salud y el vigor individual (valor reproductivo) de manera similar a la señalizada por los rasgos sexuales según el principio del handicap (Zahavi 1975; Grafen 1990; Mock et al. 2011). Según esta hipótesis, los pollos con mejor condición (i.e. con mayor valor reproductivo) deberían poder afrontar los costos energéticos de la petición y, por lo tanto, pedirán alimento con una señal más intensa que sus compañeros de nido con peor condición, recibiendo más recursos de los padres (Zahavi 1975; Grafen 1990; Mock et al. 2011). Esta hipótesis ha encontrado apoyo en numerosos estudios que muestran una mayor preferencia de los padres a alimentar pollos con mejor condición (i.e menor daño oxidativo, mayor respuesta inmune). Esta preferencia de los padres está correlacionada positivamente con la intensidad de la señal de rasgos estructurales de la petición como por ejemplo, la coloración basada en carotenoides de las boqueras (comisuras de la boca) de los pollos o la coloración de las plumas, entre otros (Saino et al. 2000a; Jourdie et al. 2004; Soler et al. 2007; Dugas 2009; Romano et al. 2016; Border et al. 2023). Los pollos con mejor condición también pueden señalizar su calidad pidiendo más intensamente que sus hermanos en peores condiciones, ante eventos de escasez. Un ejemplo se encuentra en el piquero de patas azules (*Sula nebouxii*), cuando, ante una reducción de alimento, el pollo de mayor tamaño aumenta la petición a sus padres a la vez que la agresividad hacia el pollo más pequeño y, como consecuencia, recibe más cebas por parte de los padres (Drummond and Chavelas 1989). También se ha demostrado que cuando se priva de alimento a los pollos de golondrina común (*Hirundo rustica*), solo los pollos con mejor condición pueden mantener niveles altos en componentes de la petición como la postura y la duración (Boncoraglio et al. 2012).

Por último, Mock et al. (2011) propusieron la hipótesis de la señal de hambre (*Signal of Hunger hypothesis*), donde la petición actuaría como una señal de hambre, es decir, expresaría la saciedad de un pollo (Grodzinski and Lotem 2007). La intensidad de la señal de hambre indica a los padres el tiempo transcurrido desde la última ceba y si el pollo está listo para otra. Según esta hipótesis, los padres podrían basar las decisiones de inversión en sus hijos en base a estas señales de hambre junto con la información pública proporcionada por pistas como el tamaño corporal (Mock and Parker 1997; Davis et al. 1999; Shiao et al. 2009; Mock 2016).

Asincronía de eclosión y estrategias de reparto

a) Reducción de nidada

El sesgo hacia pollos con mayor valor reproductivo se da especialmente en especies con asincronía de eclosión y en condiciones de escasez de alimento (Caro et al. 2016). En estas especies, los padres comienzan la incubación antes de que se complete la puesta, eclosionando los huevos de manera secuencial a lo largo de los días y causando asimetrías de tamaño entre los hermanos (Lack 1947; Forbes 2011; Lord et al. 2011; Wegrzyn et al. 2023). Los primeros pollos que nacen son más grandes, más fuertes y, como consecuencia, más competitivos que los últimos, y tienen más probabilidades de recibir alimento (Lack 1954; Wiebe 1996; Soler 2001). Cuando el alimento es escaso, la eclosión asincrónica es ventajosa según la hipótesis de reducción de nidada (*brood reduction hypothesis*) (Lack 1947; 1954) ya que los padres pueden hacer un rápido ajuste del tamaño de la nidada a expensas de la muerte de los pollos más pequeños (los últimos en eclosionar), ya que tienen menos valor reproductivo para los padres (Magrath 1990; Mock and Parker 1997; Caro et al. 2016; Wegrzyn et al. 2023). En estas especies, los pollos más grandes pueden obtener más alimento de sus padres incluso cuando piden menos que los más pequeños (Cotton et al. 1999; Smiseth and Amundsen 2002; Mock et al. 2011), y los padres muchas veces ignoran el comportamiento de petición de los mas pequeños (Martín-Vivaldi et al. 1999; Mock et al. 2011; Soler et al. 2022b). De hecho, en un metaanálisis reciente, Caro et al. (2016a) demostraron que en especies con reducción de nidada y cuando hay poco alimento (i.e . un elevado conflicto familiar), los padres, o bien alimentan preferentemente a los pollos con señales estructurales más intensas, o bien ignoran las señales de petición y se basen en otros indicadores de calidad como el tamaño corporal.

b) Conflicto sexual y estrategias de los sexos

En las aves , como en otras especies con cuidados biparentales, las decisiones de inversión parental no sólo van a estar influenciadas por las peticiones de alimento de los hijos, sino que además también van a estar condicionadas por la inversión que realiza la pareja, generando un conflicto sexual (Trivers 1972). Este conflicto surge porque en el cuidado biparental los costos y beneficios de la inversión no se comparten de forma equitativa entre los dos sexos. Así, cada padre se beneficia de la inversión total de la pareja mientras que sólo paga el coste de su propia contribución (Lessells 1999; Houston et al. 2005; Lessells 2006; 2012). Por lo tanto, cada padre está bajo selección para dejar la mayor carga de trabajo a su pareja, mientras reduce la suya propia (Lessells 2012).

Al igual que en el conflicto paterno-filial, los modelos teóricos sugieren que el conflicto sexual puede resolverse mediante tres mecanismos: negociación, concordancia y decisiones de aporte fijo (*negotiation, matching and sealed-bid decisions* respectivamente) (Lessells 2012; Lessells and McNamara 2012). Las decisiones de aporte fijo ocurren cuando un padre toma una decisión fija inicial sobre cuánto esfuerzo va a brindar a la descendencia, independientemente del esfuerzo de su pareja (Houston and Davies 1985). En los modelos de negociación y de concordancia, cada padre ajusta su nivel de esfuerzo en respuesta directa a la contribución de su pareja, aunque lo hacen de manera diferente (McNamara et al. 1999; Johnstone and Hinde 2006; Hinde and Kilner 2007; Harrison et al. 2009). Cuando hay negociación, el padre responde a una reducción en el esfuerzo de su pareja aumentando su contribución y compensando total (Sanz et al. 2000) o parcialmente (Rauter and Moore 2004; Cantarero et al. 2019) esa reducción de esfuerzo de su pareja. Por otro lado, cuando hay concordancia, el padre responde igualando cualquier aumento o reducción en la contribución de su pareja, es decir, ajustan su esfuerzo en la misma dirección que su pareja (Hinde 2006; Hinde and Kilner 2007).

La especialización en las diferentes tareas del cuidado parental por parte de las hembras y de los machos afectaría al resultado del conflicto sexual, ya que podría reducir el grado en que uno de los progenitores puede explotar los esfuerzos del otro, favoreciendo a su vez el cuidado biparental (Lessells 2012; Barta et al. 2014). Muchas aves, como los calaos (Orden *Bucerotiformes*) y las abubillas (Orden *Upupiformes*) y como las rapaces (incluyendo Orden *Accipitriformes*, Orden *Falconiformes* y Orden *Strigiformes)* muestran este reparto de tareas en función del sexo (Mikkola 1983; Martín-Vivaldi et al. 1999; Newton 2010). En la mayoría de las aves rapaces, la hembra es la que se encarga de la incubación, de la crianza de los pollos y de la preparación o manipulación de la comida, mientras que el macho captura las presas (Cramp 1998). En estas especies, las presas que lleva el macho suelen ser grandes y se necesita la asistencia de la hembra para desmembrar el alimento y ofrecérselo a sus pollos (Cramp 1998; Sonerud et al. 2013). Estas aves suelen presentar dimorfismo sexual, siendo generalmente el macho más pequeño que la hembra (Cramp 1998). Este reparto de tareas entre machos y hembras en estos grupos puede provocar que los dos sexos dependan del otro para reproducirse, por lo que sería más difícil que pudieran cuidar solos a los pollos (Houston et al. 2005; Barta et al. 2014). Por otro lado, este reparto puede limitar la respuesta de cada padre a los cambios de comportamiento de su pareja, al menos, mientras dure esta división de las tareas (Harrison et al. 2009; Barta et al. 2014).

Los padres, además de diferir en las tareas reproductivas, también pueden mostrar diferentes estrategias a la hora de alimentar a los pollos dentro de la nidada (Lessells 2012). Cada uno de los padres puede mostrar preferencia de alimentar a sus crías en relación con el tamaño, posición en el nido, sexo y petición (Tanner et al. 2008; Budden and Beissinger 2009; Mainwaring et al. 2011; Lessells 2012). En especies con asincronía de eclosión dónde hay varios tamaños y edades de pollos (Magrath 1990), algunos estudios han encontrado que los machos tienden a alimentar a los pollos más grandes o más cercanos, mientras que las hembras alimentan a los pollos más pequeños. Se ha encontrado este favoritismo en la golondrina bicolor (*Tachycineta bicolor*) (Leonard and Horn 1996), el herrerillo común (*Cyanistes caeruleus*) (Dickens and Hartley 2007), el periquito coliverde (*Forpus passerinus*) (Budden and Beissinger 2009), el papamoscas cerrojillo (*Ficedula hypoleuca*) (Wiebe and Slagsvold 2009). Se ha sugerido entre otras explicaciones, que las hembras pueden conocer mejor las necesidades nutricionales de los pollos, ya que pasan más tiempo dentro del nido (Gottlander 1987; Slagsvold 1997). Por lo tanto, puede que la hembra se muestre más sensible a las peticiones de necesidad (Gottlander 1987). Este patrón de asignación podría reducir la mortalidad de los pollos más pequeños, como se cree que pasa en la abubilla. Ryser et al. (2016) encontraron que los machos alimentaban a los pollos desde la entrada de la caja nido cebando a los pollos más grandes. En cambio, la hembra entraba dentro de la caja-nido y alimentaba de forma equitativa, beneficiando a los más pequeños (Ryser et al. 2016), lo que podría suponer la supervivencia de un número de pollos mayor al final de la época de reproducción.

Limitaciones de las hipótesis disponibles sobre el reparto de alimento

El tamaño de puesta es muy variable tanto entre especies como dentro de ellas. La selección natural favorece un tamaño de puesta óptimo que maximice el éxito reproductivo a lo largo de la vida del individuo, en un hábitat determinado (Stearns 1992). La realización de puestas optimistas por parte de especies con eclosión asincrónica se ha considerado principalmente como una adaptación que facilita la reducción de nidada cuando las condiciones son ambientales son adversas (Lack 1947; Lack 1954; Magrath 1990). Sin embargo, varios estudios han mostrado que la muerte de los pollos más pequeños en especies con eclosión asincrónica se produce incluso cuando hay alimento para toda la nidada (revisado en Kloskowski 2019; Amundsen and Stokland 1988; Stouffer and Power 1990; Wiebe and Bortolotti 1995; Soler and Soler 1996; Brommer et al. 2004). La producción inicial de pollos en exceso en nidadas jerarquizadas por la eclosión asincrónica puede tener otras funciones diferentes además de la reducción de nidada (revisado en Wegrzyn et al. 2023). Por ejemplo, los pollos extra pueden temporalmente aumentar los requerimientos de la nidada y así manipular al macho para que siga aprovisionando (*Sexual Conflict over Parental Investment Hypothesis*; (Slagsvold and Lifjeld 1989; Soler et al. 2022c). Tener huevos o pollos de sobra también permitiría que si se producen fallos en la eclosión o se produce la muerte de una parte de la nidada, tener pollos de “repuesto” (*Insurance Hypothesis*; Forbes 1990; 1991). O bien, como se ha encontrado en la abubilla recientemente, que estos pollos extra sirvan como alimento para sus hermanos más grandes (*The Ice-box Hypothesis*; Soler et al. 2022; Barón et al. 2023).

3. La abubilla como especie modelo para comprobar hipótesis sobre el reparto de alimento

Nuestro modelo de estudio en esta tesis es la abubilla (*Upupa epops*). Sus características la hacen un modelo excelente para probar hipótesis sobre las decisiones de los padres a la hora de distribuir y asignar alimentos a la descendencia a lo largo del ciclo reproductivo. En primer lugar, las decisiones de aprovisionamiento parental pueden estar influenciadas por el hecho de que la abubilla es una especie de vida corta (baja probabilidad de supervivencia anual: 0,38%) especialmente cuando la disponibilidad de presas es limitada en el ambiente (Cramp 1998; Hamel et al. 2010; Schaub et al. 2012). En segundo lugar sólo pueden cargar una presa en el pico por viaje (Cramp 1998), por lo que deberán tomar decisiones sobre el tamaño, digestibilidad y destino de cada presa llevada al nido (Orians and Pearson 1979) y cada presa utilizada para autoalimentarse ellos. En tercer lugar, son especies con asincronía de eclosión (Martín-Vivaldi et al. 1999) por lo que la asignación de presas por parte de la hembra a cada pollo de la nidada estará influenciada por las señales de petición de sus pollos, por las jerarquías de tamaño de cada pollo y por la disponibilidad de alimento para el nido (Caro et al. 2016). En cuarto lugar, los padres difieren en sus tareas parentales, estrategias de búsqueda de alimento específicas de cada sexo y costos reproductivos (Martín-Vivaldi et al. 1999; Guillod et al. 2016; Plard et al. 2018) por lo que el valor de cada presa para cada sexo puede cambiar a lo largo del período de reproducción. La especialización de tareas se produce porque la hembra permanece en el nido durante el periodo de incubación y la primera semana del periodo de pollos, mientras el macho recoge y proporciona todo el alimento a la familia (Martín-Vivaldi et al. 1999; Arlettaz et al. 2010a). Tras esta primera semana, ambos progenitores recogen la comida y alimentan a los pollos, aunque los machos siguen ofreciendo comida a las hembras fuera del nido. Existen diferentes estrategias de búsqueda de alimento entre los padres porque mientras los machos transportan presas de mayor tamaño al nido, las hembras transportan las de menor tamaño (Fournier and Arlettaz 2001; Arlettaz et al. 2010a; Guillod et al. 2016; Ryser et al. 2016). Además, mientras las hembras priorizan el éxito de cada evento reproductivo a expensas de su futura reproducción y supervivencia, los machos limitan su esfuerzo reproductivo dentro de un temporada de reproducción (Plard et al. 2018) difiriendo en sus costes reproductivos. En quinto lugar, el éxito de reproducción de las abubillas en cautividad (Martín-Vivaldi et al. 2014) nos permite manejar experimentalmente la disponibilidad de alimento fuera del nido y manipular las presas, tanto en términos de cantidad como de calidad (tamaño y digestibilidad). La cautividad nos permite seguir el conjunto completo de decisiones de aprovisionamiento que toman los padres para cada presa, desde su captura hasta su asignación a cada pollo o su propio consumo, con diferentes presas y diferente disponibilidad de alimento. Además, las condiciones de cautividad permiten el testado de las hipótesis expuestas anteriormente simulando condiciones ambientales óptimas, es decir, alimento *ad libitum*.

4. Explotación del sistema de reparto por parásitos de cría

Las especies que brindan cuidado parental corren el riesgo de ser explotadas por parte de parásitos de cría (Roldán and Soler 2011; Spottiswoode et al. 2012). La selección natural ha favorecido una gran variedad de adaptaciones por parte de los hospedadores para no ser parasitados, como construir nidos más ocultos, más pequeños o de más difícil acceso, defender el nido atacando o expulsando al parásito y reconocer y rechazar los huevos parásitos (Soler et al. 1999a; Soler et al. 1999b; Muñoz et al. 2007; Abernathy and Peer 2015). De la misma forma, se seleccionan respuestas o contra-adaptaciones por parte del parásito para evadir esas estrategias, como la observación del comportamiento de la pareja hospedadora antes de que comience la puesta de los huevos, ser más sigiloso, desarrollar patrones de plumaje que se parecen mucho a los de los depredadores, mimetismo de los huevos del hospedador, etc. (revisado en Soler 2017). Esta serie de adaptaciones y contra-adaptaciones da lugar a la carrera de armamentos coevolutiva entre parásito y hospedador (Soler 2017). Cuando todas estas defensas del hospedador son superadas por el parásito y los huevos eclosionan, los pollos parásitos deben conseguir niveles adecuados de cuidado parental explotando a sus padres adoptivos en su propio beneficio (Spottiswoode et al. 2012).

Engaño y sintonización

La explotación del hospedador se puede lograr mediante dos mecanismos no mutuamente excluyentes: el mecanismo del engaño (*trickering*) y los mecanismos de sintonización (*tuning*) (Davies 2011; Rojas Ripari et al. 2021).

El mecanismo del engaño implica el mimetismo del pollo parásito, permitiendo que los hospedadores acepten a los pollos parásitos como si fueran suyos propios (Spottiswoode et al. 2012). Existen varios ejemplos sobre este mimetismo visual y vocal (Rojas Ripari et al. 2021). Un ejemplo son los pollos parásitos del cuclillo menudo (*Chrysococcyx minutillus*) que son imitaciones visuales de los pollos de los gerygones, sus principales hospedadores (*Gerygone magnirostris y Gerygone laevigaster*), coincidiendo su piel oscura, plumas blancas y el color de las comisuras (Langmore et al. 2011; Soler 2017). Los parásitos de cría del género *Vidua*, también se parecen mucho a sus hospedadores (familia *Estrildidae*) en los colores, patrones de coloración de sus bocas y en las llamadas de petición (Payne 2005; Jamie et al. 2020). El mimetismo también se ha documentado durante la etapa de volantón, en el parásito de cría tordo chillón (*Molothrus rufoaxillaris*) (Fraga 1998; De Mársico et al. 2012). En esta especie, el volantón tiene un parecido asombroso con la coloración del plumaje y las llamadas de petición de su hospedador, el tordo músico (*Agelaioides badius*) (De Mársico et al. 2017). Este parecido dura hasta que los parásitos consiguen ser independientes nutricionalmente (Fraga 1998).

Los mecanismos de sintonización ayudan a asegurar el éxito de los pollos parásitos una vez que ya han sido aceptados por el hospedador (Davies 2011; Rojas Ripari et al. 2021). Esto implica la explotación de los sistemas de comunicación que median la resolución del conflicto entre padres e hijos (Godfray 1995a; Rojas Ripari et al. 2021). En el caso de que el pollo parásito no mate a los pollos del hospedador, estos tendrán que sintonizar su señales de petición (acústicas o visuales) a las de sus hermanos adoptivos y competir por el alimento dentro de las nidadas (Soler 2017; Rojas Ripari et al. 2021). En los casos en los que los parásitos eliminan a todos los pollos hospedadores, los parásitos a través de la petición deben estimular a los padres para que les proporcione comida suficiente en ausencia de sus hermanos adoptivos (Soler 2017; Rojas Ripari et al. 2021). Estos mecanismos de sintonización se pueden dividir según la revisión de Rojas Ripari et al. (2021) en tres grupos:

1) Comportamiento petitorio exagerado: Este comportamiento por parte del pollo parásito se ha podido observar en multitud de taxones (Redondo 1993; Davies et al. 1998; Grim 2008; Gloag and Kacelnik 2013). La visión general es que los pollos parásitos realizan llamadas de petición más exageradas que sus compañeros de nido para así poder obtener más alimento de sus padres adoptivos (Redondo 1993; Kilner et al.

1999; Dearborn and Lichtenstein 2002). Sin embargo, numerosos trabajos sugieren que también estas peticiones pueden expresar señales honestas de necesidad (Hauber and Ramsey 2003; Soler et al. 2012; Bortolato et al. 2019). Además, existen muchas evidencias de que el éxito de los parásitos que no expulsan a los pollos hospedadores, no está relacionado con estas peticiones exageradas, sino con la relación de su tamaño con el resto de sus hermanos adoptivos unido a la capacidad de poder modular su petición según el ambiente del nido (Tuero et al. 2016; Soler 2017; Bortolato et al. 2019).

2) Llamadas de petición sintonizadas con las del hospedador: Este mecanismo implica la capacidad de los pollos parásitos de imitar la estructura acústica de las llamadas de petición del hospedador para así explotar el esfuerzo de aprovisionamiento de los adultos (Madden and Davies 2006; Langmore et al. 2008; Roldán et al. 2013; Jamie et al. 2020).

3) Explotación sensorial: Este mecanismo de explotación consiste en que los pollos parásitos exhiben señales estructurales que no se utilizan en la comunicación entre padres e hijos, pero en cambio estimulan los sesgos sensoriales del hospedador (Tanaka and Ueda 2005).

Explotando nidadas jerarquizadas

El críalo europeo es un parásito de cría obligado, cuyo principal hospedador en Europa es la urraca (*Pica pica*). La principal característica de este parásito de cría es que sus pollos no expulsan los huevos o los pollos de la especie hospedadora. Además, su hospedador, la urraca, es una especie con reducción de nidada que alimenta preferentemente a los pollos de mayor tamaño. El críalo, presenta una serie de adaptaciones para la explotación de hospedadores como la urraca. En primer lugar, el periodo de incubación del críalo es menor que el de la urraca (Soler et al. 1995). La tasa de crecimiento de los pollos de críalo es mayor que la de los pollos del hospedador (Soler and Soler 1991), por lo que su eclosión más temprana y su rápido crecimiento hacen que tengan un tamaño mayor que el de los pollos de urraca (Soler et al. 1995). Por lo tanto, los críalos tienen una ventaja frente a sus hermanos a la hora de conseguir alimento, monopolizando la comida entregada en los nidos de urraca (Soler and Soler 1991; Soler et al. 1995). Además, los críalos poseen unas papilas palatales blancas (que no poseen los pollos de urraca) que van a influir en la distribución del alimento (explotación sensorial) (Soler et al. 1995). En cambio, esta ventaja desaparece en especies hospedadoras de mayor tamaño como la corneja (Soler et al. 2002), a pesar de que el críalo muestre un exagerado comportamiento de petición (Soler et al. 2002; Martín-Gálvez et al. 2012). Por último, los adultos de críalo pueden romper algunos huevos de la especie hospedadora (Soler et al. 1997) eliminando, por tanto, competencia para sus futuros pollos.

Aunque el principal hospedador del críalo es la urraca, también utiliza con frecuencia otras especies de córvidos y otros grupos que nidifican en agujeros, como grajillas (*Corvus monedula*) y chovas (*Pyrrhocorax pyrrhocorax*) en España (Soler 1990) o estorninos del Cabo (*Lamprotornis nitens*) y estorninos africanos (*Spreo bicolor*) en el Sur de África (Johnsgard 1997; Erritzøe et al. 2012). Junto a alguna cita ocasional de parasitismo en la abubilla (Amor-García et al. 2020), esta información sugiere que otras especies de aves medianas podrían ser hospedadores potenciales para el críalo en España, pero se desconoce si la causa de su escaso uso podría deberse a una historia coevolutiva que haya originado defensas efectivas en esas especies.

Reconocimiento de pollos parásitos por los padres adoptivos

En las etapas de pollo y de volantón, las defensas del hospedador contra el parásito son menos frecuentes y han recibido menos atención que en la fase de huevos (De Mársico et al. 2017; Grim 2017). Se ha asumido que la carrera de armamentos entre parásitos de cría y sus hospedadores estaba limitada a la fase de huevos, al existir muy pocas evidencias de discriminación de pollos, incluso en especies que son capaces de discriminar los huevos miméticos (Davies and Brooke 1989; Davies et al. 1996). Además, Lotem (1993) propuso una modelo que sugería que el reconocimiento del pollo parásito puede imponer costes muy altos. Según este modelo, si en un primer intento de reproducción un hospedador es parasitado por un pollo parásito que mata a todos sus pollos, dejaría en el hospedador una huella mental equivocada de cómo serían sus propios pollos, con consecuencias nefastas para un siguiente intento de reproducción. Esta teoría fue ampliamente aceptada, dedicando menos atención a la fase de pollos (Grim 2017). Actualmente hay evidencias de que el reconocimiento de pollos parásitos es más frecuente de lo que se esperaba (Soler 2009). Sigue siendo menos común que el reconocimiento de huevos, porque el beneficio del hospedador aumenta si rechaza huevos en vez de pollos (Soler 2009), ya que el coste del parasitismo de cría va aumentando según vaya avanzando el ciclo reproductor (i.e. mayor inversión gastada en un parásito) (Davies 2011; Feeney et al. 2014).

De esta forma, para evitar una inversión aún mayor en los pollos de parásito que ya han nacido, los padres hospedadores pueden desarrollar defensas que permitan discriminarlos (Spottiswoode et al. 2012). Se han encontrado hospedadores capaces de discriminar a los pollos y a los volantones de parásitos, sobre todo en especie de parásitos de cría muy virulentos (Spottiswoode et al. 2012; Rojas Ripari et al. 2021). Un ejemplo de reconocimiento de pollos parásitos lo muestra el maluro soberbio (*Malurus cyaneus*) que reconoce al pollo del cuclillo de Horsfield (*Chrysococcyx basalis*) por la presencia de un único pollo en el nido (Langmore et al. 2003). En esta fase, el parásito con sus huevos miméticos ha conseguido superar las líneas anteriores de defensa del hospedador (Langmore et al. 2009), por lo que el hospedador ve limitada sus defensas al reconocimiento de pollos parásitos. En otros casos, el hospedador, como el carricero común (*Acrocephalus scirpaceus*), abandona el nido con el pollo parásito, el cuco común (*Cuculus canorus*). Los cuidados parentales del cuco son más largos que la inversión que hace esta especie de carricero, por lo que una vez superados los costes "previstos", el carricero abandona el nido con el pollo parásito (Grim 2007). Otro ejemplo de reconocimiento de volantones ocurre en el tordo músico (*Agelaioides badius*) al que parasita el tordo chillón (*Molothrus rufoaxillaris*), que es un parásito especialista, y el tordo común (*Molothrus bonariensis*) que es un parásito generalista. De Mársico et al. (2017) descubrieron que el tordo músico alimenta a los volantones del parásito especialista, que imitan visual y vocalmente a los volantones del hospedador, pero rechaza alimentar a los volantones del parásito de cría generalista, que no imita a los volantones de la especie hospedadora.

Algunas especies hospedadoras no desarrollan defensas frente al parasitismo y no reconocen a los pollos parásitos. Existen varias hipótesis evolutivas que tratan de explicar esta falta de reconocimiento. La hipótesis del retraso evolutivo propone que no ha habido suficiente tiempo de interacción o variación genética para que las defensas evolucionen en el hospedador (Davies and Brooke 1988). La hipótesis del equilibrio evolutivo postula que los costes de la defensa frente al parásito superan los beneficios de aceptarlo, y por lo tanto, es adaptativo que las defensas no evolucionen (Aviles et al. 2005). Por último, si las primeras líneas de defensa son efectivas, como la defensa de los nidos y el rechazo de los huevos, se podría impedir la evolución de líneas de defensa posteriores según la estrategia de bloqueo (*blocking model*) (Britton et al. 2007). Esto implica que las defensas en etapas posteriores serán menos comunes, si la línea de defensa anterior es eficiente

(Britton et al. 2007; Feeney et al. 2012). De manera similar, si una especie no presenta reconocimiento de huevos podría presentar defensas a nivel de pollo o volantón.

Una pregunta que queda sin responder en la bibliografía es el por qué especies que podrían ser idóneas como hospedadores de parásitos de cría, no son parasitadas. Estas especies presentan rasgos potencialmente beneficiosos para un parásito de cría, como, por ejemplo, dieta y tamaño similares o estrategias de reparto de alimento adecuadas. Algunos de estos potenciales hospedadores siguen una estrategia de reducción de nidada, alimentando preferentemente a los pollos más grandes (ver el ejemplo del sistema parásito-hospedador urraca-críalo explicado más arriba). En principio, las especies insectívoras de tamaño mediano y nidadas jerarquizadas con frecuente reducción de nidada serían hospedadores potenciales para el críalo, que, con su comportamiento petitorio exagerado podría acaparar el alimento aportado al nido. Una especie con estas características que nidifica habitualmente en hábitats utilizados por el críalo es la abubilla, para la que no se conocen defensas frente al parasitismo de cría, a pesar de que se ha documentado que ocasionalmente puede ser parasitada (Amor-García et al. 2020). En el contexto del estudio de la toma de decisiones sobre el reparto de alimento en el nido por parte de las abubillas adultas, en esta tesis se aborda también hasta qué punto, el que esta especie no sea un hospedador habitual del críalo, se puede deber a la existencia de defensas como el reconocimiento de los pollos parásitos.

OBJETIVOS

HIPÓTESIS, OBJETIVOS Y PREDICCIONES:

Partimos de la hipótesis general de que las condiciones del nido, como la disponibilidad de alimento o el parasitismo de cría, afectarán a las decisiones de ambos progenitores a la hora de aprovisionar a la nidada, dentro y fuera del nido, además de al comportamiento petitorio de los pollos.

Para poder comprobar esta hipótesis, planteamos los siguientes objetivos específicos:

1) Explorar las decisiones parentales sobre cómo ambos padres de abubilla distribuyen los alimentos entre ellos y su descendencia en función de la disponibilidad, tamaño y calidad de las presas. El reparto de alimento en abubillas está basado en que son forrajeadoras de un lugar central y cargadoras de una única presa. Por lo tanto, esperamos que los padres ofrezcan selectivamente presas más grandes y más nutritivas a sus pollos, mientras que ellos consumirán presas más pequeñas y menos nutritivas (**Capítulo 1**).
2) Comprobar cómo afectan las condiciones de escasez al reparto de alimento realizado por ambos padres. La abubilla es una especie de vida corta, por lo que esperamos que, en condiciones de escasez de comida, los padres no reduzcan la cantidad de biomasa ofrecida a sus pollos, sino que den prioridad al éxito de la nidada frente a su propia supervivencia futura (**Capítulo 1**).
3) Comprobar si la escasez de alimento afecta de forma diferencial a las estrategias seguidas por los dos progenitores. La hembra y el macho difieren en sus tareas parentales y tienen diferentes costes reproductivos (aparentemente mayores en las hembras), por lo que esperamos que, en condiciones de escasez, la hembra reduzca su consumo de presas a expensas de alimentar a sus pollos (**Capítulo 1**).
4) Explorar las decisiones de asignación de presas por parte de la hembra de abubilla a sus pollos en función de las señales de petición y bajo diferentes condiciones de disponibilidad de alimento. La abubilla presenta una marcada asincronía de eclosión, por lo que en los nidos de estas aves habrá pollos de diferentes tamaños. Esperamos que cuando la comida sea abundante, la hembra distribuya las presas de manera más equitativa entre los pollos según las señales de hambre o necesidad, independientemente del tamaño de los pollos. Por el contrario, cuando la comida sea

escasa, esperamos que la hembra asigne las presas a los pollos que muestren mejores condiciones a través de señales de calidad o pistas de tamaño corporal (**Capítulo 2**).

5) Comprobar si la abubilla presenta defensas contra el parasitismo tanto en la fase de pollo como en la fase de volantón. La abubilla reúne rasgos idóneos para ser potencial hospedador del críalo, y por tanto, esperamos que presente defensas contra el parasitismo, en alguna de estas fases. En concreto, sería esperable que las abubillas alimenten a los críalos en menor medida que a sus propios pollos, y que, por tanto, los críalos sufran una alta tasa de mortalidad (**Capítulo 3**).
6) Comprobar si el reconocimiento de pollos se ve afectada por la posibilidad de comparar con sus propios pollos. Esperamos que los pollos de críalo criados en nidadas mixtas (compartiendo nido con pollos de abubilla) experimentaran un mayor descenso de cebas y mayor mortalidad que los pollos de críalos criados solos, ya que los padres de abubilla tendrán menos posibilidades de comparar el pollo parásito con una abubilla (**Capítulo 3**).

MATERIAL Y MÉTODOS

Especies de estudio

La abubilla

La abubilla (*Upupa epops*) es un ave perteneciente al Orden *Upupiformes* y que se distribuye por el sur de Europa, Asía y África, existiendo poblaciones migrantes y sedentarias (Reichlin et al. 2009; Reichlin et al. 2013; van Wijk et al. 2018). En general se trata de una especie solitaria, aunque puede formar grupos pequeños durante la época de migración (Cramp 1998; Martín-Vivaldi et al. 2016). Es un ave que se alimenta buscando presas en el suelo o bajo las piedras que levanta con el pico (Cramp 1998), por lo que prefieren hábitats abiertos, con parches de pastizal de baja altura o terrenos de cultivo con acceso al suelo desnudo. Anida principalmente en cavidades naturales de árboles, paredes, etc., y pueden usar cajas-nido para reproducirse (Cramp 1998; Arlettaz et al. 2010a). La abubilla no construye nidos, sino que usan cavidades ya existentes normalmente con restos de material blando que puede provenir de reproducciones anteriores, tanto de congéneres como de heteroespecíficos, donde realizan una pequeña depresión y ponen la puesta (Martín-Vivaldi et al. 1999; Hoffmann et al. 2015).

Es un ave de mediano tamaño (26-28 cm) con un plumaje de color marrón anaranjado en la parte superior y un dibujo bandeado de plumas blancas y negras en las alas, en el dorso y en la cola. Su cresta es de color naranja en forma de abanico y con puntos negros en los extremos de las plumas. Tiene un largo pico curvado hacia abajo de aproximadamente 5-6 cm de longitud, especializado en la captura de invertebrados subterráneos e incluso pequeños reptiles (Cramp 1998; Martín-Vivaldi et al. 2016).

La hembra puede llegar a poner dos puestas de entre seis y ocho huevos entre los meses de febrero y julio, y si fracasa el intento reproductor (depredación o fallo en la eclosión) suele realizar una puesta de reposición (Martín-Vivaldi et al. 1999). El sistema de emparejamiento es monógamo pero se han descrito casos de poliginia, poliandria y poliginandria por lo que parece más flexible (Martin-Vivaldi et al. 2002).

El críalo

El críalo (*Clamator glandarius*) es un ave parásita de cría obligada perteneciente al Orden *Cuculiformes* (Cramp 1998). Se caracteriza por parasitar, mediante la puesta de uno o varios huevos, los nidos reproductivamente activos de otras aves, principalmente especies de la Familia *Corvidae* (Orden *Passeriformes*), tales como la urraca (*Pica pica*), la grajilla (*Corvus monedula*), la corneja (*Corvus corone*) o la chova piquirroja (*Pyrrhocorax phyrrocorax)* (Soler 1990; Johnsgard 1997; Erritzøe et al. 2012).

Es un ave de tamaño medio (38-40 cm) con un tono marrón grisáceo en el dorso y salpicado de motas blancas, la parte ventral es de color claro amarillento, su cola es larga con el borde blanco. Su pico es negro, robusto y ligeramente curvado hacia abajo (Cramp 1998; Soler 2016). Se alimenta principalmente de larvas de lepidóptero tóxicas como la procesionaria del pino (*Thaumetopoea pityocampa*), aunque también de otros artrópodos como escarabajos (Orden *Coleoptera*) y hormigas (Familia *Formicidae*) (Cramp 1985). Es un ave migratoria que pasa los inviernos en África y regresa al sur de Europa por el mes de febrero para reproducirse (Ibáñez-Álamo et al. 2019), siguiendo la fenología de la especie que parasita.

Las hembras pueden llegar a poner 15 huevos por temporada de cría y una misma hembra puede poner más de un huevo en un mismo nido (Martínez et al. 1998).

Alojamiento de las aves experimentales

Se partió de una población de abubillas mantenida en cautividad desde 2008 (Martín-Vivaldi et al. 2014). Durante el otoño y el invierno, las abubillas se mantuvieron, separadas por sexos, en instalaciones situadas en la Facultad de Ciencias de la Universidad de Granada (Granada, España). Estas instalaciones consistían en un aviario grande (13,5 m de largo x 7 m de ancho x 4 m de altura) y tres jaulas de tamaño medio (7 m de largo x 6 m de ancho x 3 m de altura), con una densidad aproximada de 0,072 aves/m3. Las hembras se alojaron en el aviario grande y los machos en las jaulas medianas. El aviario y cada jaula estaban equipados con techos de aluminio que protegían los comederos de plástico de la lluvia y la insolación.

Las parejas reproductoras se establecieron a principios de marzo, cuando se emparejaron un macho y una hembra por jaula. Las aves reproductoras se capturaron en las jaulas del aviario y en las jaulas medianas con redes japonesas y se transportaron a las jaulas de cría en bolsas opacas de tela para reducir el estrés. Ningún ave sufrió daño alguno durante la captura y el transporte. Las jaulas se visitaron diariamente para alimentar a las aves y vigilar su salud.

Durante la época de cría, las parejas se mantuvieron en jaulas montadas durante la temporada de cría de 2011 (Figura 1) en un pinar de la Hoya de Guadix (37º 21’ N, 003º 05’ W, provincia de Granada, sur de España) (Figura 2). En este estudio, se utilizaron

27 jaulas (Figura 3) de 3 m de largo, 2 m de ancho y 2 m de altura, separadas entre sí al menos 50 m. El suelo de las jaulas tenía acceso directo a la tierra, y las jaulas estaban parcialmente protegidas con un techo de plástico ondulado o una tela de rafia para dar sombra. Las jaulas estaban equipadas con una caja-nido de corcho (40 cm de alto x 20 cm de ancho x 20 cm de profundo, 5,5 cm de diámetro de agujero) similar a los empleadas en nuestra área de estudio y utilizadas frecuentemente por las abubillas

Figura 1. Proceso de montaje de una jaula individual de cría. (A) En primer lugar se excavaron las cuatro esquinas que servirán de pilares de anclaje. (B) A continuación, se excavó pequeños canales donde irían enterrados los paños laterales y del fondo. (C y D) Se colocaron los paños, (E) y se atornillaron entre ellos (F). (G) Se colocó el techo y (H) se atornilló. (I y J) se colocó el paño frontal con la puerta y (K) se atornilló al resto de la jaula. (L) Se acondiciono el interior ablandando el terreno y se enterraron los laterales. (M) Finalmente se ajustaron todos los tornillos. (Fotografías cortesía de Juan M. Peralta-Sánchez).

silvestres (Martín-Vivaldi et al. 2006). Las cajas nido se rellenaron hasta 2 cm con corteza de pino picada. Un pequeño techo interior de aluminio (50 de 12 cm y 12,5 cm de alto) protegía del sol y la lluvia a los comederos (Figura 3).

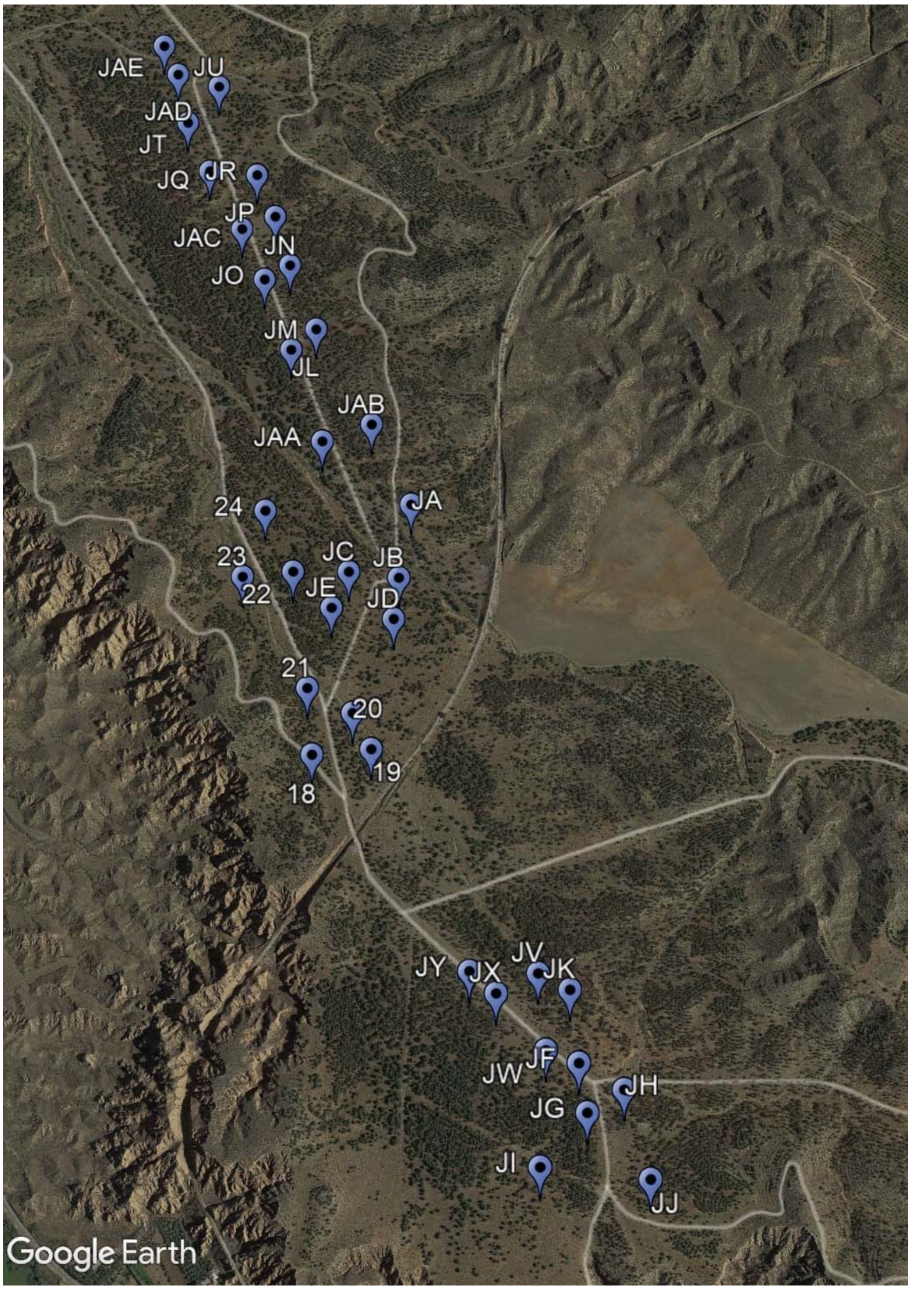

Figura 2. Mapa mostrando la disposición de treinta y dos jaulas colocadas en 2011 en el Pinar próximo a Benalúa de Guadix. Estas jaulas son un subconjunto del total de 75 jaulas colocadas entre Granada, Guadix y Almería (España).

Figura 3. Jaula tipo donde criaron las parejas de abubilla en las temporadas de 2011 a 2013 en el pinar de Benalúa de Guadix. Se puede observar en el interior de la jaula una caja nido y un techo de aluminio para proteger de la lluvia y el sol los dos comederos, uno grande para albergar a grillos y unos más pequeño para las larvas y pupas de mosca (Fotografía cortesía de Juan M. Peralta-Sánchez).

Las abubillas fueron alimentadas diariamente con larvas vivas y pupas de las moscas *Calliphora* y *Sarcophaga*, así como con carne (corazón de ternera) enriquecida con vitaminas ad libitum durante todo el año. No se suministró agua, ya que las abubillas la obtienen de la dieta. En la temporada de cría, además se les proporcionaron grillos vivos (*Gryllus bimaculatus*) adquiridos a la empresa Krik Krik.

Montaje experimental de las jaulas

Los experimentos se realizaron durante las temporadas de cría de 2012 (**Capítulo 1** y **2**) y 2013 (**Capítulo 3**), entre los meses de marzo y julio.

El día anterior a la sesión de control (**Capitulo 1** y **2**), se prepararon las jaulas con el equipo necesario para habituar a los adultos. Se colocó una alfombra de 3 x 2 m sobre el suelo de la jaula para impedir el acceso a presas salvajes o restos de comida de días anteriores. Un tubo de PVC opaco de 4 cm de diámetro y 1,80 m de longitud sirvió para suministrar presas directamente desde el exterior de la jaula a una bandeja de plástico blanco de 25 x 15 cm. Se colocó un panel de madera de 2 x 1 m (3 mm de grosor) en una de las paredes exteriores de la jaula, lo que permitía ocultar al investigador. El panel tenía dos agujeros, uno para que el investigador observara el interior de la jaula y otro para el tubo de PVC (Figura 3). Se instaló una micro-cámara (540TVL SONY CCD Color) en el interior del nido. Esta microcámara se conectó a un grabador externo (mini_dvr, eBoTrade) con una tarjeta SD de 32 MB. Tanto la cámara como el grabador estaban conectados a una batería externa de camión de 12 V (12 AH). Un pequeño monitor (KKMoon 3,5" TFT LED, OWSOO-EU) conectado a la microcámara permitía al investigador observar lo que ocurría dentro del nido y comprobar si la cámara estaba bien colocada y la grabadora funcionaba. Además, esta microcámara permitía saber en tiempo real si la hembra consumía la presa o se la ofrecía a uno de los pollos. Para poder reconocer en la grabaciones al pollo al que la hembra le asignaban la ceba, marcamos aleatoriamente los pollos de abubilla con puntos y rayas azules en el píleo con un marcador permanente. Cada pollo fue marcado con un patrón distinto de puntos y rayas, por ejemplo, pollo1: dos puntos; pollo2: un punto y una raya; pollo3: cuatro puntos, y así sucesivamente. Nunca observamos a los padres picoteando las marcas de los pollos.

Alimento proporcionado a los individuos durante los experimentos

Dependiendo de la fase en la que se encontraban los pollos, el investigador proveyó de diferentes presas a los adultos, que representaban diferencias en la calidad del alimento en términos de digestibilidad y/o tamaño. En todo momento de la fase de pollos, el investigador proporcionó presas pequeñas, i.e. pupas y larvas de las moscas *Calliphora* y *Sarcophaga* (asticot) (**Capítulo 1, 2** y **3**). Con pollos grandes (fase NS2), y volantones, se proporcionaron además presas de mayor tamaño, i.e. grillos adultos, *G. bimaculatus* (**Capítulo 1** y **3**), y larvas de gusano de seda en fase tardía, *Bombyx mori* (**Capítulo 1**).

El uso de presas en cada capítulo queda reflejado en la Tabla 1.

Tabla 1. Distribución de comida y fases de pollos y volantones para cada capítulo de esta tesis.

Cap.	Especies modelo	Fase pollos **NS1**	Fase volantones **NS2**	Pupas	Larvas	Grillos	Gusanos de seda
1	Abubilla (*Upupa epops*)	X	X	X	X	X	X
2	Abubilla (*Upupa epops*)	X	-	X	X		
3	Abubilla (*Upupa epops*) Críalo (*Clamator glandarius*)	X	X	X	X	X	

Procedimientos experimentales

Condiciones de escasez y abundancia de alimento en las abubillas (Capítulo 1 y 2)

Los experimentos sobre el reparto de comida en abubillas (**Capitulo 1** y **2**) se realizaron en dos fases diferentes del periodo de nidificación. La fase de nidificación 1 (**NS1**) se corresponde a la fase temprana de pollos, es decir, 4-6 días tras la eclosión del primer huevo. En esta fase, las hembras de abubilla permanecen en el interior de la caja-nido y los machos proporcionan todo el alimento a la familia (**Capitulo 1** y **2**). La fase de nidificación 2 (**NS2**) se corresponde a la fase tardía de pollos, 16 días tras la eclosión del primer huevo (**Capitulo 1**). En esta fase, tanto las hembras como los machos participan en la alimentación de la familia. Aunque ambos progenitores buscan comida fuera del nido (Martín-Vivaldi et al. 1999), los machos siguen ofreciendo presas a las hembras.

Las diferentes fases de pollos utilizadas en cada capítulo quedan reflejadas en la Tabla 1.

Para determinar la cantidad de alimento necesaria para simular la situación de "abundancia" para cada nido en el tratamiento experimental (**Capítulos 1** y **2**), realizamos dos pruebas de alimentación ad libitum (una por la mañana y otra por la tarde), el día anterior a cada sesión experimental. Media hora antes de empezar, limpiábamos la jaula de restos de comida. A continuación, comenzábamos a alimentar a las aves con larvas y pupas (tanto para **NS1** como **NS2**), aportadas de una en una a través del tubo de PVC hasta que se habituaron a él y tomaban el alimento sin prestar atención al aparato. A partir de ese momento se registró el número total de presas consumidas durante 1 h. A continuación, se les proporcionó presas ad libitum en su comedero durante 1 hora, y se registró el número de presas consumidas, sumándolo al número de presas consumidas del tubo. A continuación, utilizamos el número medio consumido en las sesiones de la mañana y de la tarde como el nivel para cada tratamiento de "abundancia" de nidos. Este enfoque adaptó específicamente la cantidad de alimento suplementario a cada nido, en función del tamaño de la nidada.

El orden de presentación de los alimentos en las sesiones de control (primero tubo de PVC y luego la bandeja llena o viceversa) se cambió entre las observaciones de la mañana y las de la tarde y entre nidos consecutivos. El orden de suministro de cada tipo de presa a través del tubo de PVC se hizo siguiendo una serie de números aleatorios para cada observación y nido (obtenida con el programa STATISTICA 12, Statsoft Inc., Tulsa, OK, EE.UU).

En cada fase de los pollos (**NS1** y **NS2**) (**Capítulos 1** y **2**), se realizaron dos tratamientos (abundancia/ escasez), uno por la mañana y otro por la tarde, alternando este orden en nidos consecutivos. Cada tratamiento duró 2 h, suministrando siempre las presas una a una a través del tubo de PVC. Las sesiones de control y experimental empezaban media hora después del amanecer y las de la tarde comenzaban 3 h antes de la puesta de sol. Entre los ensayos y después del tratamiento de la tarde, se proporcionó comida ad libitum para que los padres pudieran alimentar a los pollos durante la última hora del día.

En el tratamiento de abundancia en **NS1**, proporcionamos el mismo número de presas que en la sesión control con comida ad libitum. Este número de presas se distribuyó como 50% larvas y 50% pupas. El intervalo entre las adiciones de presas se ajustó según la sesión de control anterior (120 min/número de presas consumidas en la sesión de control = minutos para suministrar cada presa en la sesión experimental).

Del mismo modo, para NS2, el número de presas utilizadas para el tratamiento de abundancia se estimó durante la sesión de control, en este caso con los cuatro tipos de presa. Para este cálculo, asumimos de forma conservadora que una presa grande equivalía a dos presas pequeñas. La cantidad de alimento a proporcionar en el tratamiento de abundancia se calculó como el número de presas de los cuatro tipos: larvas 33,3%, pupas 33,3%, gusanos de seda 16,7% y grillos 16,7%. Así, cada tipo equivalía a cerca del 25% de la cantidad total del alimento calculado. El intervalo entre adiciones de presas se ajustó con respecto a la sesión control (120 min/número de presas resultantes del cálculo anterior de la biomasa = minutos para suministrar cada presa durante la sesión experimental). Si una presa no se consumía en 10 minutos, se consideraba rechazada y el ensayo continuaba con la siguiente presa.

Para generar el tratamiento de escasez para cada nido en cada una de las fases (**NS1** y **NS2**), multiplicamos el valor de abundancia por 0,6. La decisión de reducir el alimento al 60% se tomó porque consideramos que era una reducción adecuada para obtener una clara situación de escasez de alimento sin comprometer la supervivencia de los pollos.

Para estimar la biomasa de presas, 20 individuos de cada tipo de presa se secaron en un horno durante 24 h a 70 ºC. A continuación, calculamos la biomasa media (g de peso seco ± SE) (larvas: 0,014 ± 0,0015; pupas: 0,028 ± 0,0008; gusanos de seda: 0,180

± 0,0120; grillos: 0.159 ± 0.0080).

Cuantificación de la asignación de los padres y la petición de los hijos (Capítulo 2)

Para medir el comportamiento de petición de los pollos del **Capítulo 2** se utilizaron cinco componentes de la petición que pueden aportar diferente información a los padres. En primer lugar, medimos la intensidad y la duración de la petición que puede reflejar la necesidad o el hambre de los pollos (Godfray 1995b; Grodzinski and Lotem 2007; Mock et al. 2011). En segundo lugar, medimos la altura de la cabeza, la posición (cercanía a los padres) y el orden de petición según la rapidez con que cada pollo comienza a pedir, que nos puede dar información sobre el tamaño y la calidad de los pollos (Mock et al. 2011; Caro et al. 2016). También medimos el peso de los pollos, considerado como una señal pública (Mock et al. 2011). Observamos en las grabaciones de video que los pollos pedían alimento incluso cuando no había eventos de alimentación. Por lo tanto, también cuantificamos este comportamiento extra de petición.

Todos los comportamientos de petición en los videos fueron calificados por un observador (LA) para reducir el sesgo, utilizando un software de análisis de video (VLC media player, versión 3.0.18, Francia). Analizamos 591 eventos de alimentación. Para cada pollo en cada evento de alimentación, anotamos (a) si pedía o no y (b) si era alimentado o no. A cada pollo que pedía se le asignó una puntuación para las siguientes variables: (1) "orden": el orden en el que cada pollo pidió comida a la llegada de los machos; (2) "intensidad": intensidad postural máxima basada en la siguiente escala según Ryser et al. (2016): 0 (no pedir), 1 (boca abierta), 2 (boca abierta y cuello estirado), 3 (boca abierta, cuello estirado y levantarse), 4 (las tres medidas anteriores más aleteo); (3) "posición": distancia entre los picos de los pollos que piden y la cabeza de la hembra que los alimenta; (4) "altura": el orden relativo de la altura de la cabeza entre los pollos cuando piden (Moreno-Rueda et al. 2009); y (5) "duración de la petición" tiempo(s) desde que el pollo levanta la cabeza y abre la boca hasta que la cierra y baja la cabeza. Fueron incluidos en los análisis solo los eventos de alimentación en los que la hembra alimentó a un pollo, excluyendo aquellos eventos de alimentación dónde la hembra consumía presas ofrecidas por el macho. Finalmente, algunos pollos pidieron comida entre eventos de alimentación, donde el macho no llevó presas al nido. También anotamos la duración e intensidad de la petición de estos pollos.

Tipos de nidos experimentales con abubillas y críalos (Capítulo 3)

En la temporada de cría de 2013, creamos dos tipos de nidos experimentales: nidadas mixtas con un pollo de críalo y un número variable de pollos de abubilla (de 1 a 5 pollos de abubilla); y nidos sólo de críalos, con uno o dos pollos de críalo, solos en el nido. El tamaño de pollada está dentro del rango natural de nidos en libertad (Martín-Vivaldi et al. 1999).

En nidadas mixtas, se introdujeron pollos de críalo 1 ó 2 días más jóvenes que el primer pollo de abubilla. Esto permitió que ambas especies tuvieran un tamaño similar al inicio del periodo de estancia de los pollos en el nido para asegurar la supervivencia de los pollos de ambas especies hasta que fuesen volantones. Los pollos de críalo son más grandes que los de abubilla, alcanzando un peso medio al nacer de 7,8 g, frente a los 3,5 g de los de abubilla (Soler and Soler 1991; Hildebrandt and Schaub 2018). Al final del periodo de nidificación, esta diferencia entre especies es mayor (el peso medio es de 133,7 g en los pollos de críalo; y de 69,6 g en los pollos de abubilla (Soler and Soler 1991; Hildebrandt and Schaub 2018). Además, la introducción de pollos de críalo más jóvenes que las abubillas hace coincidir el tiempo de estancia de los pollos en el nido para ambas especies, ya que los críalos pasan de 19 a 25 días y las abubillas 27,1 días en el nido (Soler and Soler 1991; Martín-Vivaldi et al. 1999).

En los nidos de sólo críalo, se introdujeron pollos de críalo de 1 ó 2 días de edad en nidadas de abubilla que habían tenido un fracaso total de eclosión. La viabilidad de los huevos de abubilla se controló mediante el monitor de pulso cardiaco digital Egg Buddy (Avitronics, Reino Unido). Se introdujo el pollo de críalo en la fecha prevista de eclosión de los huevos de abubilla, asegurando su aceptación por parte de la hembra. En el momento de introducir el pollo de críalo, se retiraron los huevos de abubilla. La razón de utilizar nidadas fallidas de abubilla para obtener nidadas de sólo críalo y mantener el número de pollos de abubilla original en nidadas mixtas obedece a consideraciones éticas. Por un lado, no podíamos trasladar los pollos de abubilla a otros nidos debido a las limitaciones en el número de jaulas y a la falta de sincronía en la fecha de puesta entre los nidos de abubilla. Por otro lado, no teníamos la intención de sacrificar ningún pollo de abubilla en el procedimiento experimental.

Los pollos de críalo fueron transportados en un nido artificial de algodón y mantenidos a una temperatura entre 25 y 30 °C (para más detalles, véase Ibáñez-Álamo et al. (2012)). Ningún críalo murió durante el transporte.

Se crearon 8 nidadas mixtas y 7 nidadas de sólo críalo (4 nidadas con dos pollos de críalo y 3 nidadas con un solo pollo de críalo).

El comportamiento de aprovisionamiento parental se analizó en dos momentos de la reproducción: con pollos pequeños dentro de la caja nido y volantones fuera de la caja. Con pollos pequeños, el interior de las cajas nido se grabó con micro-cámaras (KPC-S500, eSentia Systems Inc., Baton Rouge, LA, EE.UU.) conectadas a grabadores de vídeo siguiendo el protocolo puesto a punto por (Martín-Gálvez et al. 2011). El reparto de alimento a los volantones de abubilla y críalo se cuantificó mediante observación directa utilizando un *hide* situado a unos tres metros de la jaula. De este modo, el investigador tenía una perspectiva de toda la jaula y de la posición de adultos y volantones en todo momento.

Durante la fase de pollos dentro de la caja-nido, se filmaron una vez tanto las nidadas mixtas como las de sólo críalo, cuando los pollos de críalo tenían entre 13 y 18 días de edad. Consideramos este intervalo porque los cañones de las plumas en el críalo aparecen entre los días 12 y 13 (Soler and Soler 1991) y, en la abubilla, la cresta ya se está desarrollando en el día 14 (Kristin 2001). Por lo tanto, a estas edades las diferencias de desarrollo y color del plumaje entre las dos especies son más visibles y evidentes, lo que facilitaría su reconocimiento. En las nidadas mixtas con más de un pollo de abubilla, los pollos de abubilla fueron marcados individualmente al azar sobre el píleo con un número diferente de puntos azules, utilizando un rotulador permanente (excepto un pollo que permaneció sin marcar) con el fin de identificar al individuo alimentado en cada ceba. No encontramos razones para esperar que la presencia del punto azul pueda afectar a la preferencia de los padres por un pollo de abubilla. Decidimos no marcar al críalo, ya que se distingue fácilmente de las abubillas. En las nidadas de sólo críalo, con dos pollos de críalo, estos se distinguían entre sí por su desarrollo, por lo que tampoco los marcamos. La entrega de alimento por parte de los padres se filmó en 8 cajas nido de nidadas mixtas y en 6 de nidadas de sólo críalo (un críalo de una nidada de sólo críalo murió pocos días después del inicio del experimento). Perdimos algunas grabaciones de vídeo porque uno de los videograbadores falló durante los procedimientos experimentales, por lo que nos quedamos con 5 grabaciones de nidadas mixtas y 5 de nidadas de sólo críalo (Tabla suplementaria 3 del **Capítulo 3**). La tasa de cebas de cada pollo (cebas por hora) se calculó como la proporción de cebas por hora de grabación.

Las grabaciones duraron aproximadamente dos horas y media y comenzaron media hora después de la salida del sol (el periodo más activo de las abubillas adultas) y después del suministro diario de comida a la jaula. La información que contiene la edad y el peso de los pollos (críalos y abubillas), así como el tamaño de la nidada antes de las grabaciones de vídeo, se proporciona en la Tabla Suplementaria 7 del **Capítulo 3**.

Durante la fase de volantones fuera de la caja-nido, las observaciones comenzaron el primer día en que todos los individuos estaban fuera del nido. Las observaciones duraron aproximadamente dos horas y se realizaron media hora después del amanecer, después del suministro diario de alimento a la jaula.

En cada evento de alimentación, anotamos la identidad del volantón que recibía la ceba. En nidadas mixtas, marcamos el tarso de los volantones de abubilla con un marcador permanente rojo y azul para distinguirlos entre sí. Sin embargo, no siempre fue posible asignar una ceba a cada volantón en nidadas mixtas debido a la velocidad de los eventos de alimentación. Por lo tanto, la tasa de cebas de las abubillas en una familia se calculó como el número de cebas de todos los volantones de abubilla dividido por el número de volantones y por el número de horas. En las nidadas de sólo críalo, distinguimos un volantón de otro por su tamaño y posición en la jaula. La tasa de cebas por críalo se calculó de manera similar en los casos en que había dos volantones de críalo en la jaula. El número de observaciones por nido varió entre los nidos con un rango de 1 a 4 observaciones (Tabla complementaria 9 del **Capítulo 3**), por lo que promediamos las tasas de cebas de las diferentes observaciones de los nidos. En la Tabla complementaria 2 del **Capítulo 3** se proporciona información que contiene la edad de los volantones (críalos y abubillas), así como el tamaño de la nidada durante cada evento de observación. También anotamos la estrategia de aproximación de los padres y los volantones. La tasa de aproximación de un adulto es el número de cebas en las que una abubilla adulta se acerca al volantón y lo alimenta por hora. La tasa de aproximación de los volantones es el número de veces que los volantones de abubilla/críalo se acercaron a una abubilla adulta pidiendo comida por hora. En este sentido, también distinguimos entre enfoques exitosos (cuando los volantones se acercaron a los adultos y fueron alimentados) y enfoques fallidos (cuando los volantones se acercaron a los adultos y no fueron alimentados). En la fase de volantón observamos sólo seis nidadas mixtas ya que en un caso el críalo murió al día siguiente de abandonar el nido y, en otro, los dos volantones de abubilla murieron y solo el volantón de críalo sobrevivió. En nidadas de sólo críalo, se observó el comportamiento de alimentación en cinco nidadas, ya que una se perdió debido a la depredación de un zorro (*Vulpes vulpes*) que entró en la jaula excavando debajo de la malla de alambre. Este incidente ocurrió antes de que se pudiera realizar cualquier observación (Tabla complementaria 8 del **Capítulo 3**). El período de tiempo durante el cual se observó a los volantones de críalo para registrar su supervivencia duró desde el día en que abandonaron el nido hasta que alcanzaron la independencia (cuando podían alimentarse por sí mismos). El período de dependencia post-volantón osciló entre 40 y 64 días, lo que está dentro del rango encontrado por Soler et al. (1994) en estado salvaje (25 a 59 días). Los críalos supervivientes los liberamos en la zona de Guadix a finales de julio, ya que los pollos suelen abandonar la zona de cría en la segunda semana de agosto, para iniciar su migración hacia las zonas de invernada del África subsahariana (Soler et al. 1994).

Estadística y análisis de datos

Para los análisis de datos en los **Capítulos 1** y **2**, se realizaron modelos mixtos lineales. La razón para utilizar esta aproximación es que se midieron las distintas variables, especialmente las relacionadas con el reparto de alimento a nivel de nido (**Capítulo 1**) mientras que el comportamiento de petición (*begging*) se midió a nivel de pollo (**Capítulo 2**). Debido a que en cada nido hay diferente número de pollos y para poder controlar por la variación que hay entre nidos, se incluyó la variable "identidad de nido" como variable de tipo aleatorio.

En el caso de que la variable dependiente tuviese una naturaleza binaria, se ajustó el modelo con una distribución binomial. En el caso de que la variable dependiente se midiera mediante conteos se ajustó con una distribución de Poisson. En el caso de variables dependientes en proporciones, el modelo fue ajustado mediante una binomial. Y si los datos seguían una distribución normal, el modelo se ajustaban según una distribución gaussiana. En estos modelos se incluyó el tratamiento (escasez-abundancia) como factor fijo. Cuando fue necesario, se incluyeron como factores fijos el tipo de presa (larvas-pupas al inicio de la estancia de pollos en el nido; larvas-pupas-grillos-gusanos al final de dicha estancia) y el miembro de la familia (hembra-macho-pollos); y el ranking del pollo dentro de la nidada como covariable.

Los valores de P se calcularon mediante la comparación de modelos, entre el completo frente al modelo reducido, es decir, el modelo completo sin la variable de interés. Todos los modelos de los **Capítulos 1** y **2** fueron realizados en R v4.0.3 (R Core Team, 2013), utilizando la función glmmTMB implementada en el paquete glmmTMB

(Magnusson et al., 2017).

En el **Capítulo 3**, se hicieron dos tipos de conjuntos de análisis. En un primer conjunto de análisis se compararon la tasa de cebas y las tasas de aproximación de pollos entre abubillas y críalos. En estos análisis se incluyó en el nido como efecto aleatorio y la especie como factor fijo. En una segundo conjunto de análisis, se compararon críalos criados en los dos tipos de nido (mixtos y solos), utilizando el tamaño de nidada como covariable y el experimento (tipo de nido) como factor fijo. Los modelos se ajustaron según la distribución de la variable respuesta ya fuese normal o binomial.

Estos análisis del **Capítulo 3** se realizaron con el programa estadístico STATISTICA 12.0 (Statsoft Inc., OK, EE.UU.).

CAPÍTULOS

CAPÍTULO I. *Provisioning challenge: self-consumption versus nestling provisioning, an experimental study*

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PROVISIONING CHALLENGE: SELF-CONSUMPTION VERSUS NESTLING PROVISIONING, AN EXPERIMENTAL STUDY

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ABSTRACT

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/scarce) 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.

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

INTRODUCTION

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-Alvarez & 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, Szekely, & McNamara, 2005; Lessells & McNamara, 2012). Thus, each parent profits if it leaves the highest workload for its partner (Lessells, 1999; Royle, Smiseth, & Kölliker, 2012). If there is a reduction in the partner's effort, parents can adjust their provisioning behaviour by following different evolutionarily stable strategies (Harrison, Barta, Cuthill, & Szekely, 2009; Johnstone & Hinde, 2006). In negotiation models, parents fully (Sanz, Kranenbarg, & Tinbergen, 2000) or partially (Rauter & Moore, 2004) compensate for this reduction by increasing their effort (McNamara, Gasson, & Houston, 1999), while in the matching strategy, parents adjust their effort in the same direction as their partner (Iserbyt, Griffioen, Eens, & Muller, 2019; Johnstone & Hinde, 2006). In sealed bid models, parents invest an a priori fixed effort, independently of their partner's effort (Houston & Davies, 1985; Nakagawa, Gillespie, Hatchwell, & Burke, 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, Pinshow, & Wright, 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, Dugger, Nur, & Ainley, 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, Kruger, & Pogany, 2017; long lived: Gonzalez, Margalida, Sanchez, & Oria, 2006).

In birds, the time and energy costs of transporting each prey also influence parental food allocation decisions (Mullers, Navarro, Daan, Tinbergen, & Meijer, 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, Daunt, & Wanless, 2004). These circumstances can lead to dietary differences between parents and their nestlings, especially in single-prey loaders (Alonso et al., 2012; Danhardt, Fresemann, & Becker, 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, Postma, & Schaub, 2015; Martín-Vivaldi, Palomino, Soler, & Soler, 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, Schaad, Reichlin, & Schaub, 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, Guillod, Bottini, Arlettaz, & Jacot, 2016), whereas females carry smaller prey (Guillod, Arlettaz, & Jacot, 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, Arlettaz, and Schaub (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/scarce 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, Salo, Koivisto, Banks, & Korpimaki, 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; Hernandez-Pliego, Rodriguez, & Bustamante, 2017; Robinson, Franke, & Derocher, 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 m x 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 cm x 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 cm x 12 cm and 12.5 cm high) from sun and rain.

During autumn and winter, hoopoes were maintained, separated by sexes in facilities located in the University of Granada (Granada, Spain). These consisted of one large aviary (13.5 m x 7 m and 4 m high) and three medium-size cages (7 m x 6 m and 3 m high), with an approximated density of 0.072 birds/m^3. We housed females in the large aviary while males were housed in the medium-size 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 capture with mist-nests and transported to breeding cages in opaque cloth bags to reduce stress. No bird experience 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 x 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 x 15 cm tray of white plastic. A 2 x 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 (Figure 4). 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.

Figure 4. (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.

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, Fox, & Barnes, 1994). Chitin is difficult or impossible for birds to digest (Duke, 1997; Jackson, Place, & Seiderer, 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, Shin, & Shin, 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).

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 ºC. Afterwards, average biomass (g dry weight ± SE) was calculated (larvae: 0.014 ±0.0015; pupae: 0.028 ±0.0008; silkworms: 0.180 ±0.0120; crickets: 0.159 ±0.0080).

Statistical Analyses

Descriptive estimators for groups are presented as average ± 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 x eight nests). In NS1, the number of prey collected from the tray by males differed significantly between the two treatments (Supplementary table 1; 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 (Supplementary table 1; 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 x two treatments x eight nests), while in NS2 the total number of units of replication is 64 (four prey types x two treatments x 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 (Supplementary Tables 2 and 3). Males rejected a smaller proportion of prey in the scarce food treatment (Supplementary table 2; 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 (Supplementary Tables 2, 3 and 4).

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 2, Figure 5a). 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 2, Figure 5a) 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 2).

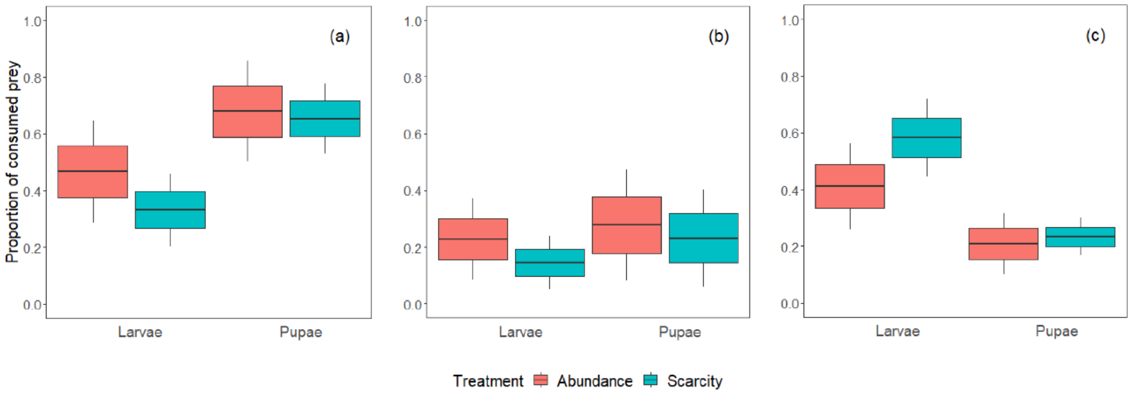

Figure 5. Proportion of larvae and pupae consumed by (a) males, (b) females and (c) nestlings in abundant and scarce food treatments at nestling stage 1 (day 4 after hatching of the first egg). At this stage, all prey were brought to the nest by males. Bold lines, boxes and whiskers show mean, standard error and its 95% confidence interval from raw data, respectively.

Females were more likely to consume pupae than larvae (GLMM 1.2, Table 2, Figure 5b) 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 2, Figure 5b) 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 2).

Nestlings were more likely to be fed larvae than pupae (GLMM 1.3, Table 2, Figure 5c). 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 2, Figure 5c). Biomass obtained by nestlings differed neither by type of prey nor by treatment (GLMM 3.3, Table 2).

Table 2. 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		C-P: 5.01(±0.51)				
		Type of prey	C-L: 4.38(±0.49)	Fixed	3,55	374.70	**<0.001**
			C-S: 1.73(±0.51)				
		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		C-P: 4.05(±0.50)				
		Type of prey	C-L: 4.67(±0.51)	Fixed	3,52	224.52	**<0.001**
			C-S: 1.87(±0.52)				
		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		C-P: -4.56(±0.37)				
		Type of prey	C-L: -4.92(±0.38)	Fixed	3,55	521.28	**<0.001**
			C-S: -1.92(±0.37)				
		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		C-P: 0.08(±0.02)				
		Type of prey	C-L: 0.04(±0.02)	Fixed	3,58	14.51	**0.002**
			C-S: 0.08(±0.02)				
		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		C-P: 0.08(±0.02)				
		Type of prey	C-L: 0.02(±0.02)	Fixed	3,58	13.64	**0.003**
			C-S: 0.07(±0.02)				
		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).

Food Distribution and Consumption in NS2

Males

In NS2, the probability of males consuming each type of prey differed significantly (GLMM 2.1, Table 2) in the following order: pupae > larvae > silkworms > crickets (Fisher LSD post hoc tests: *P* < 0.008; Figure 6a). 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 2, Figure 6a) from the prey they handled.

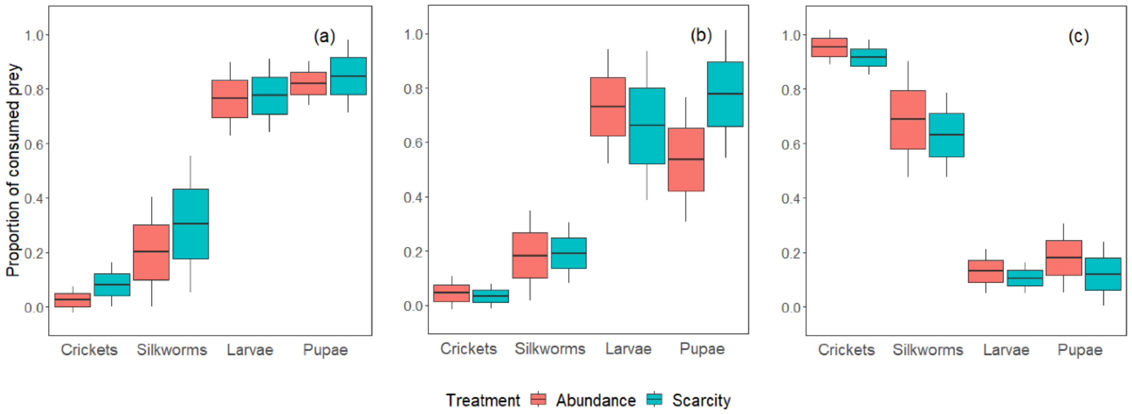

Figure 6. Proportion of each type of prey (crickets, silkworms, larvae and pupae) consumed by (a) males, (b) females and (c) nestlings in abundant and scarce food treatments at nestling stage 2 (day 16 after hatching of the first egg). At this stage both parents brought prey to the nest. Bold lines, boxes and whiskers show mean, standard error and its 95% confidence interval from raw data, respectively.

Males obtained a similar amount of biomass in both treatments (GLMM 3.4, Table 2, Figure 7a). 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; Figure 4a), while they obtained similar biomass from pupae, larvae and silkworms (Fisher LSD post hoc test: *P* > 0.091; Figure 7a).

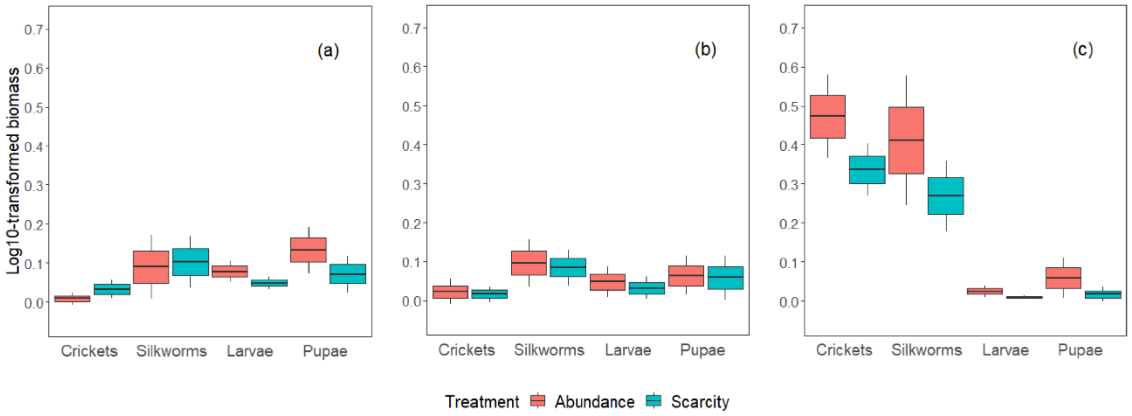

Figure 7. Biomass (g, after $\log_{10}$ transformation) of each type of prey (crickets, silkworms, larvae and pupae) consumed by (a) males, (b) females and (c) nestlings in abundant and scarce food treatments at nestling stage 2 (day 16 after hatching of the first egg). Bold lines, boxes and whiskers show mean, standard error and its 95% confidence interval from raw data, respectively.

Females

Females also were selective in the type of prey consumed (GLMM 2.2, Table 2), following a different order of preferences than males: larvae > pupae > silkworms > crickets (Fisher LSD post hoc tests: $P < 0.032$; Figure 6b). 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 2, Figure 6b) delivering the remaining to nestlings.

Females consumed a similar amount of biomass in both treatments (GLMM 3.5, Table 2, Figure 7b). They obtained significantly more biomass from silkworms and pupae than from crickets (Fisher LSD post hoc test: $P < 0.030$; Figure 7b) and more from silkworms than from larvae (Fisher LSD post hoc test: $P = 0.010$; Figure 7b).

Nestlings

Nestlings were more likely to be fed crickets than any other prey type (GLMM 2.3, Table 2; Fisher LSD post hoc test: $P < 0.001$; Figure 6c). Nestlings were also fed a higher proportion of silkworms than larvae or pupae (Fisher LSD post hoc test: $P < 0.001$; Figure 6c). Finally, nestlings consumed a similar proportion of larvae and pupae (Fisher LSD post hoc test: $P = 0.109$; Figure 6c). 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 2, Figure 6c) 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 2, Figure 7c). Crickets and silkworms provided nestlings with significantly more biomass than larvae and pupae (Fisher LSD post hoc test: $P < 0.001$; Figure 7c). Biomass consumption did not differ between crickets and silkworms or between larvae and pupae (Fisher LSD post hoc test: $P > 0.052$; Figure 7c).

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 3), 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 3, Figure 8); 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: $P < 0.032$).

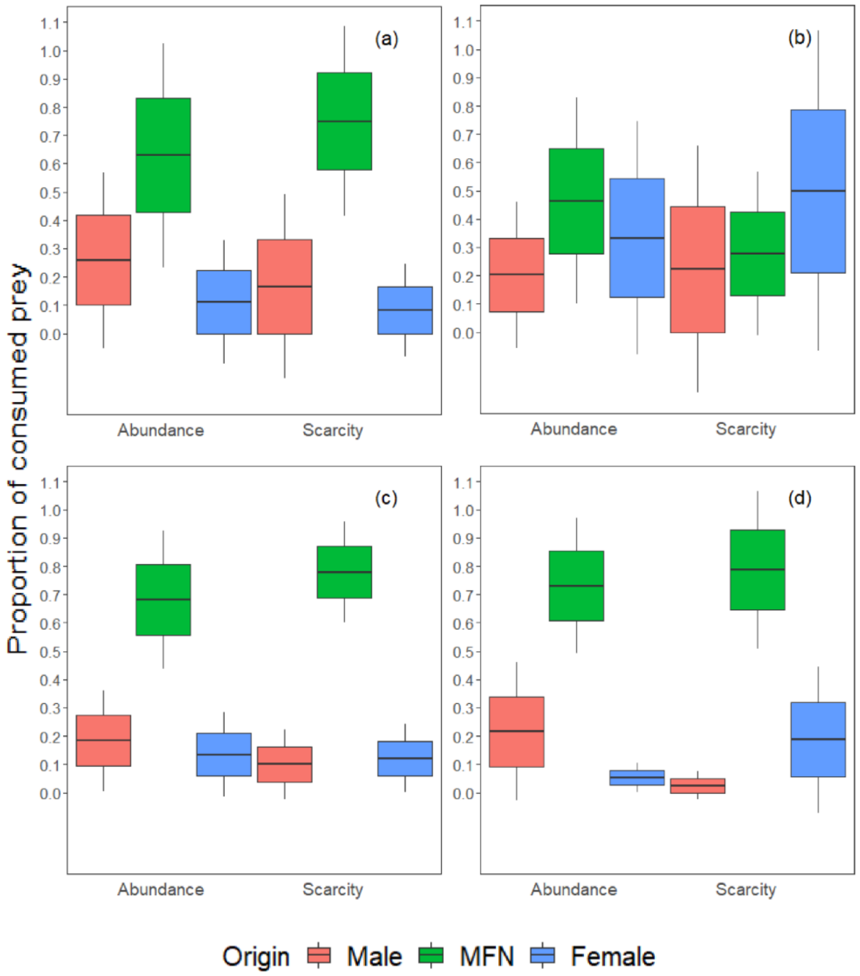

Figure 8. Proportion of (a) larvae, (b) pupae, (c) crickets and (d) silkworms consumed by nestlings in abundant and scarce food treatments at nestling stage 2 (day 16 after hatching of the first egg) and according to the origin of the prey (MFN: sequence male-female-nestling). Bold lines, boxes and whiskers show mean, standard error and its 95% confidence interval from raw data, respectively.

Table 3. 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 (±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(±0.65) C-L: -1.83(±0.67) C-S: 0.79(±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(±0.64) C-L: 0.77(±0.86) C-S: 0.46(±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).

DISCUSSION

In line with central-place foraging theory (Kacelnik & Cuthill, 1990; Orians & 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 (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, Ciancio, Marchisio, & Frere, 2018; Tveraa, Saether, Aanes, & Erikstad, 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* (Orlowski, Rusiecki, & Karg, 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, Schaefer, Mambelli, & Dawson, 2008), Cory's shearwaters, *Calonectris borealis* (Alonso et al., 2012) and grey-headed albatrosses, *Thalassarche chrysostoma* (Richoux, Jaquemet, Bonnevie, Cherel, & McQuaid, 2010).

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; Guillod 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-Ioset, Schaub, Reichlin, Weisshaupt, & Arlettaz, 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, Catry, Alho, Franco, & Moreira, 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 (Martinez-Garcia et al., 2016). Moreover, mole crickets in Switzerland (Fournier & Arlettaz, 2001) and adult field crickets, *Gryllus campestris* (Barbaro, Couzi, Bretagnolle, Nezan, & Vetillard, 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, Bernardi, & Ghiraldo, 2000). This extra time spent handling silkworms can reduce their profitability (Banbura, Lambrechts, Blondel, Perret, & Cartan-Son, 1999; Cansse, Fauchet, Wells, & Arnould, 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 (Orlowski, Wuczynski, & Karg, 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, Svetlik, Eckenfellner, Knauer, & Hoi, 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; Korpimaki, 1989). Indeed, species where males feed their females are also those where males invest more in feeding their offspring (Moller & 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 (Galvan & 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 ± SD = 39.6 ± 25.4 ha, Tagmann-Ioset et al., 2012), between 7.41 and 30.76 ha in France (mean ± 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, Makan, & Castro, 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.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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).

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 Juarez García-Pelayo: Investigation;

Writing – review & editing. Manuel Soler: Conceptualization; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Writing – review & editing.

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SUPPLEMENTARY MATERIAL

Supplementary Table 1. Confirmatory analyses to test whether the experimental treatment had an effect.

Nestling stage	Dependent variable	Factors	Estimate (±SE)	Factor type	*df*	χ^2	*P*
NS1	No. of prey collected by males	Treatment	-0.18 (±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 (±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/scarce 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.

Supplementary Table 2. Confirmatory analyses to test whether parents rejected specific prey.

Nestling stage	Dependent variable	Factors	Estimate (±SE)	Factor type	*df*	χ^2	*P*
NS1	Proportion of prey rejected by males	Type of prey	1.35 (±0.57)	Fixed	3,28	25.38	**<0.001**
		Treatment	-3.37 (±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	Type of prey	C-P: -3.41(±1.08) C-L: -1.17(±1.13) C-S:- 0.05(±1.45)	Fixed	3,58	44.63	**<0.001**
		Treatment	-0.84 (±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/scarce 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).

Supplementary Table 3. Mean (±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 (±0.006)	0.087 (±0.040)	-	-
NS2	0.009 (±0.005)	0.211 (±0.098)	0.009 (±0.009)	0.004 (±0.004)

Nonrejected prey were consumed by parents or offspring.

Supplementary Table 4. 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.

CAPÍTULO II. *Food allocation among nestlings by female hoopoes in ad libitum conditions*

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FOOD ALLOCATION AMONG NESTLINGS BY FEMALE HOOPOES IN *AD LIBITUM* CONDITIONS

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ABSTRACT

In altricial birds, offspring demand food from their parents through conspicuous begging signals and parents respond to these signals by making decisions about how to optimize food allocation among nestlings. Both nestling signalling and parental provisioning strategies can vary depending on environmental predictability and food availability. In unpredictable environments where broods may suffer brood-reduction and when food is scarce, it has been hypothesized that nestlings indicate their quality to parents through structural signals and body size cues and parents feed nestlings in better condition and with a higher probability of survival. We tested this hypothesis in hoopoes, a species with a marked hatching asynchrony and brood reduction, in which the last hatched nestlings usually die. For this purpose, we conducted an experiment with two conditions of food availability (scarce and abundant food), measured the components of nestlings begging and analysed food allocation by the female. We predict that in abundance conditions, the allocation of food by the female would be more equitable among the nestlings, feeding the most needy or hungry ones, while in scarcity the allocation will be biased towards the larger nestlings, feeding those that show higher reproductive value .

We found that reliable predictors of whether a nestling would be fed or not were nestling rank (size) and begging components related to nestling size and quality. In contrast, female food allocation was not influenced by begging intensity, as all nestlings begged with the same intensity, signalling their hunger rather than their need or their quality. Thus, the female preferentially fed the larger nestlings over the smaller ones. In contrast to our predictions, this strategy was held independently whether food was abundant or scarce. Moreover, food limitation further accentuated this difference among siblings.

Two non-exclusive possibilities would explain this result. On the one hand, our experiment with small prey items could not have satiated large nestlings even if they are available *ad libitum*, as all nestlings were hungry. Alternatively, small nestlings could be destined to die, even if there is enough food. These results suggest that carrying large prey could satiate larger nestlings, increasing the survival prospects of small ones and hence increasing fledging success.

Keywords: Nestlings signalling, food provisioning, *Upupa epops*, brood-reduction, food limitation, signals of hunger

INTRODUCTION

In altricial birds, offspring demand food from their parents through conspicuous begging signals (Kilner and Johnstone 1997; Bradbury and Vehrencamp 2011; Caro et al. 2016b) and parents respond to these signals by making decisions about how to optimize food allocation among offspring (Leonard and Horn 2001; Li et al. 2019). Different hypotheses have been proposed to explain the type of information that nestlings transmit to parents through begging (need, quality or hunger) as well as how the parents respond to these signals (e.g. feeding or ignoring). This field has been extensively studied with theoretical and empirical studies (Grodzinski et al. 2011; Hinde and Godfray 2011; Johnstone and Kilner 2011; Mock et al. 2011; Wright 2011). Begging has been hypothesized to reveal three types of “cryptic” information about the nestling state/condition, classified as signals of need, of quality or of hunger (Godfray 1991; Royle et al. 2002; Wright et al. 2002; Mock et al. 2011). The Signal of Need (SoN) hypothesis postulates that the signal conveys information about the marginal fitness benefit gained by receiving more food (Godfray 1991; 1995; Johnstone and Godfray 2002). In this model, the most needy (i.e., in poor condition) nestlings invest more in begging and thus solicit at higher levels compared to their less needy (i.e., in better condition) nest mates, since the same amount of food means a greater increase in fitness for the neediest nestlings. According to this hypothesis, more needy nestlings should beg louder or more intensively and will be preferentially fed by their parents (Godfray 1991; Kilner and Johnstone 1997). Conversely, the Signal of Quality (SoQ) hypothesis postulates that the signal provides information about individual health and vigour (reproductive value) in a similar way to that signalled by sexual traits under the handicap principle (Zahavi 1975; Grafen 1990; Mock et al. 2011). According to this hypothesis, the nestlings with higher reproductive value (i.e., in better condition) should be able to afford the energetic costs of begging and will therefore beg more intensely than their nest mates with low reproductive value, receiving more resources from the parents (Zahavi 1975; Grafen 1990; Mock et al. 2011). Both SoN and SoQ rely on the assumptions that: (i) begging is honest and reliably conveys information about nestling need or quality to parents and that (ii) individual nestlings are able of assessing their own reproductive value, either high (indicating quality) or low (indicating need) (Zahavi 1975; Grafen 1990; Godfray 1991; Zahavi et al. 1999; Maynard Smith and Harper 2003; Searcy and Nowicki 2010; Mock et al. 2011). In a SoN scenario, the begging is negatively condition-dependent and parents favour an equal investment in all of their offspring so that they all survive to independence. In contract, in a SoQ scenario the begging is positively condition-dependent and parents favour a greatest investment in offspring in better condition and with a high probability of survival (Mock et al. 2011). Furthermore, SoN only could work assuming altruism on the part of nest mates in better condition, who would choose not to exert their physical advantage (Godfray 1991; Godfray and Johnstone 2000; Mock et al. 2011). The signal of hunger (SoH) hypothesis was proposed by Mock et al. (2011). In this model, begging express the satiety of a nestling (Grodzinski and Lotem 2007). The intensity of the signal of hunger indicates to the parents the time elapsed since the last feeding and whether the nestling is ready for another feeding. This model is somewhat simpler because it neither requires the altruism of larger, competitively dominant nestmates nor do nestlings have to possess insider information about their own long-term prospects (i.e., need and quality). According to this hypothesis, parents could base their investment decisions on the nestling signals of hunger, along with public information provided by cues, such as body size (Mock and Parker 1997; Davis et al. 1999; Shiao et al. 2009).

The different hypotheses are not mutually exclusive, as begging behaviour and parental responses depend on variation in the predictability of food availability and the quality of available resources (i.e., good or poor environmental conditions), and thus differ among species (Caro et al. 2016a; Mock 2016). In species whose food availability is relatively predictable, parents tend to lay a clutch size that corresponds to the number of nestlings for which they can provide enough food (Lack 1947; Magrath 1990; Vander Werf 1992; Stoleson and Beissinger 1995). In these cases, parents initiate incubation after their clutch is complete, resulting in hatching of all the eggs within a few hours. In these synchronous hatching broods, all nestlings are about the same age and size, which reduces competitive hierarchies among them and favours an equitable allocation of food. In this scenario and with good environmental conditions (i.e., plentiful food), parents preferentially should feed the neediest nestlings that beg more intensely (SoN), in order to increase the probability that all offspring survive (Soler 2001; Caro et al. 2016a; Fresneau and Muller 2016). In contrast, when food availability is unpredictable, parents tend to lay optimistic clutches, raising all their nestlings only when there is enough food (Lack 1947; Mock and Parker 1997; Cotton et al. 1999). In this reproductive strategy, parents start incubation before clutch completion resulting in sequential hatching of nestlings and thus size asymmetries among siblings (Lack 1947; Forbes 2011; Lord et al. 2011; Wegrzyn et al. 2023). In these asynchronous hatching broods, the first-hatched nestlings are larger, stronger and more competitive than the last-hatched ones, and are more likely to receive food (Lack 1954; Wiebe 1996; Soler 2001).When food is scarce (i.e., poor environmental conditions), the hatching asynchrony is advantageous according to the brood reduction hypothesis (Lack 1947; Lack 1968). Parents would make a rapid adjustment of brood size at the expense of the death of the last-hatching nestlings, which have less reproductive value to the parents and often die by starvation (Magrath 1990; Mock and Parker 1997; Caro et al. 2016a; Wegrzyn et al. 2023). Larger nestlings may obtain more food from their parents even when they beg less than smaller nestlings (Cotton et al. 1999; Smiseth and Amundsen 2002; Mock et al. 2011), with parents ignoring the offspring begging behaviour (Martín-Vivaldi et al. 1999; Mock et al. 2011; Soler et al. 2022b). Indeed, in a recent meta-analysis, Caro et al. (2016a) have shown that in species with brood reduction parents preferentially feed the largest nestlings among those signalling their hungry by begging, regardless of their begging intensity.

The hoopoe (*Upupa epops*) is a good model for examining the effect of food availability on both nestling begging behaviour and parental responses (Wild et al. 2017). This bird is a hole-nesting species and its marked asynchronous hatching pattern results in brood reduction (Cramp 1998; Martín-Vivaldi et al. 1999; Ryser et al. 2016; Hildebrandt and Schaub 2018). The male provides all food to the nest during the incubation period and the first 8-10 days after the hatching of the first nestling, while the female remains inside the nest allocating the food among the nestlings. It is around this 10th day when most of the nestling deaths have occurred, being the smallest one the most likely to die first (Martín-Vivaldi et al. 1999; Arlettaz et al. 2010a). Later, the female stops brooding and leaves the nest, and both parents provide food to the nestlings. In this late nestling stage when brood reduction has already occurred and brood size is adjusted to the actual food availability, Ryser et al. (2016) found that parental allocation of feeding to hoopoe nestlings is sex-specific. While the males fed the nestlings from outside the nest box, where the larger and more competitive nestlings received most food (i.e. there is not active allocation by the adult), the females entered the nest box and fed the nestlings more evenly, showing a preference for the smallest and hungriest nestlings. However, this female strategy cannot account for the clear disadvantage of small nestlings at the beginning of the nestling period. Indeed, there is evidence that at this early stage when all allocation decisions are taken by females, females prefer to feed the largest nestlings (Martín-Vivaldi et al. 1999; Ferrer-Pereira et al. 2023). Until now, experimental studies of female hoopoe strategies when allocating food among nestlings have been performed in the field, either with the natural availability of food (Ryser et al. 2016) or experimentally providing extra food at the nest during the first days of the nestling period (Ferrer-Pereira et al. 2023). These conditions probably have not created real scenarios of abundance of food causing a change in female allocation strategies, given that extra food is provided only in short daily periods and only during the beginning of the nestling period (Ferrer-Pereira et al. 2023). While in the field it is not easy to create experimental scenarios of food abundance, this can be easily performed in captivity conditions (Arco et al. 2022).

In a captive hoopoe population fed ad libitum, experimental reduction of food availability did not affect male and female strategies when allocating food between the brood and themselves in the early nestling period (Arco et al. 2022). In this study, the same experimental approach creating two food availability treatments (abundant/scarce food) modifies the hunger level of the whole brood (parents and nestlings). The main objective of the present study is to determinate how the female hoopoe allocates prey among nestlings as a function of both nestling begging behaviour and food availability. We focus on the early nestling stage because the brood reduction has not yet occurred and because females have control over food allocation, with low sibling competition (Martín-Vivaldi et al. 1999). The novelty of our experimental approach is that the hoopoe population was maintained with food ad libitum throughout the breeding season. This approach should provide enough food for raising whole broods. If food availability is the determinant factor in female decisions for investing in the neediest or the fittest nestlings, we should find a different pattern than that found in other field studies where the availability of food is not plentiful (Ferrer-Pereira et al. 2023). Moreover, we marked each nestling individually and we followed the final destiny of each prey from the bill of the female to the gape of the nestling, so this approach allowed us to study the begging behaviour of each nestling, at each feeding event and for the entire brood.

We predict that when food is abundant, the female should allocate prey more equally among the nestlings according to their need or hunger signals. Thus, begging success would be similar among nestlings of different sizes. Conversely, when food is scarce, the female should allocate prey to nestlings that show best condition through their quality signals or body size cues. Thus, begging success would be higher for larger nestlings, while begging by smaller nestlings should be ignored. In natural nests it is known that that the probability of a nestling being fed depends on whether the larger nestlings beg or not (Ferrer-Pereira et al. 2023). This successful feeding would depend if a larger nestling is begging for food, so we predict that a successful feeding of a small nestling would be more probable when a larger sibling is not begging for food. This relationship would be even stronger in scarcity.

MATERIAL AND METHODS

Fieldwork and experimental set-up

The experiment was performed during the 2012 breeding season (March - July) in a population maintained in captivity since 2008 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 x 2 m and 2 m high, at least 50 m apart each other. The cages had a soil floor and were equipped with a roof to provide shade, with plastic poultry feeders (50 x 12 cm and 12.5 cm high) and with an internal aluminium roof that protected these feeders from sun and rain. We also installed in each cage a cork nestbox (40 x 20 cm and 20 cm high, 5.5 cm hole diameter) filled up to 2 cm with chopped pine bark.

Outside the breeding season (autumn and winter), hoopoes were maintained separated by sexes in facilities located in the University of Granada (Granada, Spain). 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. During the breeding season (early March), one male and one female were paired in each cage. Breeding birds were captured with mist-nests and transported to the breeding cages in opaque cloth bags to reduce stress. Cages were visited daily to ensure hoopoes care and maintenance.

The day before the control session, cages were prepared with the necessary equipment to habituate the adults. A carpet of 3 m x 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 provided prey directly from outside the cage onto a 25 cm x 15 cm tray of white plastic. A 2 m x 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. To record the prey allocation by females to nestlings, we installed inside the nestbox a microcamera (540TVL SONY CCD Color). This microcamera was connected to an external recorder (mini_dvr, eBoTrade) with a 32MB SD card. Both the camera and the recorder were connected to an external 12V battery (12AH). A small monitor (KKMoon 3.5" TFT LED, OWSOO-EU) connected to the microcamera allowed the researcher to observe what was happening inside the nest and to check if the camera was properly positioned and the recorder was working.

For further details about the cages and captivity conditions see Arco et al. (2022).

Experimental Procedure

The experiment was conducted 4-6 days after the first egg hatched. At this stage, females remain inside the nest and males provide all food to the family (Martín-Vivaldi et al., 1999). The experiment was performed to ten hoopoe pairs but some experiments could not be completed in two nests due to adverse weather conditions or failures in the recording equipment, and the final number of pairs with available information was eight.

Control Session

To calculate 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. Then, we started feeding larvae and pupae, one by one, through the PVC pipe until the birds habituated to it and took food without paying attention to the setup. From that moment, we provided prey continuously for 1 h, recording the number of consumed prey. After that, in the next hour, we provided prey ad libitum by filling their normal feeding tray. Then, we recorded the number of eaten prey by summing those taken from the tray and those consumed from the pipe. We then used the average number consumed across the morning and afternoon sessions as the level to be used for each nest in the '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

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. At that moment, we weighed the nestlings for ranking them to determine their age/size. For nestling recognition during recording, we randomly marked hoopoe nestlings with blue dots and stripes on the crown with permanent marker. Each nestling was marked with a distinct pattern of dots and stripes, e.g., nestling one: two dots; nestling two: one dot and one stripe; nestling three: four dots, and so on. We never observed the parents pecking at the nestling marks. 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, 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).

To generate the scarce food treatment for each nest, we multiplied the abundant food value by 0.6.

Video analyses

The begging behaviour of the nestlings was measured using five begging variables that provided different information to the parents. First, the intensity of begging and the duration of begging may reflect the need or hunger of the nestlings (Godfray 1991; Grodzinski and Lotem 2007; Mock et al. 2011). Second, begging height, position (proximity to parents) and begging order (the speed with which nestlings start begging) may also provide information about nestling size and quality (Mock et al. 2011; Caro et al. 2016a). We also measured body mass of nestlings considered as public cues (Mock et al. 2011). We observed in the video-recordings that nestlings were begging for food even when there were not feeding events. Therefore, we also quantified this nestling begging behaviour.

All begging behaviours in the videos were scored by one observer (LA) to reduce bias, using video analysis software (VLC media player, version 3.0.18, France). We analysed 591 feeding events. For each nestling at each feeding event, we noted (a) whether it begged or not and (b) whether it was fed or not. Each begging nestling was assigned a score for the following variables: (1) "order": the order in which each nestling begged for food upon the arrival of the males; (2) "intensity": maximum postural intensity based on the following scale according to Ryser et al. (2016): 0 (not begging), 1 (gapping), 2 (gaping and neck stretching), 3 (gaping, neck stretching and standing), 4 (all former three measures plus wing flapping); (3) "position": distance between the beaks of the begging nestlings and the head of the feeding female; (4) "height": the relative order of head height among nestlings when begging (Moreno-Rueda et al. 2009); and (5) "begging duration" time (s) from the nestling raising its head and gaping until closing its gape and putting its head down. Only feeding events in which the female fed a nestling were included in the analyses, excluding those events in which the female ate prey offered by the male. Finally, some nestlings begged for food between feeding events, where the male did not bring prey to the nest. We also noted the duration and intensity of the begging of these nestlings.

Statistical analyses

A Generalized Linear Mixed Model (GLMM 1.1), analysed the probability of successful begging for each nestling, where the probability of successful begging (binomially distributed response variable: 1 = beg and successful, it was fed; 0 = beg and failed, it was not fed) depended on the treatment (fixed factor), the nestling rank (covariate) and their interaction (treatment and nestling rank). We included nest ID as a random effect.

To explore the probability that a nestling is fed when a larger (and older) nestling is begging for food, we used a Generalized Linear Mixed Model (GLMM 1.2), where the probability of being fed (binomially distributed response variable; 1 = nestling fed; 0 = nestling not fed) depended on the begging of any other older nestlings as a fixed factor (1 = beg ; 0 = not beg), the treatment as a fixed factor, nestling rank as a covariate and the interaction between begging of nestling older and nestling rank. We included nest ID as a random effect.

We also analysed a subset of data of successful feedings, taking into account if a larger fledgling is begging for food or not. For this purpose, we performed Generalized Linear Mixed Model (GLMM 1.3), with the successful feeding as binomially distributed response variable (1 = nestling fed when larger nestlings begging; 0 = nestling fed when larger nestlings not begging) depended on the treatment (fixed factor), the nestling rank (covariate) and their interaction (treatment and nestling rank). We included nest ID as random effect.

To explore the effects of order, intensity, position and height (as covariates) in the probability of successful begging for each nestling, we used separated Generalized Linear Mixed Model (GLMMs 2) for each covariate, where the probability of successful begging (binomially distributed response variable: 1 = beg and successful, it was fed; 0 = beg and failed, it was not fed) depended on the covariate, the treatment (fixed factor), the nestling rank (covariate) and nest ID (random effect).

To explore how nestling height, position, order and begging intensity varied as a function of nestling rank and food availability, we performed a Generalized Linear Mixed Model (GLMMs 3) where each variable was used as response variable in separated models with Poisson distribution and log link functions. In each model, treatment was included as a fixed factor, nestling rank as a covariate and their interaction (treatment and nestling rank). We included nest ID as a random effect.

Moreover, we performed Generalized Linear Mixed Model (GLMMs 4, ESM) where the duration of begging was used as response variable with Gaussian distribution and log link functions. Treatment was included as a fixed factor, nestling rank as a covariate and their interaction (treatment and nestling rank). We included nest ID as a random effect. Duration of begging was log transformed to fit parametric assumptions. The residuals of response variable followed a Gaussian distribution (Kolmogorov - Smirnov normality test: $P > 0.20$).

Finally, we explored the intensity and duration of begging between each feeding event, where nestlings begged for food without any stimuli (no prey to provide). On the one hand, we performed Generalized Linear Mixed Model (GLMMs 5, ESM) where begging intensity was included as dependent variable following a Poisson distribution and log link functions, including in the model food availability as fixed factor, nestling rank as covariate, their interaction and nest ID as a random effect. In the other hand, we performed Generalized Linear Mixed Model (GLMMs 6, ESM) where the duration of begging was used as response variable with Gaussian distribution and log link functions, treatment was included as a fixed factor, nestling rank as a covariate and their interaction. We included nest ID as a random effect. Duration of begging was log transformed to fit parametric assumptions. The residuals of response variable followed a Gaussian distribution (Kolmogorov - Smirnov normality test: P > 0.20).

All P-values were calculated by model comparison between the complete ones against the reduced model, i.e. without 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 allocation by females to nestlings under different food availability conditions

Nestling begging success decreased as nestlings rank increased in both food availability conditions (GLMM 1.1, Table 4, Figure 9). These differences in begging success between nestlings of different ranks was stepper under scarcity condition (see interaction term in GLMM 1.2, Table 4, Figure 9).

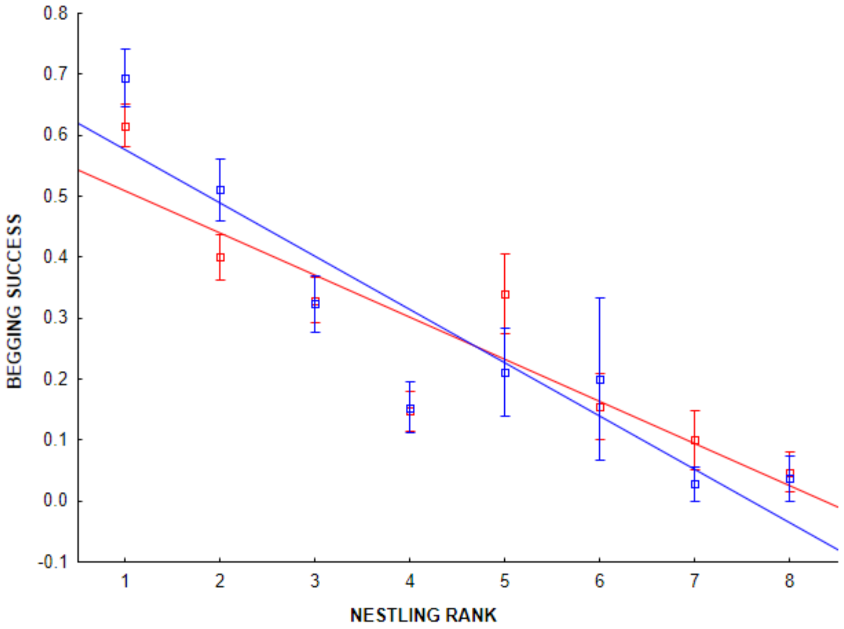

Figure 9. Probability of successful begging for each nestling (nestling that begged and was fed) according to nestling rank and treatment (food abundance in red; food scarcity in blue). Means ± standard errors are shown.

Table 4. Generalized Linear Models (GLMMs) exploring the effects the treatment (abundance and scarcity) and nestling rank (1-8) on food allocation by females to nestlings. Models were fitted with binomial distributions and logit link functions. In case of non-significant interaction, the model was performed again without this term. In GLMM 1.2, we included an additional variable, i.e. that a larger nestling was begging for food (LNB; 1 = begs, 0 = does not beg). P values were calculated by Chi square comparison between the complete model with the reduced one, i.e. without the variable of interest. Significant P-values are shown in bold.

	Dependent variable	**Factors**		**d.f.**	**Chisq**	**P**
GLMM 1.1	Probability of successful begging	Treatment	Fixed	1,1295	6.16	**0.013**
		Rank	Covariate	1,1295	0.00	1.000
		Treatment*rank	Fixed	1,1294	5.55	**0.018**
		Nest	Random	7,1295	1.38	0.240
GLMM 1.2	Probability of a nestling being fed	LNB	Fixed	1,1009	0.10	0.749
		Treatment	Fixed	1,1009	0.36	0.545
		Rank	Covariate	1,1009	0.00	**<0.001**
		LNB*rank	Fixed	1,1008	18.00	**<0.001**
		Nest	Random	7,1009	10.30	**0.001**
GLMM 1.3a	Probability of a successful feeding when a larger nestling begs	Treatment	Fixed	1,270	2.74	0.097
		Rank	Covariate	1,270	0.00	**<0.001**
		Treatment*rank	Fixed	1,269	0.45	0.501
		Nest	Random	7,270	6.37	**0.011**
GLMM 1.3b	Probability of a successful feeding when a larger nestling begs	Treatment	Fixed	1,270	7.40	**0.006**
		Rank	Covariate	1,270	1.89	0.168
		Nest	Random	7,270	6.48	**0.010**

The probability of a nestling receiving food when a larger nestling begged was lower as the rank of the nestlings increased (GLMM 1.2, Table 4, Figure 10). If a larger nestling did not beg, the probability of a smaller nestling receiving food increased as the rank of the nestlings increased (GLMM 1.2, Table 4, Figure 10).

That a nestling is fed even if a larger nestling begs for food occurred more frequently in abundance. Conversely, in situations where food is scarce, it was more frequent that a nestling was fed, the larger nestling was not begging for food (GLMM 1.3b, Table 4).

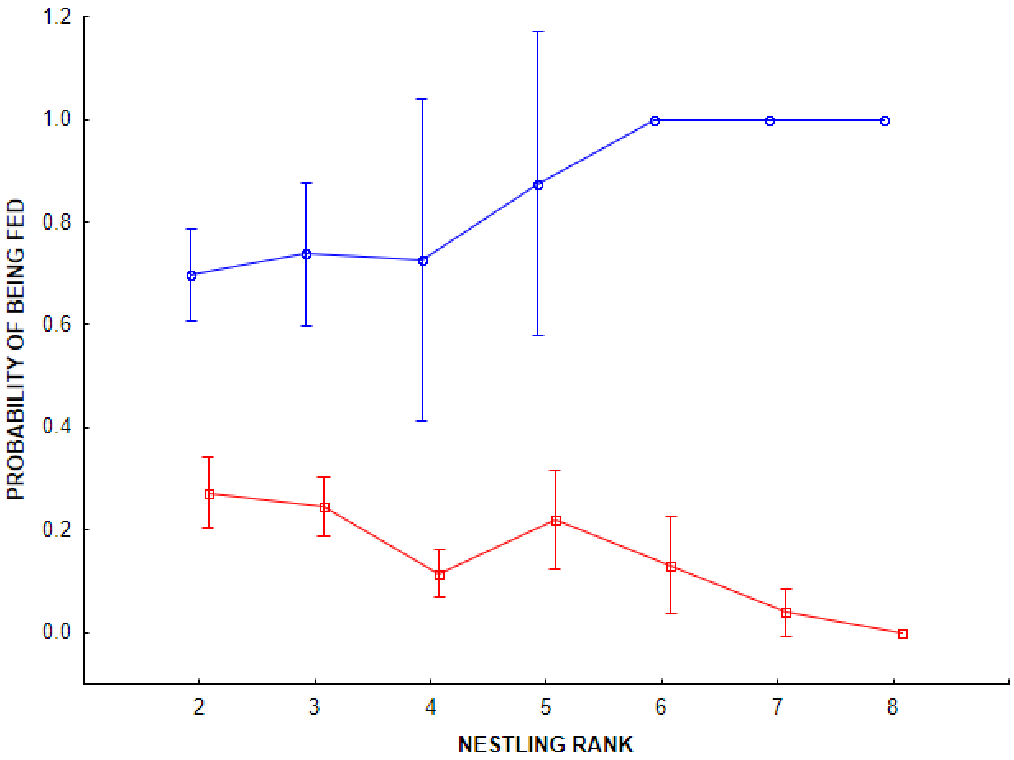

Figure 10. Probability of being fed according to nestling rank and whether larger nestlings were begging (larger nestling was begging in red; larger nestling was not begging in blue). Means ± standard errors are shown.

Influence of components of begging (order, intensity, position and height) to successful begging of nestlings

Nestlings that begged sooner (GLMM 2.1, Table 5), reached higher height (GLMM 2.2, Table 2) or with a position closer to the parents while begging (GLMM 2.3, Table 5) experienced a higher probability of being fed. However, begging intensity did not influence the probability of being fed (GLMM 2.4, Table 5).

Influence of rank and food availability on the nestling height, position, order, intensity and duration of begging

The height of the nestlings as well as the proximity to their parents when begging for food varied according to their rank and the conditions of food availability. Larger nestlings begged higher and closer to parents, but this difference with their siblings increased when food was scarce (GLMM 3.1 and GLMM 3.2, Table 6, Figure 11a and 11b).

Table 5. Generalized Linear Models (GLMMs) testing the effect of order, height, position and intensity (as covariates) in the successful begging (binomially distributed response variable: 1 = beg and successful, it was fed; 0 = beg and failed, it was not fed). Treatment (abundance and scarcity) was included as a fixed factor, nestling rank (1-8) as a covariate and nest ID as a random effect. Models were fitted with binomial distributions and logit link functions. P values were calculated comparing the complete model against the reduced one, i.e. without the variable of interest. Significant P-values are shown in bold.

	Dependent variable	**Factors**		**d.f.**	**Chisq**	**P**
GLMM 2.1	Successful begging	Order	Covariate	4,1295	48.13	**<0.001**
		Treatment	Fixed	1,1295	0.05	0.816
		Rank	Covariate	1,1295	144.83	**<0.001**
		Nest	Random	7,1295	12.19	**<0.001**
GLMM 2.2	Successful begging	Height	Covariate	4,1295	304.36	**<0.001**
		Treatment	Fixed	1,1295	3.36	0.067
		Rank	Covariate	1,1295	2.87	0.090
		Nest	Random	7,1295	16.29	**<0.001**
GLMM 2.3	Successful begging	Position	Covariate	4,1295	287.23	**<0.001**
		Treatment	Fixed	1,1295	1.25	0.263
		Rank	Covariate	1,1295	73.21	**<0.001**
		Nest	Random	7,1295	45.34	**<0.001**
GLMM 2.4	Successful begging	Intensity	Covariate	3,1295	0.29	0.588
		Treatment	Fixed	1,1295	0.82	0.365
		Rank	Covariate	1,1295	143.95	**<0.001**
		Nest	Random	7,1295	19.51	**<0.001**

Nestlings also rose more quickly to beg for food when food was scarce than when it was plentiful (GLMM 3.3b, Table 6, Figure 11c).

All nestlings begged at similar intensities in both conditions of food availability (GLMM 3.4b, Table 6, Figure 11d).

The duration of nestling begging was longer in situations of abundant food, although all nestlings begged for the same amount of time (GLMM 4.1b, Supplementary Table 5).

It was frequent that nestlings beg for food when the male was not coming with prey to the nest (between feeding events). The duration of begging in these periods was longer in small than in large nestlings in both food availability conditions (GLMM 6.1b, Supplementary Table 5). The intensity of begging, however, was similar for all nestlings and for both conditions of food availability (GLMMs 5, Supplementary Table 6).

Table 6. Separated Generalized Linear Mixed Models (GMMM) exploring the effects the treatment (abundance and scarcity) and nestling rank (1-8) on nestling order, height, position and intensity. Models were fitted with Poisson distribution and log link functions. In case of non-significant interaction, the model was performed again without this term. P values were calculated by comparing the complete model against the reduced model, .i.e. without the variable of interest. Significant P-values are shown in bold.

	Dependent variable	**Factors**		**d.f.**	**Chisq**	**P**
GLMM 3.1	Height	Treatment	Fixed	1,1295	1.49	0.221
		Rank	Covariate	1,1295	0.00	**<0.001**
		Treatment*rank	Fixed	1,1294	4.49	**0.034**
		Nest	Random	7,1295	36.82	**<0.001**
GLMM 3.2	Position	Treatment	Fixed	1,1295	3.99	**0.046**
		Rank	Covariate	1,1295	0.00	**<0.001**
		Treatment*rank	Fixed	1,1294	11.19	**<0.001**
		Nest	Random	7,1295	27.05	**<0.001**
GLMM 3.3a	Order	Treatment	Fixed	1,1295	0.29	0.586
		Rank	Covariate	1,1295	0.00	1.000
		Treatment*rank	Fixed	1,1294	0.73	0.392
		Nest	Random	7,1295	1.13	0.288
GLMM 3.3b	Order	Treatment	Fixed	1,1295	6.15	**0.013**
		Rank	Covariate	1,1295	2.31	0.128
		Nest	Random	7,1295	1.19	0.274
GLMM 3.4a	Intensity	Treatment	Fixed	1,1295	0.72	0.395
		Rank	Covariate	1,1295	0.00	1.000
		Treatment*rank	Fixed	1,1294	0.60	0.436
		Nest	Random	7,1295	10.03	**<0.001**
GLMM 3.4b	Intensity	Treatment	Fixed	1,1295	0.12	0.723
		Rank	Covariate	1,1295	0.74	0.387
		Nest	Random	7,1295	10.06	**<0.001**

DISCUSSION

In this study, we hypothesized that food availability in the hoopoe, a species with strong hatching asynchrony, would influence the allocation of food by the female among her nestlings. We predicted that food allocation would be equally distributed between nestlings in situations of food abundance, but with a bias toward large nestlings in situations of scarcity. However, we found that the female preferentially fed the largest nestlings, and that nestling begging success decreased as nestling size was smaller, independently of the food availability. Food limitation made even more marked this difference in nestling begging success. Besides, as a large nestling begged for food, the probability that a smaller nestling would be fed decreased. In situations where food is scarce, it was more frequent that a nestling was fed, the larger nestling was not begging for food. Regarding nestling begging signals, we found that begging intensity did not change among treatments or with nestling size. Conversely, other components of nestling begging related to nestling size and quality changed in situations of food scarcity. Below, we discuss in detail the results obtained from our experimental manipulation of food on the response of nestlings and female hoopoes.

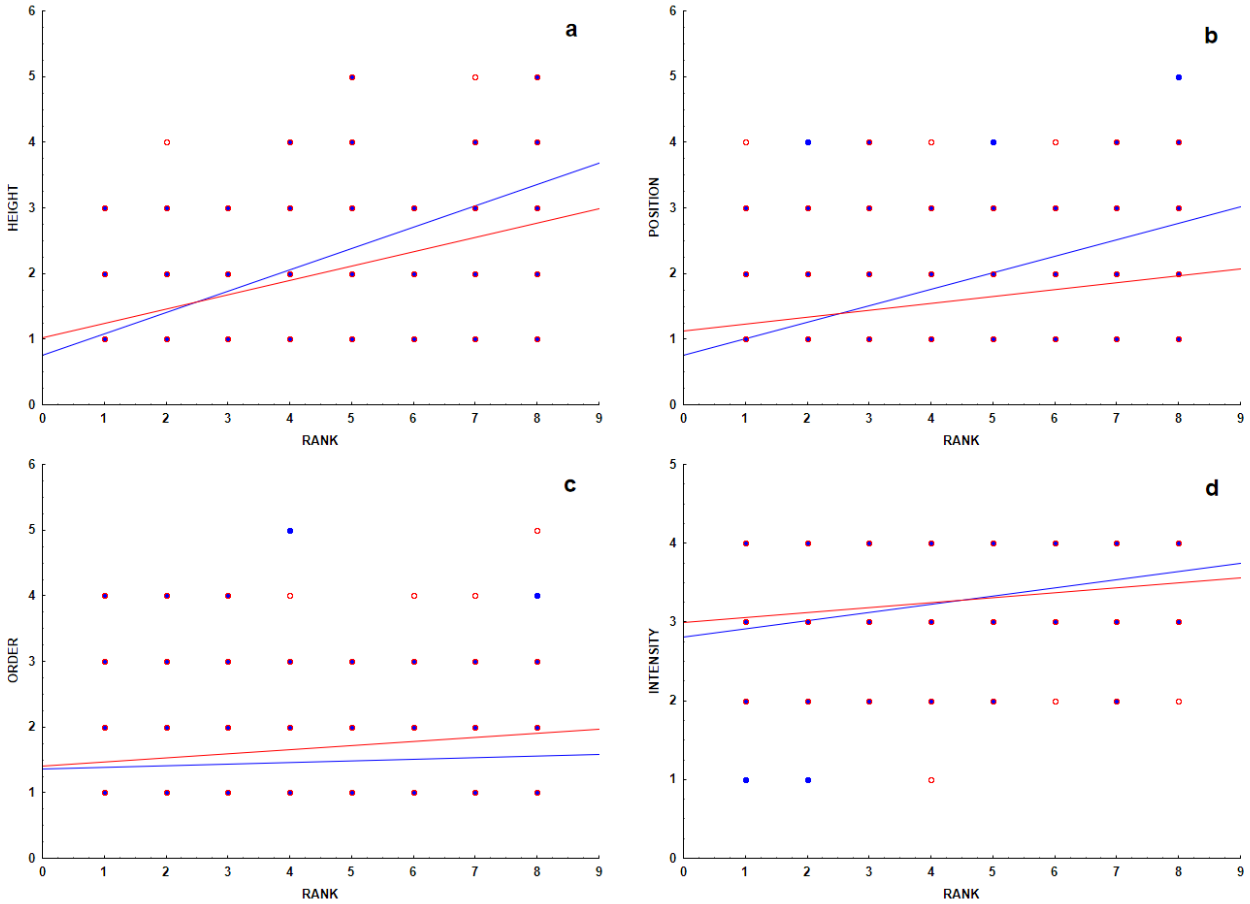

Figure 11. Effects of treatment and nestling rank on begging components (a = height; b = position; c = order; d = intensity). Food abundance is shown in red and food scarcity in blue. Means ± standard errors are shown. Height, position and order are ranges where a lower number implies a higher height, position and order. Intensity is also a range, but a lower number implies lower intensity.

Signalling of nestlings according to their rank and food availability

Nestlings can convey information to their parents about their condition through structural signals (Kilner and Davies 1998; Dugas and Rosenthal 2010), body size cues (Mock et al. 2011; Soler et al. 2022b) and begging displays (Kilner and Johnstone 1997; Gurguis and Duckworth 2022). The intensity of nestling begging is thought to reflect their need, hunger and quality, offering different types of information to parents (Godfray

1991; Royle et al. 2002; Mock et al. 2011) according to different hypothesis (SoN, SoQ and SoH). Thus, if smaller nestlings (i.e., low reproductive value) beg more intensely than larger nestlings (i.e., high reproductive value), it has been suggested that the smaller ones may be signalling their need to the parents (Leonard and Horn 2001), especially in good environments (Caro et al. 2016a). Conversely, if larger nestlings beg more intensely, nestlings may be signalling quality or merit to their parents (Zahavi 1975; Grafen 1990; Cotton et al. 1999; Mock 2016), especially in poor environments (Caro et al. 2016a). In our study, we found that all hoopoe nestlings beg with similar intensities, in both food availability conditions. One possible explanation for this result is that begging intensity would not convey information about offspring condition (need or quality) in the hoopoe. It would be possible that the nestling begging intensity simply expresses nestling hunger (Grodzinski and Lotem 2007; Mock et al. 2011; Mock 2016). Hunger ("short-term need") can be defined as the amount of food needed to achieve satiety (Johnstone and Kilner 2011; Mock et al. 2011). Thus, signals of hunger may convey information about short-term changes in offspring digestive-system fullness (empty to full) (Grodzinski and Lotem 2007; Mock et al. 2011). In our experiment, we only used small prey (fly larvae and pupae) since some of the nestlings were newly hatched or very small and they could have difficulties ingesting or digesting the prey, as proposed by the feeding constraint hypothesis (Slagsvold and Wiebe 2007). In this way, we avoided prey size being a factor affecting the food provided to the smallest nestlings and were able to test the effect of food abundance on female decisions without influence of prey size. With this design, the result that all nestlings beg with similar intensities regardless of whether food was abundant or scarce could be interpreted as evidence that all nestlings were always hungry (Caro et al 2016a). The use of small prey as food source could have caused that the larger nestlings never reach satiety, despite receiving a greater number of prey than their smaller siblings. Since hoopoes only carry one prey per trip, the size of the food item provided in one trip may affect the probability that the nestling that received the prey would be satiated in the next male visit. It has been suggested that a main determinant of breeding success of hoopoes in Switzerland is the availability of molecrickets (Arlettaz et al. 2010b). While there is not any apparent reason why this would be a better food than other insects, probably the main effect of its availability is that molecrickets are big prey that keep large nestlings satiated until the next food item arrive to the nest, thus letting smaller nestlings to get some feedings (this study, Ferrer-Pereira et al. 2023). In the same sense, a small nestling used as a food item when hoopoes cannibalize them (Soler et al. 2022a) may keep a larger nestling satiated for a long while, thus increasing survival prospects of the rest of the siblings.

The experimental food limitation had an effect on components of nestling begging behavior that convey information about nestling quality or size, in accordance to our predictions. Thus, all the nestlings responded to scarcity by starting to beg sooner (upon the arrival of the male in the nest-box) in line with other studies (Smiseth et al. 2003; Porkert and Spinka 2006). In addition, as expected in asynchronous species, the larger nestlings reached a greater height and a position closer to the female than their smaller siblings did when begging (Cotton et al. 1999; Glassey 2000; Moreno-Rueda et al. 2009). Again, this difference was even more pronounced when food was scarce. This effect was due to the larger siblings begging higher and closer to the female, and the smaller siblings begging at lower heights and with less proximity to the female than in situations of food abundance. Furthermore, we found in line with Ferrer-Pereira et al. (2023) study that the probability of small nestlings receiving food decreased if larger nestlings begged for food. Additionally, we found that a successful feeding even if a larger nestling begs for food occurred more frequently in abundance. Conversely, in situations where food is scarce, it is more frequent that if a nestling is fed, the larger nestling was not begging for food. We can speculate that smaller nestlings may choose to expend less energy stretching their necks when larger nestlings display their full physical size potential due to food scarcity (Smiseth and Amundsen 2002; Forbes 2007; Griffith 2007). In this situation, smaller nestlings would have little to gain by increasing their efforts, instead they could divert it and use it later or in functions such as their growth and development (Forbes 2007). In fact, the smallest nestlings begged longer between feeding events. This result could suggest that smaller nestlings may be increasing the duration of their begging to induce the parents to bring more prey, as suggested by Smiseth and Amundsen (2002) or simply showing that they are hungry (Sacchi et al. 2002; Dickens et al. 2008).

Food allocation by females according to chick rank, begging components and food availability

In species with hatching asynchrony and brood reduction, such as hoopoes, there is often a bias towards larger nestlings (Lack 1954; Cotton et al. 1999; Smiseth et al. 2003; Soler et al. 2022b; Wegrzyn et al. 2023). If smaller nestlings are at risk of starvation, parents will feed the larger, better quality nestlings (Mock and Parker 1997; Caro et al. 2016b; Savagian and Riehl 2023) even ignoring begging of smaller nestlings, as occurs in hoopoes (Martín-Vivaldi et al. 1999). We hypothesized that when food is abundant, the allocation of food from females to their nestlings would be more equitable, reducing the preference for larger nestlings. However, our results did not support this hypothesis, as females fed larger nestlings more frequently than the smaller ones, regardless of whether the food was abundant or scarce. A possible explanation could be related to the fact that all the nestlings beg with the same intensity in both conditions of food availability. In our study, the intensity of begging reflects that all the nestlings are hungry and therefore does not provide useful information to the parents about the need or quality of the nestlings (Mock et al. 2011; Caro et al. 2016a). Some studies have proposed that parents in this scenario may obtain information about nestlings condition through body size cues (Mock et al. 2011) as well as from low-cost signals that conveyed size-like information such as begging height (Caro et al. 2016a; Wild et al. 2017). Our results support this hypothesis since those nestlings that reached a greater height, were closer to the female and started begging earlier, were the most likely to be fed. Therefore, it is possible that in a scenario where all nestlings are hungry in both abundance and scarcity conditions, the female allocates food according to nestling rank by using both body size cues and begging components related to nestling size and quality (Mock et al. 2011; Caro et al. 2016a) with no differences between the two feeding conditions.

Another possible explanation for the female allocating prey in a similar way under different conditions of food availability could be because, in hoopoes, the last hatched nestlings is doomed to die, even if there is enough food. In hoopoes, a recent study by Soler et al. (2022a) found evidence that females used their last hatched nestlings to feed older siblings (sibling cannibalism). These authors conducted another supplementation experiment with large prey such as crickets (*Gryllus campestris*) to determine the influence of food availability on brood reduction and sibling cannibalism (Ferrer-Pereira et al. 2023). The experiment started a few days before hatching of the first egg and ended a few days after hatching of the last egg. In this study, food supply did not influence the probability of brood reduction, even using large prey that would satiate the larger nestlings, although the probability of sibling cannibalism was reduced. In a similar setup, food supplementation decreased the begging success of smaller nestlings when they were the only ones begging for food, as the female used those prey for self-feeding (Ferrer-Pereira et al. 2023). Therefore, whether there is scarcity or abundance, the smallest hoopoe nestlings within a brood are neglected by females and tend to die. Other studies in asynchronous species also found that death of smaller nestlings is frequent even if there is enough food for all offspring (Soler and Soler 1996; Brommer et al. 2004; Kontiainen et al. 2010) supporting this hypothesis.

In hoopoes, as in other species with hatching asynchrony, brood reduction occurs in the first days after hatching, when sibling rivalry and nestling demand for food is still low (Martín-Vivaldi et al. 1999; Slagsvold and Wiebe 2007; Ryser et al. 2016). Therefore, the decision to sacrifice nestlings at this early stage reflected female selection to assign care mostly to high-value nestlings and avoid the high cost of investing in nestlings with lower survival prospects. On the contrary, Ryser et al. (2016) found that at a later stage (11-15 days after hatching of the first egg), just after brood reduction had occurred, the female hoopoe fed the smaller surviving hungrier nestlings and the male hoopoe fed the larger, more competitive nestlings, thus maintaining the whole size-adjusted brood. As the age of the offspring increases, the costs and benefits of both the offspring begging and parental provisioning of food may change (Royle et al. 2002; Hinde et al. 2010). Thus, it would be possible that female hoopoes conform to the quality-signal hypothesis until the smallest nestlings die and then follow the need-signal hypothesis to get the rest of the brood to fledging (Bowers et al. 2019).

In conclusion, our experiment has shown that in the early nestling period, before brood reduction has occurred, female hoopoes keep a strategy of feeding preferentially the larger, higher ranked siblings in the size hierarchy caused by hatching, even in conditions of *ad libitum* food supply. Begging by nestlings reflects hunger levels and at this stage, only satiation of large nestlings let smaller nestlings to receive food, but this rarely happen when available prey are of small size, even if they are available ad *libitum*. These results suggest that carrying large prey could satiate larger nestlings, increasing the survival prospects of small ones and hence increasing fledging success.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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).

AUTHORS CONTRIBUTION

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

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SUPPLEMENTARY MATERIAL

Supplementary Table 5. Generalized Linear Mixed Models (GLMMs) exploring the effects of treatment (abundance and scarcity) and nestling rank (1-8) on nestling begging duration. The "only nestlings fed" includes the feeding events where only nestlings were fed; and the "between each feeding event" includes the events where nestlings beg, between feeding events. Models were fitted with a Gaussian distribution and log link functions after log transformation. We included models without non-significant interaction. Significant P-values are shown in bold.

	Dependent variable	**Factors**		**d.f.**	**F**	**P**
Only nestlings fed						
GLMM 4.1a	Duration of begging	Treatment	Fixed	1,55	2.61	0.111
		Rank	Covariate	1,55	3.82	0.055
		Treatment*rank	Fixed	1,55	0.33	0.568
		Nest	Random	7,55	1.68	0.131
GLMM 4.1b	Duration of begging	Treatment	Fixed	1,56	4.77	**0.033**
		Rank	Covariate	1,56	3.87	0.054
		Nest	Random	7,56	1.70	0.126
Between each feeding event						
GLMM 6.1a	Duration of begging	Treatment	Fixed	1,55	0.04	0.826
		Rank	Covariate	1,55	16.11	**<0.001**
		Treatment*rank	Fixed	1,55	0.17	0.679
		Nest	Random	7,55	6.02	**<0.001**
GLMM 6.1b	Duration of begging	Treatment	Fixed	1,56	0.06	0.794
		Rank	Covariate	1,56	16.35	**<0.001**
		Nest	Random	7,56	6.11	**<0.001**

Supplementary Table 6. Generalized Linear Mixed Models (GLMM) exploring the effects of treatment (abundance and scarcity) and nestling rank (1-8) on nestling intensity. The “between each feeding event" includes the events where nestlings beg, without there being a feeding event. Models were fitted with Poisson distribution and log link functions We performed new models without non-significant interactions. P values were calculated by comparing the complete model against the reduced model, .i.e. without the variable of interest. Significant P-values are shown in bold.

	Dependent variable	**Factors**		**d.f.**	**Chisq**	**P**
Between each feeding event						
GLMM 5.1	Intensity	Treatment	Fixed	1,1059	0.73	0.391
		Rank	Covariate	1,1059	0.00	1.000
		Treatment*rank	Fixed	1,1058	0.06	0.804
		Nest	Random	7,1059	0.00	1.000
GLMM 5.1b	Intensity	Treatment	Fixed	1,1059	1.53	0.215
		Rank	Covariate	1,1059	1.81	0.178
		Nest	Random	7,1059	0.00	1.000

CAPÍTULO III. *Fledgling discrimination in the hoopoe, a potential host species of the great spotted cuckoo*

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FLEDGLING DISCRIMINATION IN THE HOOPOE, A POTENTIAL HOST SPECIES OF THE GREAT SPOTTED CUCKOO

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ABSTRACT

Obligate brood parasites lay their eggs in nests of other species, with host parents bearing the cost of raising their offspring. These costs imposed on hosts select for the evolution of host defenses against parasitism at all stages of the reproductive cycle. The most effective defense is egg rejection at early stages of the breeding cycle, with later-stage defenses (nestling and fledgling discrimination) being less common. In this study, we tested whether the hoopoe (*Upupa epops*), a potential host of the great spotted cuckoo (*Clamator glandarius*) without egg rejection ability, presents defenses after the egg stage. We experimentally parasitized hoopoe nests with great spotted cuckoo nestlings creating mixed broods (with hoopoe and cuckoo nestlings) and broods with only cuckoo nestlings and measured parental feeding behavior and survival of nestlings and fledglings of both species. Cuckoo fledglings were fed fewer often than hoopoe fledglings in mixed broods, and adults approached more often to feed hoopoe fledglings than cuckoo fledglings. Consequently, the survival of cuckoo fledglings in both mixed and only-cuckoo-broods, was significantly lower than that of hoopoe fledglings. These results suggest that hoopoes would discriminate great spotted cuckoo fledglings, with or without direct comparison with their own fledglings. However, the survival of some cuckoos suggests that hoopoes have not reached highly efficient defenses so, other life history traits hindering parasitism by cuckoos may explain low parasitism rates and low levels of defenses in this species.

Keywords: Brood parasitism, *Clamator glandarius*, coevolution, fledgling discrimination, host defenses, *Upupa epops*

SIGNIFICANCE STATEMENT

Brood parasites lay their eggs in nests of other species, tricking hosts into raising their parasitic offspring. However, hosts may fight back impeding successful parasitism by developing defences at any of the stages of their breeding cycle. We investigated why the hoopoe is not parasitized by the great spotted cuckoo despite this potential host apparently does not show such anti-parasitic defenses. We found that hoopoes have evolved the less common host defense: discrimination of parasite fledglings, even in the absence of their own fledgling for comparison. Our study supports the idea that discrimination during the later stages of the nesting cycle (i.e. nestling and fledgling periods) may be more common that previously assumed.

INTRODUCTION

Obligate brood parasite females lay their eggs in the nests of other species (a type of parental-care parasitism: Roldán and Soler 2011). This means that brood parasites evade all parental care, fooling hosts into raising their parasitic offspring and thus diverting resources away from their own nestlings (Soler 2017a). Brood parasitic nestlings usually outcompete host nestlings because they hatch earlier, are larger and beg at a higher intensity than host nestlings (Soler 2017b). Therefore, brood parasitism imposes important fitness costs on hosts, reducing their reproductive success to nearly zero in many cases (Moskát et al. 2017). These severe costs imposed by brood parasites on hosts select for the evolution of host defenses, which in turn drives selection for the brood parasite to evolve counter-defenses, triggering improved host defenses, further parasitic adaptations and so on (Davies 2000; Soler and Soler 2000; Stokke et al. 2005; Feeney et al. 2014; Soler 2014). These reciprocal evolutionary changes, so-called coevolutionary arms race, have proven to be excellent systems for understanding coevolution, in which some of the clearest experimental demonstrations of a coevolutionary process have been reported (e.g. Brooke and Davies 1988; Soler and Møller 1990).

Despite egg-rejection being the most common and effective host defense against brood parasites, nowadays it is widely accepted that adaptations and counter-adaptations may occur at any stage of the breeding cycle; moreover, defenses at an early stage can influence the evolution of subsequent defenses and counter-defenses at later stages (Davies 2011; Feeney et al. 2014; Soler 2014, 2017a). An efficient line of defense at an earlier stage of the breeding cycle would be more beneficial because costs of brood parasitism accumulate as the breeding cycle advances (Britton et al. 2007; Davies 2011; Feeney et al. 2014; Soler 2014, 2017a). Such early lines of defense would prevent the evolution of later-stage defenses (nestling and fledgling discrimination) which may explain why the latter is less common than the former (frontline defenses and egg rejection). Nevertheless, when effective defenses have not evolved at earlier stages, a host defense at a later stage of the breeding cycle would be more likely to evolve (Britton et al. 2007; Feeney et al. 2012, 2014; Soler 2017a).

The great spotted cuckoo (*Clamator glandarius*) is a non-evictor specialist brood parasite which, in the Palearctic, lay most of their eggs in the nests of its main host: the common magpie (*Pica pica*), with carrion crow (*Corvus corone*) being its secondary host.

Other corvid and non-corvid species are also parasitized in some populations (Soler 1990; Johnsgard 1997; Erritzøe et al. 2012). The coevolutionary relationships between the great spotted cuckoo and its hosts are well studied (Soler and Soler 2000; Roldán et al. 2013a; Bolopo et al. 2015). This brood parasite chooses brood-reducing host species that selectively feed larger nestlings (Soler 2001, 2002, 2017b). The appearance of great spotted cuckoo eggs does not mimic that of the host eggs (Soler et al. 2003), and there is no evidence for begging-call mimicry of hosts by great spotted cuckoo nestlings either (Roldán et al. 2013b). The average body mass of cuckoo females is 152 g and that of males is 157 (Macías-Sánchez et al. 2013). The magpie is slightly larger than the great spotted cuckoo while the carrion crow is more than twice the weight of the brood parasite (Soler et al. 2002). When parasitizing the magpie, the breeding success of the parasite is very high and that of the host very low (on average, only 0.7 magpie nestlings fledge per parasitized nest compared to 3.6 magpie nestlings that fledge in unparasitized nest (Soler et al. 2002)). Conversely, the cost of brood parasitism is lower in the carrion crows (on average 1.6 carrion crow nestlings fledge per parasitized nest compared to 3.1 in unparasitized nests (Soler et al. 2002)); the larger size of host nestlings makes cuckoo nestlings less efficient in obtaining food from their foster parents than their larger host nest mates (Bolopo et al. 2015).

The hoopoe (*Upupa epops*) is a hole-nesting bird with biparental care that presents a marked asynchronous hatching pattern (Cramp 1998; Martín-Vivaldi et al. 1999; Hoffmann et al. 2015; Ryser et al. 2016; Hildebrandt and Schaub 2018). It is a medium-sized bird, with a body mass ranging from 76.6 g in males to 73.1 g in females (Hildebrandt and Schaub 2018). The hoopoe could be a suitable host species for the great spotted cuckoo because the hoopoe follows a brood-reduction strategy, as hosts of the great spotted cuckoo do (Soler 2017b), and feeds its nestlings and fledglings with insects, an appropriate diet for this brood parasite. Cavity-nesting species have been traditionally considered unsuitable common cuckoo (*Cuculus canorus*) hosts (Davies and Brooke 1989b), because the small size of the nest entrance prevents the female cuckoo from laying her eggs effectively (Davies and Brooke 1989a; Moreras et al. 2021) or the young cuckoos leaving the nest at fledging time (Löhrl 1979). However, the cavities used by hoopoes many times have a larger entrance that may allow the entry of great spotted cuckoo females. In fact, the great spotted cuckoo can use other hole-nesters of medium size as hosts like jackdaws (*Corvus monedula*) and choughs (*Pyrrhocorax pyrrhocorax*) in Spain (Soler 1990) or Cape starlings (*Lamprotornis nitens)* and African pie starlings (*Spreo bicolor*) in South Africa (Johnsgard 1997; Erritzøe et al. 2012). However, to the best of our knowledge, there is only one record of possible hoopoe parasitism by the great-spotted cuckoo in Spain. In that record, hoopoe adults were observed feeding a great-spotted cuckoo fledgling in the wild (Amor-García et al. 2020). Even though the authors did not provide direct evidence that hoopoes reared this cuckoo nestling in their own nest, this observation points to the possibility of hoopoes being a potential host for this brood parasite.

Potential host defenses against brood parasitism in the hoopoe have not been thoroughly studied. Although appropriate egg-recognition experiments have not been performed in the hoopoe, experiments with other purposes that needed the introduction of foreign eggs in natural nests (Díaz-Lora et al. 2021) or introduced collared dove (*Streptopelia decaocto*) eggs and plaster model eggs in captivity nests (MM-V et al., unpublished data), never resulted in egg rejection. Thus, we can assume that egg rejection has not evolved in this potential great spotted cuckoo host species. In the Guadix area (a population located in southern Spain), the great spotted cuckoo reaches a high breeding density with parasitism of four different host species (Soler 1990). Moreover, hundreds of hoopoe nests have been monitored, in both natural cavities and nest-boxes (Martín-Vivaldi et al. 1999, 2006, 2009; Ruiz-Rodríguez et al. 2013; Díaz-Lora et al. 2019; Díaz-Lora et al. 2021). In spite of these favorable traits of the hoopoe as a host and the intense monitoring of both reproductive hoopoes and great spotted cuckoos, no trace of great spotted cuckoo parasitism in the hoopoe was found in our study area.

This observation suggests that the hoopoe would have already evolved efficient defenses against brood parasitism during the nestling or during the fledging periods, which could prevent successful parasitism by the great spotted cuckoo. This possibility is quite plausible given that nowadays it is broadly accepted that adaptations and counter adaptations in brood parasites and their hosts can evolve at all phases of the nesting cycle (Soler 2014). This is the main objective of our study: to determine whether the hoopoe, a potential host of the great spotted cuckoo without egg rejection ability, presents defenses after the egg stage. We explored this possibility by proposing two mutually exclusive hypotheses. First, the hoopoe may have evolved nestling discrimination, a potential host defense less common than egg discrimination, which is predicted to occur more frequently when an efficient adaptation at an earlier stage has not evolved (the blocking model: Britton et al. 2007). In fact, most of the hosts that discriminate parasite nestlings do not discriminate parasite eggs (Grim 2017). As the hoopoe does not have the ability to recognize foreign eggs, our first hypothesis is that the hoopoe has evolved nestling discrimination. Our second hypothesis is that fledgling discrimination could be the host defense responsible for preventing success of great spotted cuckoo parasitism on the hoopoe. However, according to the blocking model (Britton et al. 2007), it could only evolve if efficient nestling discrimination has not evolved. Furthermore, the great spotted cuckoo is non-killer brood parasite, giving the possibility to foster parents to observe both the parasite and their own nestlings (both species look quite different from each other). This comparison when they share the same nest and later out of the nest, may be an important cue to favor nestling and/or fledgling discrimination (Davies and Brooke 1988; Lotem 1993).

The main aim of this study is to test experimentally these two hypotheses using a population of hoopoes maintained in captivity. We experimentally created mixed broods with hoopoe and cuckoo nestlings and analysed the parental feeding behaviour to nestlings (feeding rate) and fledglings (feeding rate and approach rate). This experimental design allows us to analyse whether adult hoopoes are able to discriminate cuckoo nestlings when they can directly compare them with their own nestlings. With the same objective, we created only-cuckoo-broods, i.e. cuckoo nestlings raised without hoopoes, to analyze the ability of the parents to discriminate cuckoos but without any possibility of comparison.

Our first hypothesis predicts that great spotted cuckoo nestlings introduced in hoopoe nests would be fed at a lower rate (Prediction 1) and would present a higher mortality rate (Prediction 2) than hoopoe nestlings and cuckoo nestlings from only-cuckoo-broods. The second hypothesis predicts that cuckoo fledglings from mixed broods would be fed at a lower rate than hoopoe fledglings and cuckoo fledglings from only-cuckoo-broods (Prediction 3) and that cuckoo fledglings from mixed broods would present a higher mortality rate (Prediction 4) than hoopoe fledglings and cuckoos from only-cuckoo-broods. If adults have the capacity to discriminate cuckoos, we predict that: hoopoe adults would approach to hoopoe fledglings and cuckoo fledglings from only-cuckoo-broods to feed more often than cuckoo fledglings from mixed broods (Prediction 5) and that cuckoo fledglings would be fewer likely to get food than hoopoe fledglings, when they approached the adults (Prediction 6).

MATERIALS AND METHODS

Study Area

This study was performed during the 2013 breeding season (March-July) in a population of hoopoes maintained in captivity since 2008. During autumn and winter, hoopoes were maintained, separated by sex, in facilities located at the University of Granada (southern Spain). In spring, the captive pairs were housed in independent cages (3 m × 2 m × 2 m) installed outdoors in a pine forest in the Hoya de Guadix (37° 21' N, 003° 05' W, Granada province). This area is a high-altitude plateau (approx. 1000 m a.s.l.) with cereal crops, groves of almond trees (*Prunus amygdalus*) and some areas with dispersed holm-oak trees (*Quercus rotundifolia*) and reforested pine forests. We used 20 cages spaced at 50m from each other to avoid interactions between pairs and ensure successful breeding. All cages had access to soil and were equipped with a roof that provided shadow, a cork nest box (40 cm x 20 cm x 20 cm, 5.5 cm of hole diameter) and an internal roof that protected feeders from sun and rain. Great spotted cuckoo nestlings were collected from magpie nests found in the surroundings. The great spotted cuckoo is a common species in this area, involved in a high incidence of parasitism on magpie hosts with 56.8% of magpie nests parasitized by the great spotted cuckoo during the period 2008 - 2012 (Soler et al. 2014a).

Experimental design

Hoopoe breeding pairs were established in March, when one male and one female were randomly paired in each cage. Hoopoes were provided with live food (crickets, fly larvae) and meat (beef heart vitamin-enriched) ad libitum. Cages were visited daily to ensure hoopoes care and maintenance and to record laying date, clutch size, and hatching date. At the same time, we searched for magpie nests during nest-building or egg-laying phases so brood parasitism by the great spotted cuckoo was detected soon to be able to calculate hatching date accurately. Close to hatching, we visited nests daily in order to detect cuckoo hatchlings.

We created two types of experimental nests: mixed broods with one cuckoo and a variable number of hoopoe nestlings (from 1 to 5 hoopoe nestlings); and only-cuckoo-broods with one or two cuckoo nestlings. The variable number of hoopoe nestlings is within the natural range of brood sizes in the wild (Martín-Vivaldi et al. 1999). In mixed broods, cuckoo nestlings were introduced 1 to 2 days younger than the first hatched hoopoe nestling. This allowed both species to reach a similar weight at the start of the nestling period, in order to ensure survival of nestlings of both species until fledging. Cuckoo nestlings are larger than hoopoe nestlings, reaching an average weight at hatching of 7.8 g compared to 3.5 g for hoopoe nestlings (Soler and Soler 1991; Hildebrandt and Schaub 2018). At the end of the nestling period, this difference between species is greater (the average weight is 133.7 g in cuckoo nestlings; and 69.6 g in hoopoe nestlings (Soler and Soler 1991; Hildebrandt and Schaub 2018)). Furthermore, the introduction of cuckoo nestlings younger than hoopoes matches the nesting period of both species, since cuckoos spend 19-25 days and hoopoes 27.1 days in the nest (Soler and Soler 1991; Martín-Vivaldi et al. 1999). In only-cuckoo-broods, cuckoo hatchlings 1- or 2-days-old were introduced in hoopoe clutches with a total hatching failure. The viability of hoopoe eggs was monitored using an Egg Buddy Digital Heart Monitor (Avitronics, UK). This allowed us to introduce the cuckoo nestlings on the expected hatching date of the hoopoe eggs, ensuring acceptance by the hoopoe female. We removed failed hoopoe eggs after nestling introduction. The reason for using failed hoopoe clutches to obtain only-cuckoo-broods and keeping all hoopoe nestlings in mixed broods follows ethical considerations. On the one hand, we could not move hoopoe nestlings to other nests due to limitations in the number of cages and lack of synchrony in laying date between hoopoe nests. On the other hand, we were not going to sacrifice any hoopoe nestling in the experimental procedure. Cuckoo nestlings were transported in an artificial cotton nest and kept at a temperature between 25 and 30 °C (for further details see Ibáñez-Álamo et al. 2012). No cuckoo died during the transport process. We created 8 mixed broods and 7 only-cuckoo-broods (4 broods with two cuckoo nestlings and 3 broods with only one cuckoo nestling).

We analyzed parental feeding behavior during the nestling period by video recording into nest boxes, and during the fledgling period by direct observations of fledglings in the cage. Nest boxes were video-recorded using micro-cameras (KPC-S500, eSentia Systems Inc., Baton Rouge, LA, USA) connected to video recorders. Further details on the filming procedure can be found in Martín-Gálvez et al. (2011). The observations of fledglings were performed using a hide located about three meters from the cage.

During the nestling period, both mixed and only-cuckoo-broods were filmed once when cuckoo nestlings were between 13 and 18 days old. We considered this range because in the great spotted cuckoo the feathers appear in the majority of the quills between days 12 and 13 (Soler and Soler 1991) and the crest is already developing in the hoopoe by day 14 (Kristin 2001). Therefore, at these ages the differences in development and plumage color between the two species would be more visible, making recognition easier. Recordings lasted approximately two hours and a half and started half an hour after sunrise (the most active period of adult hoopoes) and after the daily food provision to the cage. Information containing age and weight of the nestlings (cuckoos and hoopoes) as well as brood size before video-recordings is provided in Supplementary Table 7. In mixed broods with more than one hoopoe nestling, hoopoe nestlings were randomly marked individually with blue points on the crown with permanent marker (except one nestling that remained unmarked) in order to identify the individual fed in each food provisioning event. There is no reason to expect that the presence of the blue dot might affect parental preference for a hoopoe nestling. Therefore, we decided not to mark the cuckoo which is easily distinguished from hoopoes. In only-cuckoo-broods with two cuckoo nestlings, cuckoo nestlings were distinguishable from each other by size, so we did not mark them either. The parental food delivery was filmed in 8 nest boxes of mixed broods and 6 of only-cuckoo-broods (one cuckoo from a single only-cuckoo-brood died a few days after the beginning of the experiment). We lost some video recordings because one of the videorecorders failed during experimental procedures, leaving us with 5 recordings of mixed broods and 5 of only-cuckoo-broods (Supplementary Table 8). The feeding rate to each nestling (feedings per hour) was calculated as the ratio of feedings events per recording hours.

During the fledgling period, the observations started on the first day that all individuals were outside the nest. The observations lasted approximately two hours and were performed half an hour after sunrise, after the daily food provision to the cage. In mixed broods, the cuckoo fledgling usually left the nest box a few days before the hoopoe fledglings, and hoopoe fledglings left the nest boxes depending on their age, starting from the oldest to youngest nestlings in consecutive days. In cuckoo broods with two fledglings, both individuals left the nest box at the same time.

In each feeding event, we annotated the identity of the fledgling. In mixed broods, we marked the tarsus of the hoopoe fledglings with a red and blue permanent marker to distinguish them from each other. However, it was not always possible to assign feedings to particular hoopoe fledglings in mixed broods due to the high speed of the feeding events. Therefore, the feeding rate to hoopoes in a family was calculated as the number of feedings to all hoopoe fledglings divided by the number of hoopoe fledglings and by the number of hours. In only-cuckoo-broods, we distinguished one fledgling from another by its size and position in the cage. The feeding rate per cuckoo was calculated in a similar way in cases where two cuckoo fledglings were in the cage. The number of observations per nest varied among nests with a range of 1-4 observations (Supplementary Table 9), so we averaged feeding rates of the different observations of nests. Information containing age of the fledglings (cuckoos and hoopoes) as well as brood size during each observation event is provided in Supplementary Table 9.

We also annotated the approaching strategy of parents and fledglings. The adult approach rate is a subsample of the feeding rate in which an adult hoopoe approached the fledgling and fed it per hour. Fledgling approach rate is the number of times that hoopoe/cuckoo fledglings approached an adult hoopoe begging for food per hour. In this sense, we also distinguished between successful (when fledglings approached adults and were fed) from unsuccessful (when fledglings approached adults and were not fed) approaches.

In the fledgling phase we observed only six mixed broods since in one case the cuckoo died the day after leaving the nest and, in another, the two hoopoe fledglings died and only the cuckoo fledgling survived. In only-cuckoo-broods, feeding behavior was observed in five broods since one brood was lost to predation by a fox (*Vulpes vulpes*) entering the cage by burrowing under the wire mesh. This incident happened before any observation could be performed (Supplementary Table 8).

It was not possible to record data blind because our study involved focal animals in the field.

The period of time during which the cuckoo fledglings were observed to record their survival lasted from day they left the nest box until they reached the post-fledgling independence (when they could feed themselves). The post-fledgling dependence period ranged from 40 to 64 days which is within the range found by Soler et al. (1994) in the wild (25-59 days).

We released the surviving cuckoos in the area of Guadix at the end of July, since the fledglings usually leave the breeding area in the second week of August, to start their migration towards the wintering areas in Subsaharian Africa (Soler et al. 1994).

Statistical analyses

Feeding rate and approach rate fitted a Gaussian distribution after log transformation (Kolmogorov–Smirnov $P > 0.20$). Therefore, any reference to feeding rate or approach rate refers to the log-transformed variable. In all cases, all dependent variables were homoscedastic ($F < 1.61$; $p > 0.232$), validating the use of parametric tests.

In the nestling and fledgling periods and for mixed broods, we used a General Linear Mixed Model (GLMM) exploring differences in feeding rate (dependent variable) between hoopoe and cuckoo nestlings (species as a fixed factor). Nest identity was included as a random effect. In addition, we explored if cuckoos received different feeding rates (dependent variable) depending on their experimental broods (fixed factor: cuckoos raised in mixed broods versus cuckoos raised in only-cuckoo-broods) and brood size as a covariate by means of a General Linear Model (GLM).

To test adult approach rate in mixed broods in the fledgling period, we used a GLMM where the adult approach rate was used as a dependent variable, species as a fixed factor and nest identity as a random effect. To test whether hoopoe adults approached cuckoo fledglings more often when they are raised in mixed broods compared to only-cuckoo-broods, we used a GLM where adult approach rate was used as a dependent variable, the type of experimental brood as a fixed factor and brood size as a covariate.

In order to establish whether cuckoo fledglings were fewer likely to be fed than hoopoe fledglings when they approached the adults, we used a GLMM, where the fledgling approach rate (dependent variable) was calculated separately for successful and unsuccessful approaches (fixed factor) for each species (fixed factor) and controlled by nest identity as a random effect.

To analyze the survival of the cuckoo, we considered that a nestling survived the nestling period when it left the nest box (0 = died before left the nest; 1 = successfully left the nest). Similarly, fledgling survival is the survival since the moment they left the nest until the end of the dependency period (40-64 days after fledging; 0 = died; 1 = survived). To analyze the probability of survival in mixed broods in both the nestling period and the fledgling period, we used a Generalized Linear Model (GLZ), where the probability of survival (binomially distributed response variable) depended of the species identity (explanatory variable; fixed factor) and the nest identity was included as a random effect. In a second model, we used a Generalized Linear Model (GLZ), where the probability of survival (binomially distributed response variable) of the cuckoo differed between type of experimental broods (raised in mixed or only-cuckoo-broods; fixed factor) and the brood size was included as a covariate both in the nestling period and in the fledgling period. Statistical analyses were performed in STATISTICA 12.0 (Statsoft Inc., OK, USA).

RESULTS

Nestling period

In mixed broods, feeding rate was similar between cuckoo and hoopoe nestlings (species, $F_{1,11} = 0.76$, $p = 0.403$; nest identity, $F_{4,11} = 8.78$, $p = 0.001$**;** Figure 12a).

The feeding rate of the cuckoo nestlings was similar when reared in only-cuckoo-broods or in mixed broods (experimental nest, $F_{1,10} = 0.73$, $p = 0.412$; brood size, $F_{1,10} = 2.99$, $p = 0.114$; Figure 12b).

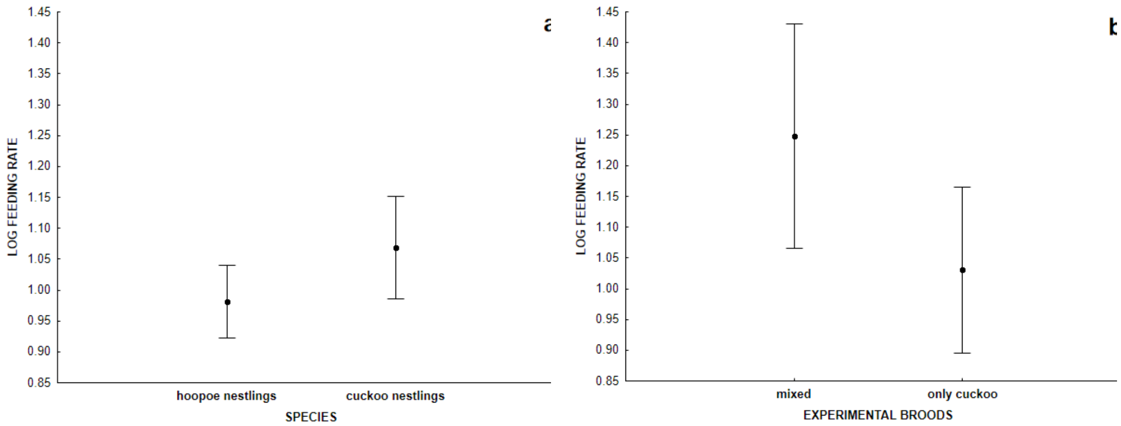

Figure 12. Comparisons of feeding rates by adult hoopoes to: (a) hoopoe (*Upupa epops*) and great spotted cuckoo (*Clamator glandarius*) nestlings raised in mixed broods; and (b) nestlings of great spotted cuckoo raised in mixed broods and in only-cuckoo-broods. The feeding rate of each nestling was calculated as the logarithm of the number of feedings they received divided by the recorded hours. Means ± standard errors are shown.

Fledgling period

In mixed broods, cuckoo fledglings received fewer feedings than hoopoe fledglings (species, $F_{1,5} = 6.70$, $p = 0.048$; nest identity, $F_{5,5} = 0.90$, $p = 0.543$; Figure 13a). Moreover, cuckoo fledglings from mixed broods received fewer feedings than those from only-cuckoo-broods (experimental broods; $F_{1,8} = 11.73$, $p = 0.009$; brood size, $F_{1,8} = 3.55$, $p = 0.096$; Figure 13b).

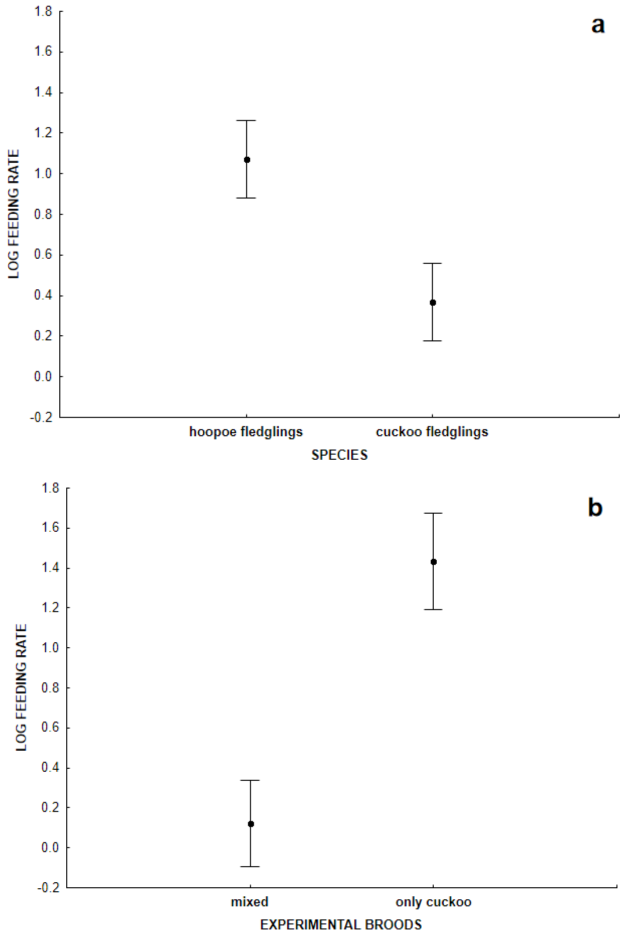

Figure 13. Comparisons of feeding rates by adult hoopoes (a) to hoopoe (*Upupa epops*) and great spotted cuckoo (*Clamator glandarius*) fledglings in mixed broods (raised in the same cage); and (b) to fledglings of great spotted cuckoo raised in mixed broods and in only-cuckoo-broods (cages only with cuckoo fledglings). The feeding rate was calculated as the logarithm of the number of feedings to all hoopoe fledglings divided by the number of hoopoe fledglings and by the number of observation hours. In only-cuckoo-broods, the feeding rate per cuckoo was calculated in a similar way. Means ± standard errors are shown.

Approaching preferences

In mixed broods, hoopoe adults approached more often to feed hoopoe fledglings than cuckoo fledglings (species, $F_{1,5} = 28.46$, $p = 0.003$; nest identity, $F_{5,5} = 2.59$, $p = 0.159$; Figure 14a). In addition, hoopoe adults approached more often to feed cuckoo fledglings from only-cuckoo-broods than cuckoo fledglings from mixed broods (experimental broods, $F_{1,8} = 6.28$, $p = 0.036$**;** brood size, $F_{1,8} = 0.002$, $p = 0.969$; Figure 14b).

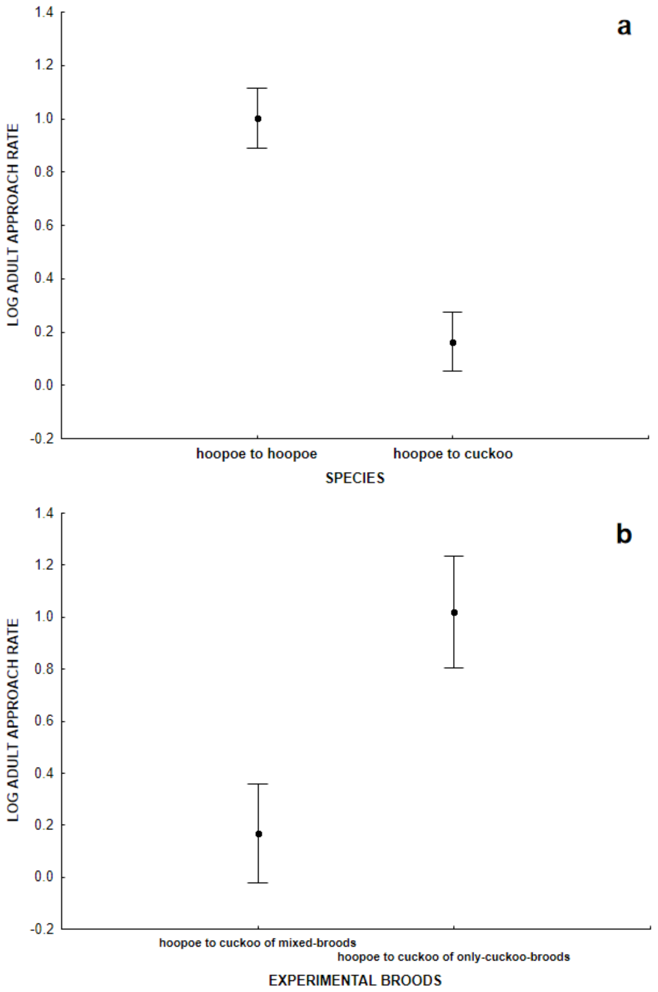

Figure 14. Adult approach rates taking into account only when adult hoopoes approached to (a) great spotted cuckoo (*Clamator glandarius*) and hoopoe (*Upupa epops*) fledglings raised in mixed broods, and (b) great spotted cuckoo fledglings raised in mixed and only-cuckoo-broods. The adult approach rate was calculated as the logarithm of the number of feedings to all hoopoe fledglings divided by the number of hoopoe fledglings and by the number of observations. In only-cuckoo-broods, the adult approach rate per cuckoo was calculated in a similar way. Means ± standard errors are shown.

In mixed broods, differences between successful and unsuccessful fledgling approach rate were similar for both species (see interaction term: successful/unsuccessful approaches, $F_{1,15} = 4.06$, $p = 0.062$; species, $F_{1,15} = 0.49$, $p = 0.495$; interaction term, $F_{1,15} = 2.48$, $p = 0.136$; nest identity, $F_{5,15} = 0.51$, $p = 0.676$; Figure 15). However, unsuccessful approach rate in cuckoo fledglings was significantly higher than their successful approach rate (LSD, $p = 0.023$; Figure 4). In contrast, no differences were found between successful and unsuccessful approach rate in fledgling hoopoes (LSD, $p = 0.759$; Figure 15).

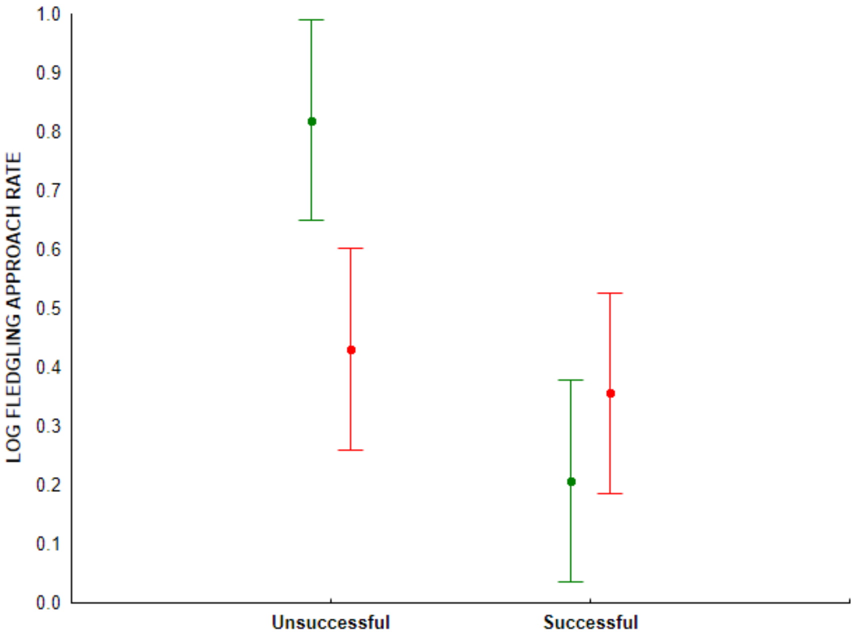

Figure 15. Comparisons of fledgling approach rates of hoopoe fledgling (*Upupa epops* – in red) and great spotted cuckoo fledgling (*Clamator glandarius* – in green) in mixed broods, distinguishing successful approach events (when fledglings approached adults and were fed) from unsuccessful approach events (when fledglings approached adults and were not fed). Fledgling approach rate was calculated as the logarithm of the number of times hoopoe/cuckoo fledglings approached an adult begging for food per hour (regardless of whether or not they were fed). Means ± standard errors are shown.

Survival

In mixed broods, the survival of hoopoe and cuckoo nestlings during the nestling period was similar (species, $x^2_1 = 1.90$, $p = 0.168$; nest identity, $x^2_7 = 0.01$, $p = 0.999$). Nevertheless, survival was significantly lower for cuckoos than for hoopoes in the fledgling period (species, $\chi^2_1 = 10.57$, $p = 0.001$; nest identity, $x^2_7 = 0.01$, $p = 0.999$; Figure 16).

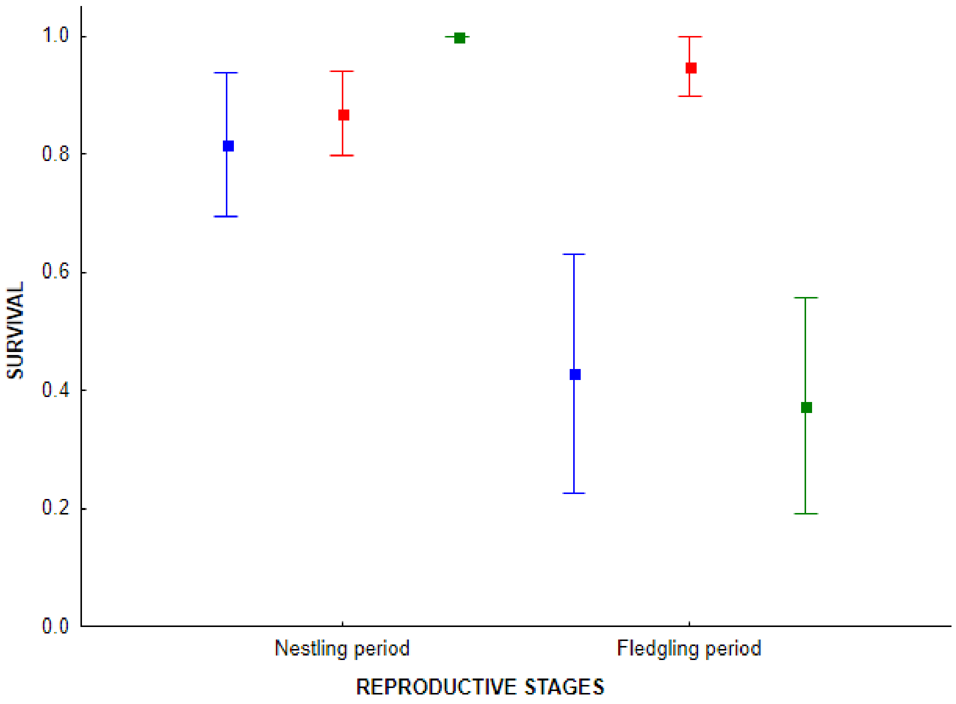

Figure 16. Probability of survival of hoopoes (*Upupa epops* – in red) and great spotted cuckoo (*Clamator glandarius*) both raised in mixed broods (nestling cuckoo raised with hoopoe nestlings -in green) and in only-cuckoo-broods (cuckoos raised alone in hoopoe nests – in blue), during the nestling and the fledgling periods. Means ± standard errors are shown.

The survival of cuckoo fledglings raised in mixed or only-cuckoo-broods was similar during the nestling period (experimental brood, $x^2_1 = 0.29$, p = 0.593; brood size, $x^2_1 = 0.58$, p = 0.445), and during the fledgling period (experimental brood, $x^2_1 = 0.63$, p = 0.425; brood size, $x^2_1 = 0.86$, p = 0.352).

Nestling survival of the great spotted cuckoo

Eighty-eight percent of cuckoos nestlings (15 up to 17) survived the nestling phase, successfully leaving the nestbox.

Survival of great spotted cuckoo and hoopoe fledglings

Survival of cuckoo fledglings (those fledglings that reached post-fledgling independence), including both experimental broods, was 6 out 15 (40%). Separately, 3 out of 7 cuckoo fledglings survived in only-cuckoo-broods (42.86%), while 3 out of 8 cuckoo fledglings survived in mixed broods (37.50%). Survival of hoopoe fledglings was 19 out 20 (95%).

Weight and age of great spotted cuckoo fledglings at death

All the cuckoo fledglings that died showed signs of undernourishment, weighing at death from 60 g to 103 g, although this information was only collected for 5 cuckoos out of 9 (Supplementary Table 8). Cuckoo fledglings died between 28 and 62 days of age (n = 9; Supplementary Table 8).

DISCUSSION

Brood parasitic cuckoos use only an extremely low proportion of available potential host species (Davies 2000; Martín-Vivaldi et al. 2013). Many of these species present a high ability of egg recognition and rejection, which preclude successful parasitism. However, a high percentage of potential host species lack egg rejection (38.5%: Soler 2014). Why then are they not parasitized? A possible answer would be that hosts have evolved an efficient defense at some of the other stages of the breeding cycle: before laying, or during nestling or fledgling periods (Feeney et al. 2014; Soler 2014, 2017c). However, the existence of defenses during these stages has been studied only in a few potential host species. In this study, we have tested experimentally whether the hoopoe, a potential host species of the great spotted cuckoo without egg rejection ability, presents defenses after the egg stage. By parasitizing hoopoe nests with great spotted cuckoo nestlings and recording brood feeding by adults, we have found an absence of defenses during the nestling period but discrimination and undernourishment of the great spotted cuckoo during the fledgling period.

During the nestling period, hoopoe adults fed great spotted cuckoo and hoopoe nestlings raised in the same nest at the same rate, and the survival of hoopoe and cuckoo nestlings was similar. These results suggest that hoopoes did not discriminate their own nestlings from experimental ones.

Host defenses at the nestling stage have been reported in several potential host species (Langmore et al. 2003; Sato et al. 2010; Tokue and Ueda 2010; Attisano et al. 2021); (reviewed in Grim 2006, 2017; Soler 2009). In several brood parasite-host systems, some brood parasites have evolved adaptations to counteract these host defenses (De Mársico et al. 2017). The evolution of any host defense is related to the absence of other efficient host defenses at earlier stages (Britton et al. 2007; Soler 2014; Grim 2017). Thus, in the hoopoe, a potential host species lacking egg-rejection defenses, the existence of nestling discrimination could be expected. However, we have found that the hoopoe does not show nestling discrimination, even when having the possibility to compare between the parasite and their own host nestlings (experimental mixed broods), which has been suggested as a crucial clue for nestling recognition (Davies and Brooke 1988; Lotem 1993). In contrast, the fan-tailed gerygone "*Gerygone flavolateralis*" and its specialist brood parasite, the shining bronze cuckoo "*Chalcites lucidus*" in New Caledonia is an example of a host that discriminates cuckoo nestlings without direct comparison with own nestlings (Sato et al. 2015; Attisano et al. 2021) Although nestling discrimination is more common among potential host species than previously suspected, this behavior is absent in egg- and fledgling-rejecters (Feeney 2017; Grim 2017), as it would be the case of the hoopoe (this study). This result is not surprising considering that absence of effective defenses at earlier stages of the nestling cycle implies stronger selection pressures for the evolution of defenses at a later stage (Britton et al. 2007; Feeney et al. 2012, 2014; Feeney 2017).

During the fledgling period, cuckoo fledglings reared in mixed broods received fewer feedings and died more frequently than hoopoe fledglings. Cuckoo fledglings died between 28 and 62 days of age, within the range in which they are dependent on their host parents (Soler et al. 1994). All the cuckoo fledglings that died were extremely thin, weighing at death from 60 g to 103 g. This range of weights is very low for a fledgling cuckoo, since they can weigh up to 133.7 g at the end of the nestling period (Soler and Soler 1991) suggesting the cause of death was undernourishment. Indeed, hoopoe adults approached to feed cuckoo fledglings fewer frequently than to hoopoe fledglings. When it was the fledglings that approached the hoopoe adults begging for food, no differences were found between cuckoo and hoopoe fledglings in successful and unsuccessful approaches (i.e. approaching an adult and received or not received food respectively). However, most of the approaches of cuckoo fledglings to adults were unsuccessful, with the fledgling not receiving food. Hoopoe fledglings, however, showed not difference in the number of successful and unsuccessful approaches (see Figure 4). Thus, our experimental study points out that hoopoe adults feed more often their own fledglings than parasitic cuckoos, which could indicate recognition and discrimination of the brood parasite in the fledgling stage. As far as we know, the hoopoe is the third potential host species showing fledgling discrimination. The relationship between foster parents and fledgling brood parasites has been studied in detail in only two brood parasite-host systems (De Mársico et al. 2017). This lack of studies at the post-fledging phase is expected because this is the least studied stage in the avian nesting cycle (Gruebler and Naef-Daenzer 2010; Matthysen et al. 2010). The best studied brood parasite, the common cuckoo only provides anecdotal information for this stage (Davies 2000; Tyller et al. 2018). Regarding other well studied brood parasites, in the brown-headed cowbird (*Molothrus ater*), parasitic fledglings are fed at a higher rate than host fledglings, which were only rarely fed, provoking a much lower survival rate of host fledglings, implying no recognition of parasites (Woodward 1983). In contrast, a recent paper by Jones et al. (2022) failed to support substantial post-fledging costs of brown-headed cowbird parasitism. The baywing (*Agelaioides badius*) is parasitized by two brood parasites, the specialist screaming cowbird (*Molothrus rufoaxillaris*) and the generalist shiny cowbird (*Molothrus bonariensis*). In a detailed study of this system, De Mársico *et al.* (2012, 2017) found that the baywing is willing to feed fledglings of the specialist parasite, which mimic both visually and vocally host fledglings, but refuse to feed fledglings of the generalist brood parasite, which does not mimic host fledglings. The relationships between foster parents and fledgling brood parasites have also been studied in detail in the great spotted cuckoo-magpie host system. The magpie feeds parasite fledglings when they have been reared in only-cuckoo-broods but were progressively more reluctant to feed parasite fledglings reared in mixed broods, implying parasite recognition (Soler et al. 2014a).

Both the cowbird and the great spotted cuckoo are non-killer brood parasites, giving the baywing and the magpie the possibility to compare the parasite and their own nestlings sharing the nest and later out of the nest, which may be an important cue to favor nestling and/or fledgling discrimination. To test this possibility in the hoopoe, we created both only-cuckoo and mixed broods in our experimental design. We found that cuckoo fledglings from mixed broods received fewer feedings than cuckoo fledglings from only-cuckoo-broods. In addition, as it occurred in the magpie (Soler et al. 2014b), the hoopoe approached more frequently to feed cuckoo fledglings from only-cuckoo-broods than to cuckoo fledglings from mixed ones. These results suggest that the presence of hoopoe fledglings helps parents in the recognition of the cuckoo fledgling in mixed broods.

Despite the difference found in willingness of parents to feed cuckoos in the two situations (reared alone or in mixed broods), the mortality was not different between both treatments, but high and significantly higher than that of hoopoe fledglings. This may indicate that, even the higher feeding rate received by cuckoo fledglings in only-cuckoo-broods did not satisfy the needs of the parasite. The hoopoes is frequently able to feed up to six hoopoe nestlings (Hildebrandt and Schaub 2018), the brood thus summing up to 450 g (6 x 75 g), and therefore should be able to rear a cuckoo nestling despite its bigger size (134 g), if the hoopoe was motivated to do so. This should be the case especially in our captivity conditions with food ad libitum. Therefore, our results suggest that, in both experimental situations, adult hoopoes were feeding cuckoo fledglings at lower rates than expected if they did not recognize them as parasites. This implies that contrary to what has been suggested (Fraga 1998; De Mársico et al. 2012; Soler et al. 2014a, b; De Mársico et al. 2017) and according to recent studies of hosts of the bronze-cuckoo (Sato et al. 2015; Attisano et al. 2018), the presence of own host fledglings for comparison is not necessary for the evolution of fledgling discrimination.

Our main conclusion is that the hoopoe would be able to discriminate parasite fledglings, even in the absence of their own fledglings for comparison. This phenomenon, inconceivable only 20 years ago (Davies 2000), is in agreement with current theory which suggests that an efficient host defense can evolve at any stage of the breeding cycle, driving the outcome of the long-term coevolution of both brood parasite and host (Soler 2014, 2017a).

The existence of discrimination ability of cuckoo fledglings by the hoopoe would indicate that this species has been parasitized at least in the past. However, the success of cuckoo fledglings in our experimentally parasitized hoopoe broods (40%) is not so low to conclude that it has been abandoned as a host by the development of defenses, as predicted by the coevolutionary alternation hypothesis (Davies and Brooke 1989a; Nuismer and Thompson 2006). Species with intermediate levels of defenses (around 50%) have been traditionally considered accepters (Davies 2000; Martín-Vivaldi et al. 2013) and therefore, the fledgling recognition ability found in the hoopoe (60%) cannot be the only reason for its rare usage as a host by the great spotted cuckoo.

It is known that host life-history variables that reduce the probability of parasitism, thereby reducing selection pressure due to parasitism, could explain low or intermediate levels of defense. It is the case of hole nesting (Aviles et al. 2005; Thomson et al. 2016), habitats without vantage points for cuckoos (Roskaft et al. 2002; Martín-Vivaldi et al. 2013), or ground nesting (Martín-Vivaldi et al. 2013). In these cases, low parasitism rates are caused by the increased difficulty of finding nests for the parasites (no perches for observation of hosts behaviors or ground nesting) or of laying the egg within nests found (because of the small size of some nest entrances in hole nesting species) (Moreras et al. 2021). The hoopoe combines both kinds of difficulties for a laying cuckoo female. First, the hoopoe does not build a nest, does not transport nest materials to the hole selected and, therefore, there is almost no clue on the place where a pair will lay eggs before eggs can be found within a particular hole. Male visits with food to the nest are only frequent after eggs hatch and, so, it is very difficult to find nests before hatching (Martín-Vivaldi et al. 1999). Second, some nests are in holes with a very narrow opening for a female cuckoo to enter or a cuckoo nestling to fledge. These two life history traits of the hoopoe may explain why the parasite pressure has not been so high to cause the evolution of higher levels of fledgling recognition. In summary, the hoopoe is a suitable but not heavily parasitized host in which only about 40% of nests found and parasitized by the great spotted cuckoo, would be successful in producing surviving cuckoo fledglings. The difficulty of finding enough usable nests would have made that this species only a secondary host, explaining low levels of defenses.

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CONFLICT OF INTERESTS

The authors declare that they have no conflict of interest.

ETHICAL APPROVAL

We performed the experiment in accordance with relevant Spanish national (Real Decreto 1201/2005, de 10 de octubre) and regional government administration (Dirección General de Gestión del Medio Natural, Junta de Andalucía). Ethical approval for this study was not required. Junta de Andalucía approved the establishment and maintenance of the captive breeding population (Resolución de 14 de abril de 2008) and conceded the permit required (Ref: SGYB/FOA/AFR/CFS) to perform the present research according to Spanish regulations (Resoluciones de 14 de abril de 2008 and 23 de marzo de 2010). Cross-fostering of great spotted cuckoo nestlings and the experimental parasitism of various species, including the hoopoe, was approved by Dirección General de Gestión del Medio Natural, Junta de Andalucía (Ref.: SGMN/GyB/JMIF).

AUTHOR CONTRIBUTIONS

Conceptualization, MS; methodology, MS, LA and MM-V; validation, MS and LA; formal analysis, LA and JMP-S; investigation, LA, MS and MM-V; resources, MS and MM-V; data curation, LA; writing - original draft preparation, MS, LA; writing - review and editing, MS, LA, JMP-S and MM-V; visualization, LA and JMP-S; supervision, MS; funding acquisition, MS and MM-V All authors have read and agreed to the published version of the manuscript.

DATA AVAILABILITY

The datasets generated during and/or analysed during the current study are available in the DIGIBUB repository, https://hdl.handle.net/10481/77885

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SUPPLEMENTARY MATERIAL

Supplementary Table 7. Information of the age and weight of the nestlings (cuckoos and hoopoes) as well as brood size before video-recordings. In mixed broods, hoopoe and great spotted cuckoo were raised together, while in only-cuckoo-broods, great spotted cuckoo were raised alone in hoopoe nests

Nest	Experimental broods	Brood size	Specie	Weight(g)	Age(days)
1	MIXED	3	Hoopoe	82	18
			Hoopoe	74	17
			Cuckoo	>100	17
2	MIXED	6	Hoopoe	77.5	18
			Hoopoe	76	18
			Hoopoe	67	18
			Hoopoe	68	17
			Hoopoe	45	16
			Cuckoo	>100	17
3	MIXED	3	Hoopoe	70	17
			Hoopoe	50	15
			Cuckoo	>100	16
4	MIXED	2	Hoopoe	36	14
			Cuckoo	>100	13
5	MIXED	3	Hoopoe	68	20
			Hoopoe	58	20
			Cuckoo	88	18
6	ONLY CUCKOO	2	Cuckoo	>100	17
			Cuckoo	77	14
7	ONLY CUCKOO	2	Cuckoo	71	13
			Cuckoo	63	14
8	ONLY CUCKOO	2	Cuckoo	>100	18
			Cuckoo	>100	18
9	ONLY CUCKOO	1	Cuckoo	112	17
10	ONLY CUCKOO	1	Cuckoo	80	18

Supplementary Table 8. Survival information (0 = died, 1= survived), at different reproductive stages and in different experimental nests (mixed broods: hoopoe and great spotted cuckoo were raised together; only-cuckoo-broods, great spotted cuckoo were raised alone in hoopoe nests). In case the nestling of the fledgling died, age and weight at died (if available) are provided as well as the completion of video-recording and additional information. We also linked the information contained in supplementary Table 1 and 2

Nest	Experimental broods	Reproductive stages	Video-recordings/ Observations	Species	Survival	Age at died	Weight at died	Additional information
1	MIXED	Nestling period	YES (nest 1, supp. table 1)	Cuckoo	1			
				Hoopoe	1			
				Hoopoe	1			
		Fledgling period	YES (nest 1, supp. table 2)	Cuckoo	0	35	60	Signs of malnourishment associated with low weight
				Hoopoe	1			
				Hoopoe	1			
2	MIXED	Nestling period	YES (nest 2, supp. table 1)	Cuckoo	1			
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			
		Fledgling period	YES (nest 2, supp. table 2)	Cuckoo	1	Survived		The fledgling was released at the age of 84 days, since it could eat by itself
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			

				Hoopoe	1			
3	MIXED	Nestling period	NO DATA (One videorecorder failed)	Cuckoo	1			
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	0			
		Fledgling period	YES (nest 4, supp. table 2)	Cuckoo	0	62	74	The fledgling gradually lost weight; at 24 days it weighed 123 grams and at 28 days it weighed 92 grams
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			
4	MIXED	Nestling period	YES (nest 3, supp. table 1)	Cuckoo	1			
				Hoopoe	1			
				Hoopoe	1			
		Fledgling period	YES (nest 6, supp. table 2)	Cuckoo	0	54	NO DATA	The fledgling was not weighed
				Hoopoe	1			but was very skinny with signs of malnourishment
				Hoopoe	1			
5	MIXED	Nestling period	NO DATA (One videorecorder failed)	Cuckoo	1			
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			

		Fledgling period	YES (nest 5, supp. table 2)	Cuckoo	1	Survived		The fledgling was released at the age of 62 days, since it could eat by itself
				Hoopoe	1			
				Hoopoe	1			
				Hoopoe	1			
6	MIXED	Nestling period	YES (nest 4, supp. table 1)	Cuckoo	1			
				Hoopoe	1			
				Hoopoe	0			
		Fledgling period	YES (nest 3, supp. table 2)	Cuckoo	0	47	76	Signs of malnourishment associated with low weight
				Hoopoe	1			
7	MIXED	Nestling period	YES (nest 5, supp. table 1)	Cuckoo	1			
				Hoopoe	1			
				Hoopoe	1			
		Fledgling period	NO DATA (The fledgling died a few days after leaving the nest-box and we were unable to make observations)	Cuckoo	0	28	103	The fledgling had a high load of ectoparasites, reflecting a poor state of health
				Hoopoe	1			
				Hoopoe	1			
8	MIXED	Nestling period	NO DATA (One videorecorder failed)	Cuckoo	1			
				Hoopoe	1			
				Hoopoe	0			
		Fledgling period	YES (nest 7, supp. table 2)	Cuckoo	1	Survived		The fledgling was released at the age of 60 days, since it could eat by itself
				Hoopoe	0			

9	ONLY CUCKOO	Nestling period	YES (nest 6, supp. table 1)	Cuckoo	1			
				Cuckoo	1			
		Fledgling period	NO DATA (The nest with both cuckoos was lost to depredation by a fox entering the cage)	Cuckoo	0			
				Cuckoo	0			
10	ONLY CUCKOO	Nestling period	YES (nest 7, supp. table 1)	Cuckoo	1			
				Cuckoo	0	26	NO DATA	The nestling was not weighed but was very skinny with signs of malnourishment
		Fledgling period	YES (nest 8, supp. table 2)	Cuckoo	0	35	NO DATA	The fledgling was not weighed but was very skinny with signs of malnourishment
11	ONLY CUCKOO	Nestling period	YES (nest 8, supp. table 1)	Cuckoo	1			
				Cuckoo	1			
		Fledgling period	YES (nest 9, supp. table 2)	Cuckoo	1	Survived		The fledgling was released at the age of 61 days, since it could eat by itself
				Cuckoo	0	54	84	Signs of malnourishment associated with low weight
12	ONLY CUCKOO	Nestling period	NO DATA (One videorecorder failed)	Cuckoo	1			
				Cuckoo	1			
		Fledgling period	YES (nest 11, supp. table 2)	Cuckoo	1	Survived		The fledgling was released at the age of 61 days, since it could eat by itself

				Cuckoo	0	54	NO DATA	The fledgling was not weighed but was very skinny with signs of malnourishment
13	ONLY CUCKOO	Nestling period	YES (nest 9, supp. table 1)	Cuckoo	1			
		Fledgling period	YES (nest 10, supp. table 2)	Cuckoo	1	Survived		The fledgling was released at the age of 65 days, since it could eat by itself
14	ONLY CUCKOO	Nestling period	YES (nest 10, supp. table 1)	Cuckoo	1			
		Fledgling period	NO DATA (The fledgling died a few days after leaving the nest-box and we were unable to make observations)	Cuckoo	0	35	50	Signs of malnourishment associated with low weight
15	ONLY CUCKOO	Nestling period	NO DATA (It was not possible to make video-recordings in this nest due to the early death of the cuckoo)	Cuckoo	0	3	NO DATA	The nestling was not weighed but was very skinny with signs of malnourishment

Supplementary Table 9. Brood size and age of fledglings in each observation event (cuckoos and hoopoes). In mixed broods, hoopoe and great spotted cuckoo were raised together, while in only-cuckoo-broods, great spotted cuckoo were raised alone in hoopoe nests

Nest	Experimental broods	Brood size	Observation number	C1	C2	H1	H2	H3	H4	H5
1	MIXED	3	1	28		29	28			
			2	32		33	32			
2	MIXED	6	1	28		29	29	29	28	27
3	MIXED	2	1	32		33				
4	MIXED	5	1	32		34	32	31	30	
			2	39		41	39	38	37	
5	MIXED	4	1	28		30	29	28		
			2	41		43	42	41		
			3	43		45	44	43		
6	MIXED	3	1	42		43	41			
7	ONLY CUCKOO	1	1	29						
			2	34						
8	ONLY CUCKOO	1	1	29						
			2	34						
9	ONLY CUCKOO	2	1	28	28					
			2	33	33					
10	ONLY CUCKOO	1	1	27						
			2	30						
			3	45						
			4	51						
11	ONLY CUCKOO	2	1	31	31					
			2	45	45					

RESULTADOS GENERALES Y DISCUSIÓN INTEGRADORA

En esta tesis se ha querido comprobar la hipótesis general de que la disponibilidad de alimento va a afectar a las decisiones parentales sobre qué cantidad y qué tipo de presas se distribuyen entre ellos y su descendencia y cómo debe asignarse esas presas entre los pollos. Estas decisiones parentales van a estar influenciadas por las características típicas de la especie, por lo que desarrollamos varias hipótesis: (I) Las abubillas son forrajeadores de un lugar central y cargadoras de una solo presa por viaje, por lo que intentarán maximizar su energía neta por viaje al nido. (II) Las abubillas son especies de vida corta por lo que favorecerán la inversión en la nidada actual a costa de su supervivencia y/o reproducción futura en situaciones de escasez. (III) Los cambios en la disponibilidad de alimentos afectarán de manera diferencial la inversión reproductiva de cada sexo. (IV) La asignación de cebas a cada pollo estará influenciada por la disponibilidad de alimento.

En términos generales encontramos que las abubillas siguieron una estrategia de búsqueda de alimento en lugares centrales, proporcionando la presa más rentable a los pollos mientras comían la de peor calidad, independientemente de la disponibilidad de alimento y en toda la etapa de los pollos. En la etapa temprana, la hembra asigna la mayor cantidad de presas a los pollos mayor tamaño, incluso en situaciones de abundancia. La probabilidad de que un pollo sea alimentando en situaciones de escasez aumenta si un pollo más grande no pide comida. En la etapa tardía, cuando aumentaron las demandas energéticas de los pollos y la actividad de aprovisionamiento de los padres, la escasez de alimento afectó a los pollos pero no a los padres. Los rasgos que limitan la capacidad energética de los padres, como un amplio área de campo y un período prolongado de estancia en el nido, podrían explicar esta respuesta atípica. A su vez, aunque ambos padres continuaron ingiriendo la misma cantidad de biomasa en ambas etapas, las hembras fueron más sensibles a los cambios en la disponibilidad de alimento, quizás debido a una diferente inversión al final de la etapa reproductiva.

Partimos de la base de que la abubilla puede ser un potencial hospedador del críalo, la cual no posee un mecanismo de rechazo de huevos y no es parasitada. Una explicación es porque haya desarrollada defensas contra el parasitismo. La hipótesis general es que las condiciones del nido, en este caso el parasitismo de cría, va a influenciar en como los padres distribuyen las presas entre sus pollos y el críalo. Tenemos dos hipótesis: (i) La abubilla ante el parasitismo de cría posee defensas como el reconocimiento de pollos (dentro del nido) y (ii) La abubilla ante el parasitismo de cría posee defensas como el reconocimiento de volantones (fuera del nido). En términos generales encontramos que los padres dentro de la caja-nido alimentan al crílalo como si fuera una de sus pollos, por lo que no hay reconocimiento. Sin embargo, cuando el crílalo sale de la caja-nido hay un 60% de probabilidad de que mueran.

A continuación, analizamos en detalle los posibles escenarios que explicarían estos resultados.

La abubilla como forrajeador de un lugar central

De acuerdo con la teoría de forrajeadores de un lugar central (*central-place foraging theory*) (Orians and Pearson 1979; Kacelnik and Cuthill 1990; Ydenberg 1994), los adultos entregarán las presas de mayor calidad a los pollos mientras que ellos consumirán las presas de baja calidad. Nuestros resultados se ven apoyados por esta teoría. En la fase temprana de pollos (NS1), tanto las hembras como los machos consumieron significativamente una mayor proporción de pupas que de larvas mientras que los pollos fueron alimentados principalmente con larvas (Figura 17). Este patrón se mantuvo en la fase tardía de pollos (NS2), consumiendo los padres una proporción mayor de presas de menor calidad (menor tamaño: larvas y pupas), mientras que alimentaron a los pollos con las presas más grandes: gusanos de seda y grillos (Figura 18).

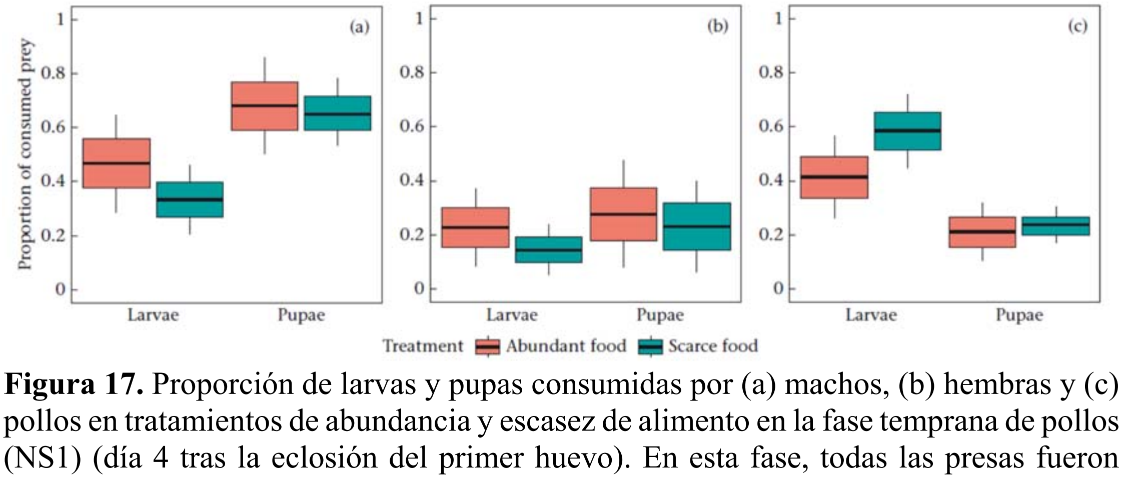

Figura 17. Proporción de larvas y pupas consumidas por (a) machos, (b) hembras y (c) pollos en tratamientos de abundancia y escasez de alimento en la fase temprana de pollos (NS1) (día 4 tras la eclosión del primer huevo). En esta fase, todas las presas fueron traídas al nido por los machos. Las líneas en negrita, los recuadros y los barras muestran la media, el error estándar y su intervalo de confianza del 95% a partir de los datos brutos, respectivamente.

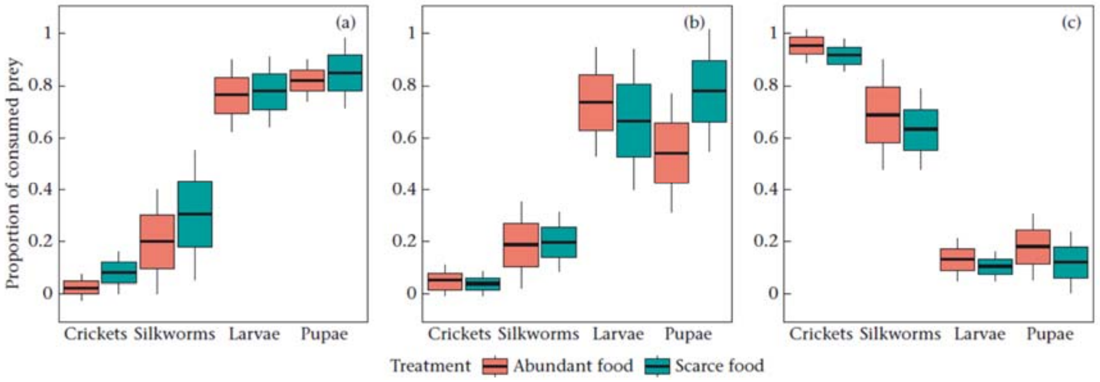

Figura 18. Proporción de cada tipo de presa (grillos, gusanos de seda, larvas y pupas) consumida por (a) machos, (b) hembras y (c) pollos en los tratamientos de abundancia y escasez de alimento en la fase tardía de pollos (NS2) (día 16 tras la eclosión del primer huevo). En esta fase, ambos progenitores llevaron presas al nido. Las líneas en negrita, los recuadros y las barras muestran la media, el error estándar y su intervalo de confianza del 95% a partir de los datos brutos, respectivamente.

En NS1, las decisiones combinadas de ambos padres (machos al recolectar y hembras al distribuir a los pollos) dan como resultado una dieta de mejor calidad para sus pollos, con una mayor proporción de larvas digeribles. Estas decisiones donde los adultos ofrecen a los pollos presas más rentables con menos quitina se han encontrado en estudios previos (Koenig et al. 2008; Richoux et al. 2010; Alonso et al. 2012; Orlowski et al. 2014). En NS2, las decisiones de ambos padres dieron como resultado una dieta para los pollos con mayor contenido energético. Este mismo patrón de alimentar a los pollos con presas grandes se ha encontrado en una población de abubillas suizas (Fournier and Arlettaz 2001; Arlettaz et al. 2010a). En esta población, la presa principal en la dieta de los pollos es el grillo topo (*Gryllotalpa grillotalpa*). Una reducción en la proporción de esta presa se asoció con una disminución significativa de la supervivencia de los pollos y por lo tanto del éxito reproductivo de los padres (Fournier and Arlettaz 2001; Arlettaz et al. 2010a; Guillod et al. 2016).

Además, la abubilla es un ave que se alimenta en el suelo buscando invertebrados subterráneos (Cramp 1998), por lo que el tiempo de búsqueda de presas depende tanto de la abundancia como de la accesibilidad de las presas que están bajo el suelo (Tagmann-Ioset et al. 2012). Por lo tanto, la mejor estrategia es maximizar el esfuerzo de aprovisionamiento por unidad de tiempo dedicado a la búsqueda de alimento. En este sentido, las abubillas adultas se comían las presas pequeñas nada más encontrarlas para satisfacer sus propias necesidades energéticas, mientras que seleccionaban presas más grandes para alimentar a sus pollos y hacer más rentable el viaje al nido como propone Kacelnik and Cuthill (1990).

Alimentación de los padres en NS1 y delegación de decisiones de aprovisionamiento del macho a la hembra en NS2

En la abubilla, ambos sexos muestran un marcado reparto de tareas a lo largo de la reproducción. Al principio de la etapa de los pollos en el nido (NS1), los machos recogen toda la comida para la familia (Martín-Vivaldi et al. 1999) y asumen todos los costes de búsqueda de alimento (Bryant 1997). Nuestros resultados muestran que los machos consumen casi la mitad de las presas que llegan al nido. Podemos especular que este alto consumo de presas quitinizadas pero con una gran biomasa, garantizaría el automantenimiento del macho. Una buena condición física de los machos puede asegurar la supervivencia de la hembra y de la nidada y, por tanto, su éxito en la reproducción (Tveraa et al. 1998; Wendeln and Becker 1999; Barrionuevo et al. 2018). En esta fase, las hembras no abandonan el nido y reciben todas las presas de los machos (Martín-Vivaldi et al. 1999), por lo que deben decidir cómo repartir las presas entre ellas mismas y los pollos, y también decidir a qué pollo alimentar **(Capítulo 2)**. Nuestros resultados muestran que las hembras comieron solo una cuarta parte del total suministrado por los machos, el resto, se lo dieron a los pollos (Figura 19). Este bajo consumo puede deberse a que las hembras ahorran energía relacionada con la búsqueda de presas, con el tiempo de manipulación de estas presas y con los viajes de aprovisionamiento, tareas que son costosas y que realizan los machos (Post and Gotmark 2006).

En la fase más tardía de los pollos en el nido (NS2), un resultado no esperado fue que las hembras decidieron el destino de la mayoría de las presas, ya que en esta fase los machos le continuaron ofreciendo más del 70% de las presas que capturaban, ofreciendo el resto a los pollos. Este resultado implica que los machos delegan las decisiones de aprovisionamiento a las hembras (Figura 19).

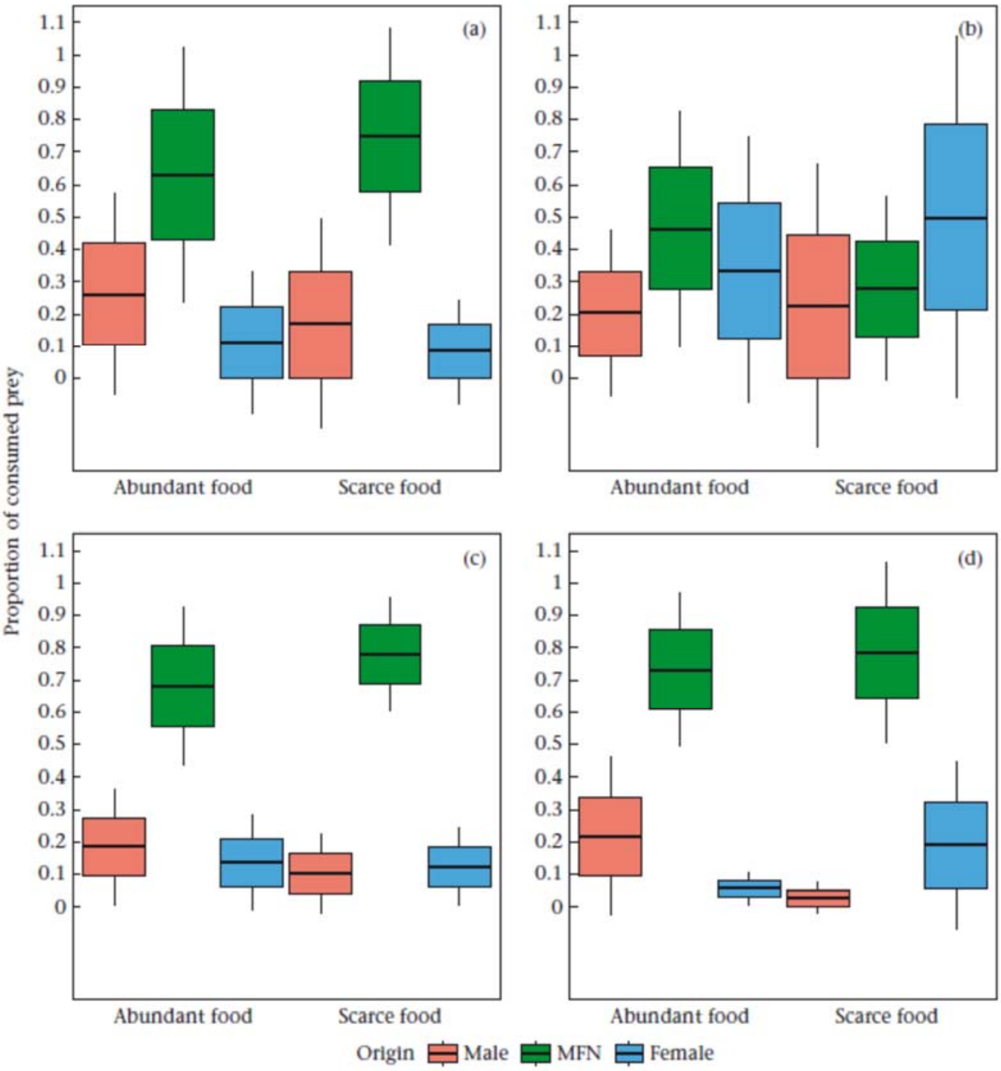

Figura 19. Decisiones parentales de distribución de presas. Proporción de (a) larvas, (b) pupas, (c) grillos y (d) gusanos de seda consumidos por los pollos en los tratamientos de abundancia y escasez de alimento en la fase de pollos tardía (NS2) (día 16 tras la eclosión del primer huevo) y según el origen de las presas (MFN: secuencia male (macho) – female (hembra) – nestlings (pollos)). Las líneas en negrita, los recuadros y las barras muestran la media, el error estándar y su intervalo de confianza del 95% a partir de los datos brutos, respectivamente.

Una posible explicación a este patrón podría ser que las hembras permanecen más tiempo dentro del nido y pueden recopilar información más fiable sobre el estado nutricional de los pollos, maximizando la asignación de alimentos entre los pollos (Gottlander 1987; Ryser et al. 2016; Nuhlickova et al. 2021). La abubilla tiene eclosión asincrónica que origina pollos de diferentes edades y tamaños (Martín-Vivaldi et al. 1999). Ryser et al. (2016) observaron que los machos de abubilla mostraban preferencia por los pollos que estaban más cerca de la entrada de la caja-nido, favoreciendo a los pollos más grandes. Las hembras entraban dentro de la caja-nido y repartían el alimento más equitativamente entre los pollos, beneficiando a los más pequeños, lo que podría aumentar el número de volantones (Ryser et al. 2016). Este comportamiento de alimentación de la pareja también puede explicarse como una muestra de la calidad del macho o como un refuerzo de los lazos de pareja (Korpimaki 1989; Costanzo et al. 2020). De hecho, las especies en las que los machos alimentan a sus hembras son también aquellas en las que los machos invierten más en alimentar a sus crías (Moller and Cuervo 2000), como ocurre en la abubilla (Martín-Vivaldi et al. 1999; Martín-Vivaldi et al. 2016). Además, las cebas del macho a la hembra podrían mantener a esta en buena condición corporal, lo que puede afectar positivamente a la eficacia biológica de ambos progenitores (Galvan and Sanz 2011). Ambas estrategias podrían aumentar la oportunidad del macho de poner una segunda puesta con la misma hembra, lo que es común en esta especie (Martín-Vivaldi et al. 1999; Hoffmann et al. 2015).

¿Cómo afecta la disponibilidad de alimento a la distribución de presas entre los adultos y la descendencia y entre sexos?

Las especies de vida corta que se enfrentan a una limitación de alimento durante la reproducción, deberían de aumentar su esfuerzo reproductor actual incluso a costa de su propia supervivencia, según la teoría de estrategias vitales (Martin 1987; Boutin 1990). Las abubillas siguen una estrategia de especie de vida corta en la fase temprana de pollos (NS1), tal y como muestran los resultados. En esta fase, el tratamiento de escasez de alimento no afectó ni a la biomasa total ofrecida ni a la entrega de las presas más rentables a los pollos. Es decir, los padres en época de escasez mantuvieron los niveles de presas ofrecidas a los pollos. Tampoco hubo cambios en la alimentación de los machos, que siguieron manteniendo el mismo consumo tanto en proporción de presas como en biomasa ingerida. En cambio, la escasez de alimento si afectó a las hembras, las cuales respondieron comiendo una menor proporción de presas (Figura 17). Sin embargo, este efecto no se vio reflejado en cambios en la biomasa ingerida entre los dos tratamientos. Es probable que se necesite una diferencia mayor entre las pupas consumidas en los dos tratamientos para producir cambios cuantificables en la biomasa ingerida. Estos resultados indican que los padres (hembras en nuestro caso) invierten en la reproducción actual por encima de su propio mantenimiento, (Grieco 2001; Markman et al. 2002; Markman 2014) como otras especies de vida corta.

Sin embargo, en la fase tardía de pollos (NS2), cuando la demanda de energía de los pollos y la actividad de aprovisionamiento es mayor, este escenario cambió. Ambos padres mantuvieron su consumo de biomasa en el tratamiento de escasez de alimento, pero esta vez los pollos sufrieron las consecuencias. Los pollos consumieron menos biomasa y una proporción menor de presas (Figura 18). Los padres a pesar de ofrecerles a los pollos las presas más rentables incluso en escasez, no compensaron el descenso en la disponibilidad de alimento que sufrió la familia, y especialmente los pollos. Este resultado contrasta con estudios realizados en especies de vida corta y forrajeadores de un lugar central, en los que los progenitores incrementaron su tasa de aprovisionamiento y, por tanto, su esfuerzo alimentario en nidadas experimentalmente aumentadas, revisado por Gow and Wiebe (2014) y en experimentos de suplementación alimentaria (Markman et al. 2002). Una posible explicación es que la abubilla podría tener limitada la capacidad para responder al aumento de la demanda de los pollos. Gow and Wiebe (2014) encontraron que el carpintero escapulario, (*Colaptes auratus)*, un ave de vida corta y forrajeadora de un lugar central, no respondía aumentando la tasa de aprovisionamiento en un experimento de aumento de nidada a corto plazo (24 h). Estos autores plantearon la hipótesis de que la falta de respuesta podría deberse a las limitaciones energéticas en esta especie, que tiene grandes áreas de campeo (>25 hectáreas) y un prolongado periodo de estancia de los pollos en el nido (25-29 días). La abubilla comparte estas características con el carpintero escapulario con medias de áreas de campeo que oscilan entre 12.79 y 39.6 ha (Barbaro et al. 2008; Tagmann-Ioset et al. 2012; Podletnik and Denac 2015) y un periodo de estancia de los pollos en el nido de 27.1 días (Martín-Vivaldi et al. 1999) por lo que podrían experimentar una respuesta atípica para especies de vida corta.

En esta fase tardía de pollos donde ninguno de los padres redujo su consumo de biomasa antes la escasez de alimentos, nos encontramos que la hembra incluso aumentó su proporción de presas consumidas (Figura 18). Este resultado podría explicarse porque un tercio de las hembras ponen una segunda nidada, mientras que solo una quinta parte de los machos lo intenta (Hoffmann et al. 2015). Es una proporción muy alta de hembras que abandonan su nidada antes de que los pollos emplumen para iniciar una segunda puesta (Arlettaz et al. 2010a; Hoffmann et al. 2015). Así, en nuestro estudio, las hembras podrían estar evaluando la disponibilidad de alimento desde el punto de vista de criar una segunda nidada con éxito. Plard et al. (2018) mostraron que las hembras experimentaban un éxito reproductivo y una supervivencia más bajas después de intensos esfuerzos reproductivos (criar segundas nidadas), especialmente en años con baja disponibilidad de alimento. En el caso de los machos, su esfuerzo reproductivo en la primera nidada en años con baja disponibilidad de alimento, afectó negativamente al éxito de la segunda nidada en la misma temporada de reproducción (Plard et al. 2018). Estos costes intraestacionales pueden limitar la inversión de los machos en la estación reproductora. Además, los machos prolongan sus cuidados parentales hasta el periodo de volantones (Arlettaz et al. 2010b; Martín-Vivaldi et al. 2016) y por lo tanto pueden ser más reacios a cambiar su patrón de consumo de presas. Nuestros resultados apoyan esta idea, ya que los machos no cambiaron la biomasa ni la proporción de presas que comieron en NS2 durante el tratamiento de escasez de alimento (Figura 18). Es posible que los machos estén conservando recursos para cuidar de los volantones hasta su independencia (Musgrove and Wiebe 2014). Mientras que los machos siguieron una estrategia de inversión fija durante el periodo de la cría de los pollos en el nido, las hembras respondieron de forma más flexible a los cambios en la disponibilidad de alimento en ambas etapas (Markman et al. 2002; Low et al. 2012). Esta respuesta diferencial puede ser el resultado de una esfuerzo parental diferente cuando los pollos están cerca de volar, ya que muestran diferentes rasgos de estrategia vital (Plard et al. 2018).

Señalización de los pollos a través de la petición de alimento

Con respecto a la señalización de los pollos a sus padres a través de la petición, encontramos en la fase temprana de pollos que todos pidieron con la misma intensidad independientemente de la disponibilidad de alimento (Figura 20). Es posible que en nuestro experimento la intensidad de petición de los pollos no transmita información sobre su condición (ni necesidad ni calidad) y puede que simplemente transmita que los pollos tienen hambre (Grodzinski and Lotem 2007; Mock et al. 2011; Mock 2016). En esta fase temprana de pollos (NS1), sólo utilizamos presas pequeñas ya que algunos de los pollos estaban recién nacidos y podían tener dificultades para ingerir la presa, como propone la hipótesis de la restricción alimentaria (Slagsvold and Wiebe 2007). De esta manera, evitamos que el tamaño de la presa fuera un factor que afectara al alimento proporcionado a los pollos más pequeños y pudimos probar el efecto de la abundancia de alimento en las decisiones de las hembras sin influencia del tamaño de la presa. El uso de presas pequeñas como fuente de alimento pudo haber provocado que los pollos de mayor tamaño nunca alcanzaran la saciedad, a pesar de recibir un mayor número de presas que sus hermanos menores. Las abubillas solo transportan una presa por viaje, y aunque en esta fase los padres le dan a sus pollos las presas más digeribles (Arco et al. 2022) la probabilidad de que un pollo grande no se saciara con una sola visita pudo influir en la intensidad de la petición. Se ha sugerido que un factor determinante principal del éxito reproductivo de las abubillas en Suiza es la disponibilidad de grillos topo (Arlettaz et al. 2010a). Si bien no hay ninguna razón aparente por la que este sería un mejor alimento que otros insectos, probablemente el efecto principal de su disponibilidad es que los grillos topo son grandes presas que mantienen saciados a los pollos grandes hasta que llega el siguiente alimento al nido, permitiendo así que los pollos más pequeños puedan obtener algo de alimento (este estudio, Ferrer-Pereira et al. 2023). En el mismo sentido, el pollo más pequeño puede ser utilizado como alimento cuando las abubillas lo canibalizan (Ferrer-Pereira et al. 2023) y puede permitir principalmente mantener saciado a un pollo grande durante más tiempo, aumentando así las perspectivas de supervivencia de sus hermanos menores.

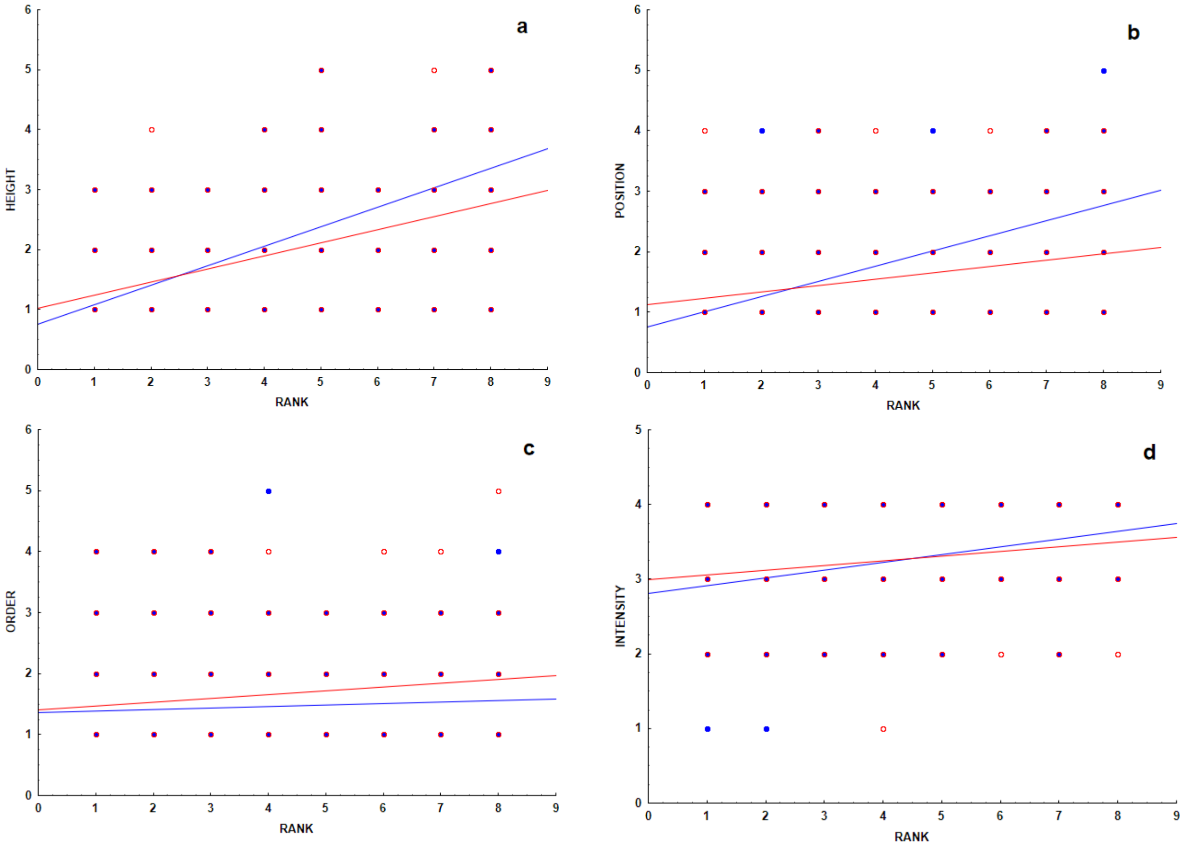

Figure 20. Efectos del tratamiento y del rango del pollo sobre los componentes de la petición (a = altura; b = posición; c = orden; d = intensidad). La abundancia de alimento se muestra en rojo y la escasez en azul. Se muestran las medias ± errores estándar.

Con respecto al resto de componentes de petición, encontramos que todos los pollos respondieron a la escasez comenzando a pedir antes (Figura 20), en línea con otros estudios (Smiseth et al. 2003; Porkert and Spinka 2006). Además, como era de esperar en especies con pollos de diferentes tamaños, los pollos más grandes cuando pedían alcanzaron una mayor altura y una posición más cercana a la hembra que sus hermanos más pequeños (Cotton et al. 1999; Glassey 2000; Moreno-Rueda et al. 2009) y esta diferencia entre los pollos se hizo más marcada en situaciones de escasez (Figura 20). Al igual que Ferrer-Pereira et al. (2023), encontramos que la probabilidad de que un pollo pequeño reciba comida, estaba supeditado a que el pollo más grande no pidiera alimento (Figura 21). Además, encontramos que cuando la comida es abundante, es más probable que un pollo sea alimentado incluso si el pollo más grande pide. En situaciones de escasez de alimento, es más frecuente que un pollo sea alimentado si un pollo grande no pide. Podríamos especular que un pollo en esta situación de escasez pueda optar por gastar menos energía estirando el cuello cuando los pollos más grandes muestran todo su potencial de tamaño físico debido a la escasez de alimentos (Smiseth and Amundsen 2002; Forbes 2007; Griffith 2007).

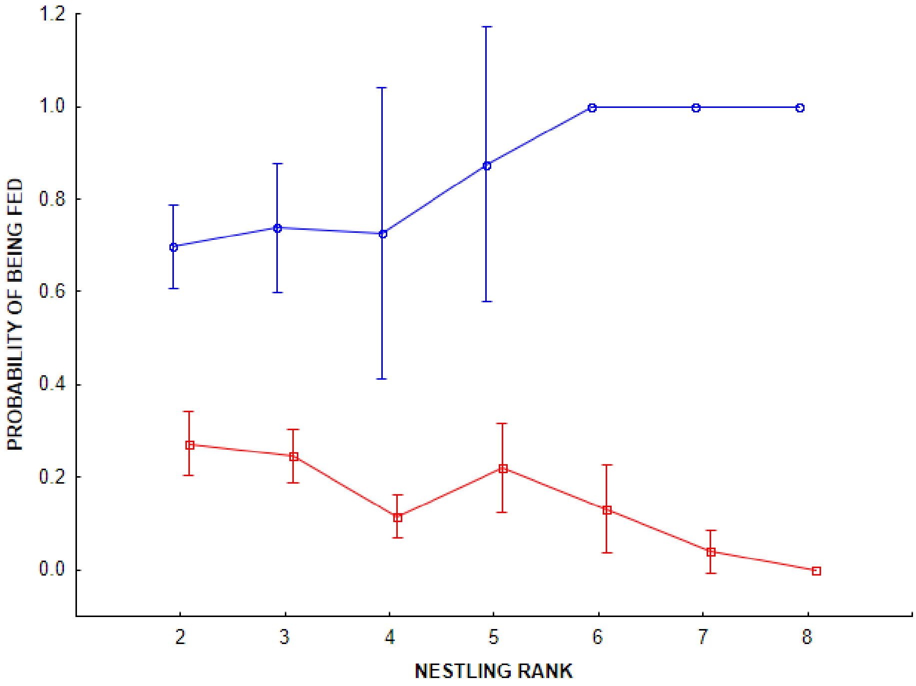

Figura 21. Probabilidad de ser alimentado según el rango de los pollos y si los pollos más grandes estaban pidiendo (el pollo más grande pedía en rojo; el pollo más grande no estaba pidiendo en azul). Se muestran las medias ± errores estándar.

En cambio, podrían desviarlo y utilizarlo más tarde en funciones como su crecimiento y desarrollo (Forbes and Glassey 2000). De hecho, los pollos más pequeños pidieron por más tiempo entre los eventos de alimentación. Este resultado podría sugerir que los pollos más pequeños pueden estar aumentando la duración de su petición para inducir a los padres a traer más presas, como sugieren Smiseth and Amundsen (2002) o simplemente mostrando que tienen hambre (Sacchi et al. 2002; Dickens et al. 2008).

Asignación de alimento a los pollos por parte de la hembra

En la fase temprana de pollos (NSI), antes de que se produzca la reducción de la nidada, la hembra alimentó preferentemente a los pollos más grandes independientemente de la disponibilidad del alimento. Además, el éxito de petición, es decir, que un pollo reciba comida cuando pide, disminuyó a medida que el tamaño de los pollos era menor y esta diferencia se acrecentó en situaciones de escasez (Figura 22). Estos resultados no apoyan la predicción de partida que establece que cuando el alimento es abundante, la asignación de alimento de las hembras a sus pollos sería más equitativa, reduciendo la preferencia por los pollos más grandes.

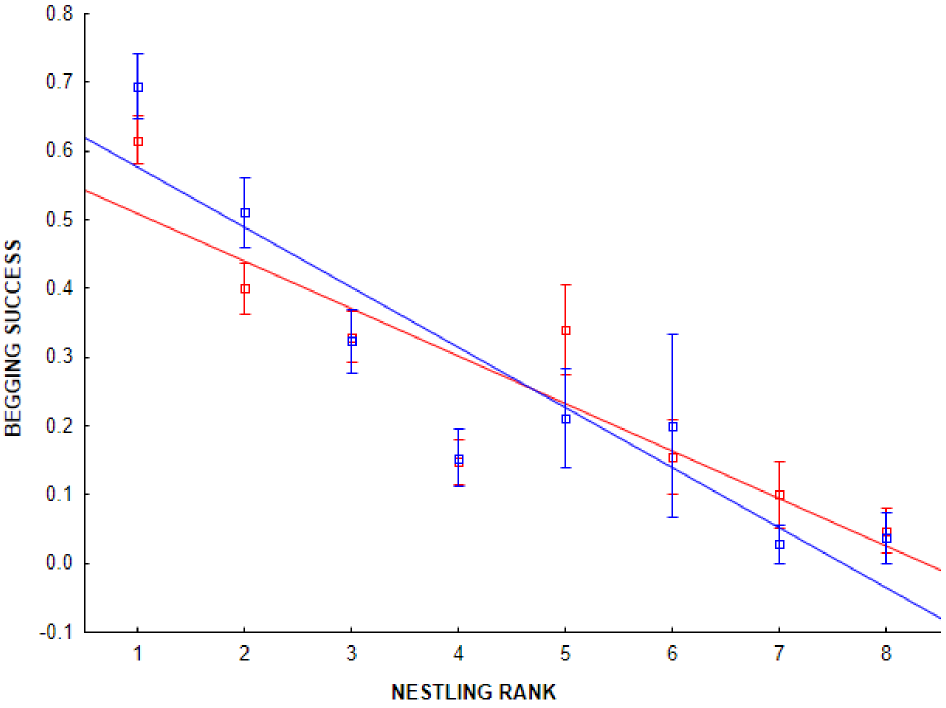

Figure 22. Probabilidad de éxito de petición para cada pollo (pollo que pidió y fue alimentado) según el rango del pollo y el tratamiento (alimento en abundancia en rojo; alimento en escasez en azul). Se muestran las medias ± errores estándar.

Una posible explicación podría estar relacionada con el hecho de que todos los pollos piden con la misma intensidad en ambas condiciones de disponibilidad de alimento, reflejando que todos los pollos tienen hambre. Por lo tanto, el nivel de petición no proporciona información útil a los padres sobre la necesidad o la calidad de los pollos (Mock et al. 2011; Caro et al. 2016). Algunos estudios han propuesto que los padres en este escenario pueden obtener información sobre el estado de los pollos a través de pistas del tamaño corporal (Mock et al. 2011), así como de señales de bajo coste que transmiten información similar al tamaño, como la altura de la petición (Caro et al. 2016; Wild et al. 2017). Obviamente, los pollos de mayor edad eran más grandes, alcanzaron una mayor altura, estaban más cerca de la hembra y empezaron a pedir antes y, por tanto, la probabilidad de ser alimentados fue mayor (Figure 22). Por lo tanto, es posible que en un escenario en el que todos los pollos están hambrientos tanto en condiciones de abundancia como de escasez, la hembra asigne el alimento en función del rango de los pollos utilizando tanto pistas de tamaño corporal como componentes de la petición relacionados con el tamaño de los pollos (Mock et al. 2011; Caro et al. 2016) no encontrando diferencias entre ambos tratamientos.

Otra posible explicación podría estar relacionada con que, en abubillas, el último pollo que eclosiona está condenado a morir, aunque haya suficiente comida. Un estudio reciente de Soler et al. (2022a) encontró evidencias de que las hembras utilizaban los últimos pollos eclosionados para alimentar a los hermanos mayores (canibalismo entre hermanos). Estos mismos autores realizaron otro experimento de suplementación con presas grandes para determinar la influencia de la disponibilidad de alimento tanto en la reducción de la nidada como en el canibalismo entre hermanos (Ferrer-Pereira et al. 2023). El experimento comenzó unos días antes de la eclosión del primer huevo y finalizó unos días después de la eclosión del último huevo. En este experimento, el suministro de alimento no influyó en la probabilidad de reducción de la nidada, incluso utilizando presas grandes que saciaron a los pollos más grandes, aunque sí se redujo la probabilidad de canibalismo entre hermanos. Además, la suplementación con estas presas disminuyó el éxito de petición de los pollos más pequeños cuando eran los únicos que pedían comida, ya que la hembra utilizaba esas presas para autoalimentarse (Ferrer-Pereira et al. 2023). En consecuencia, tanto si hay escasez como abundancia, los pollos más pequeños de abubilla dentro de una nidada son desatendidos por las hembras y tienden a morir. Otros estudios en especies asincrónicas también encontraron que la muerte de los pollos más pequeños es frecuente incluso si hay suficiente comida para todos los pollos (Soler and Soler 1996; Brommer et al. 2004; Kontiainen et al. 2010), lo que apoya esta hipótesis.

En las abubillas, como en otras especies con asincronía de eclosión, la reducción de la nidada se produce en los primeros días tras la eclosión, cuando la rivalidad entre hermanos y la demanda de alimento por parte de los pollos es todavía baja (Martín-Vivaldi et al. 1999; Slagsvold and Wiebe 2007; Ryser et al. 2016). Por lo tanto, la decisión de sacrificar a los pollos pequeños en esta fase temprana refleja la selección de la hembra de abubilla para asignar los cuidados principalmente a los pollos de mayor valor reproductivo y evitar el alto coste de invertir en pollos con menores perspectivas de supervivencia. Por el contrario, en la etapa de pollos grandes (11-15 días después de la eclosión del primer huevo), justo después de que se hubiera producido la reducción de la nidada, la hembra de abubilla alimentaba a los pollos supervivientes más pequeños y hambrientos mientras que el macho alimentaba a los pollos más grandes y competitivos, manteniendo el tamaño de la nidada ajustado (Ryser et al. 2016). A medida que aumenta la edad de las pollos, pueden cambiar los costes y beneficios tanto de la petición de las crías como de la provisión de alimento por parte de los padres (Royle et al. 2002; Hinde et al. 2010). Así, sería posible que las abubillas hembras se ajustaran a la hipótesis calidad-señal (SoQ) hasta que mueran los pollos más pequeños y luego siguieran la hipótesis necesidad-señal (SoN) para conseguir que el resto de la nidada llegue al volantón (Bowers et al. 2019).

Defensa de los padres de abubilla frente a los pollos parásitos de críalo

Las especies que brindan cuidado parental corren el riesgo de ser explotados por los parásitos de cría (Spottiswoode et al. 2012). Muchas especies presentan una gran variedad de adaptaciones como el reconocimiento y el rechazo de huevos, para no ser parasitadas. Sin embargo, un alto porcentaje de potenciales especies hospedadoras carecen de rechazo de huevos contra el parasitismo de cría, un 38,5% según Soler (2014). Una posible respuesta a por qué estas especies no son parasitadas sería que los hospedadores han evolucionado defensas eficientes en otras etapas del ciclo reproductor, tanto antes de la puesta como durante periodos de pollos o volantones (Feeney et al. 2014; Soler 2014; 2017). Sin embargo, la existencia de defensas durante estas etapas sólo se ha estudiado en unas pocas especies de hospedadores potenciales (De Mársico et al. 2012; De Mársico et al. 2017).

En el caso de las defensas frente al parasitismo del críalo en la abubilla, encontramos que en nidadas mixtas (críalo y abubillas) durante el periodo en el que los pollos están dentro del nido, los adultos alimentaron por igual al pollo de críalo que a los suyos propios de abubilla. Además, la supervivencia de los pollos de ambas especies fue similar (Figura 23). Estos resultados sugieren que la abubilla no discrimina al pollo de críalo de sus propios pollos dentro del nido. Sin embargo, cuando los pollos salen de la caja nido, en la fase de volantones, encontramos que el críalo es alimentado con menos frecuencia que los volantones de abubilla. De hecho, los adultos de abubilla se acercaban a alimentar a los volantones de críalo con menos frecuencia que a los volantones de abubilla. Cuando fueron los volantones de críalos los que se acercaron a los adultos pidiendo comida, la mayoría de los acercamientos de los volantones de críalo a los adultos no tuvieron éxito y el volantón no recibió alimento. Los volantones de abubilla, sin embargo, no mostraron diferencias en el número de aproximaciones exitosas y fallidas para conseguir alimento (Figura 24). En consecuencia, la supervivencia de los volantones de críalo en nidadas mixtas fue significativamente menor que la de los volantones de abubilla. Estos volantones de críalo terminaron

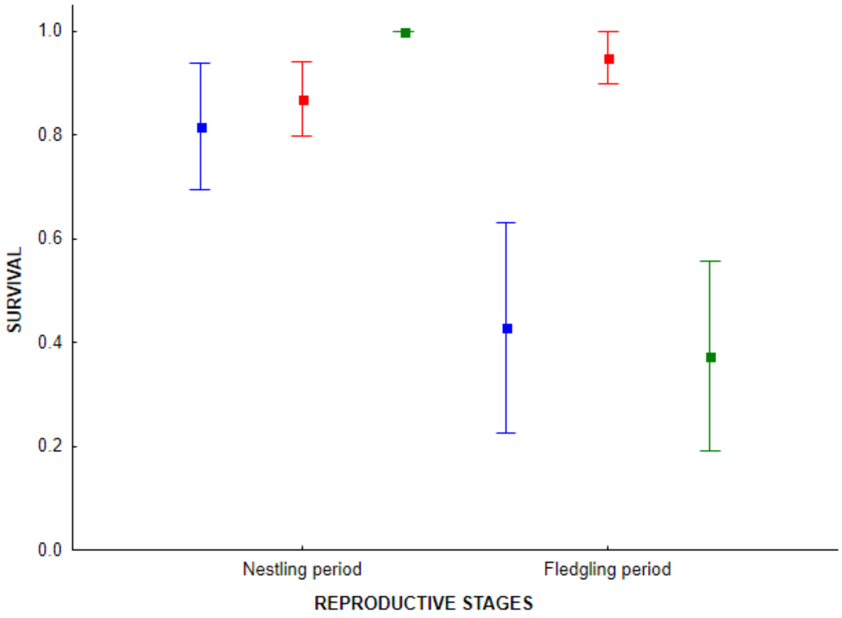

Figura 23. Probabilidad de supervivencia de las abubillas (*Upupa epops* – en rojo) y del críalo (*Clamator glandarius*) tanto criados en nidadas mixtas (críalo criado con pollos de abubilla – en verde) como en nidadas de solo críalo (críalos criados solos) en los nidos de abubilla – en azul), durante los períodos de pollo y volantón. Se muestran las medias ± errores estándar.

muriendo debido a una pérdida importante de peso y, por tanto, de desnutrición, durante las primeras fases de la etapa de volantón, cuando todavía dependen de sus padres hospedadores (Soler et al. 1994). Estos resultados podrían indicar reconocimiento y discriminación del parásito de cría en la etapa de volantón.

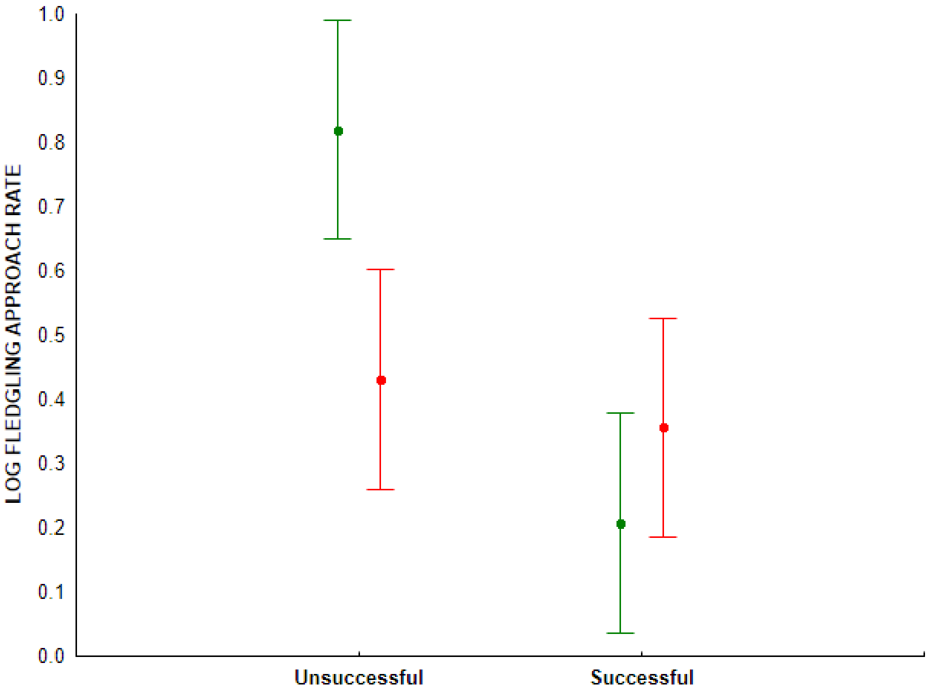

Figura 24. Comparaciones de las tasas de aproximación de los volantones de abubilla (*Upupa epops* – en rojo) y de críalo (*Clamator glandarius* – en verde) en nidadas mixtas, distinguiendo eventos de aproximación exitosos (cuando los volantones se acercaron a los adultos y fueron alimentados) de los eventos de aproximación fallida (cuando los volantones se acercaron a los adultos y no fueron alimentados). La tasa de aproximación de los volantones se calculó como el logaritmo del número de veces por hora que los volantones de abubilla/cuco se acercaron a un adulto pidiendo comida (independientemente de si fueron alimentados o no). Se muestran las medias ± errores estándar.

La fase más tardía del ciclo de pollos, es decir, cuando salen del nido y continúan con sus padres durante un cierto tiempo, es una de las etapa menos estudiada del ciclo de nidificación de las aves (Gruebler and Naef-Daenzer 2010; Matthysen et al. 2010). La discriminación de volantones parásitos solo se ha estudiado en detalle en dos sistemas parásito de cría-hospedador (De Mársico et al. 2017). El hospedador tordo músico (*Agelaioides badius*) tiene dos parásitos de cría, el tordo chillón que es especialista y el tordo brillante que es generalista (*Molothrus rufoaxillaris* y *Molothrus bonariensis* respectivamente). En este caso, el hospedador le da alimento preferentemente a los pollos del parásito especialista, ya que imitan vocal y visualmente a sus propios pollos (De Mársico et al. 2012; De Mársico et al. 2017). Otro ejemplo es la urraca (*Pica pica*) que es el hospedador principal del críalo. En este caso el hospedador es más reticente a alimentar al críalo que ha compartido nido con pollos de urracas que a críalos que se han criado solos en el nido (Soler et al. 2014a). Ambos parásitos son "no letales", por lo que darían la posibilidad al hospedador de comparar entre el parásito y sus propios pollos tanto en el nido cómo más tarde fuera de él, lo que puede ser una pista importante para favorecer la discriminación de pollos y/o volantones. Por esta razón nuestro diseño experimental también creo nidos de abubillas, pero solo con críalos. En la fase de los volantones fuera del nido, descubrimos que los volantones de críalo de nidadas mixtas recibieron menos alimentación que los volantones de críalo de nidadas exclusivas de críalo. Además, la abubilla se acercaba con más frecuencia para alimentar a los volantones de críalo criados solos, que a los volantones de críalo de nidadas mixtas, como también ocurría en las urracas (Soler et al. 2014b).

Estos resultados sugieren que la presencia de volantones de abubilla puede ayudar a los padres en el reconocimiento de los volantones de críalo en nidadas mixtas. Sin embargo, los volantones de críalo que se criaron solos en el nido (sin posibilidad de discriminación con sus hermanos) también murieron igual que los criados en nidadas mixtas (Figura 23). Este implica que, contrariamente a lo que se ha sugerido (Fraga 1998; De Mársico et al. 2012; Soler et al. 2014a; De Mársico et al. 2017) y de acuerdo con estudios recientes de hospedadores del cuclillo menudo (*Chrysococcyx minutillus)* (Sato et al. 2015; Attisano et al. 2018), no es necesaria la presencia de volantones propios del hospedador para la evolución de la discriminación de volantones del parásito.

La existencia de capacidad de discriminación de los volantones de críalo por parte de la abubilla indicaría que esta especie ha sido parasitada al menos en el pasado. Sin embargo, el éxito de los volantones de críalo en nuestras nidadas de abubillas parasitadas experimentalmente (40%) no es tan bajo como para concluir que ha sido abandonado como huésped por el desarrollo de defensas, como lo predice la hipótesis de alternancia coevolutiva (Davies and Brooke 1989; Nuismer and Thompson 2006).

Una posibilidad es que los niveles bajos de defensa de la abubilla (60%) podrían explicarse porque las variables de la historia de la vida del hospedador pueden reducir la probabilidad de parasitismo, disminuyendo la presión del parásito por el hospedador y no provocando niveles más altos de reconocimiento (Roskaft et al. 2002; Aviles et al. 2005; Martín-Vivaldi et al. 2013; Thomson et al. 2016). Las abubillas tienen dos características que habrían dificultado el parasitismo del críalo a lo largo de la historia evolutiva de ambos. Por un lado, la dificultad de encontrar nidos para los parásitos y por otro, la dificultad de poner el huevo dentro de los nidos (debido al pequeño tamaño de algunas entradas de nido en especies que anidan en agujeros) (Moreras et al. 2021). En resumen, la abubilla es un huésped adecuado, pero no muy parasitado ya que la dificultad de encontrar suficientes nidos utilizables habría hecho que esta especie fuera sólo un hospedador secundario, lo que explica sus bajos niveles de defensas.

CONCLUSIONES

1. Las abubillas siguen una estrategia de forrajeador de un lugar central, proporcionando las presas más rentables a los pollos y comiendo las de peor calidad. Mientras que los progenitores suministran presas más digeribles (menos contenido de quitina) a los pollos en su fase temprana de estancia en el nido, en la fase tardía los alimentan con las presas de mayor tamaño.

2. Los padres mantienen la estrategia de aprovisionamiento selectivo a la nidada, independientemente de la disponibilidad de alimento. Por tanto, aunque las condiciones ambientales sean desfavorables y la disponibilidad de alimento se vea reducida, las abubillas continúan alimentando a los pollos con las presas de mayor calidad e eficiencia energética, maximizando la entrega de energía por viaje al nido.

3. En la fase temprana de pollos, las abubillas adultas aprovisionan a los pollos con una biomasa similar tanto en condiciones de abundancia como de escasez. Sin embargo, en la fase tardía de pollos, cuando la demanda energética de la nidada y la actividad de aprovisionamiento es alta, la escasez de alimento afecta negativamente a la biomasa ingerida por los pollos, pero no a la de los progenitores. Por tanto, las abubillas no siguen la estrategia de una especie de vida corta, ya que reducen su inversión en la reproducción presente ante condiciones de escasez de alimento. De este modo, los pollos son los miembros de la familia que se ven afectados ante situaciones de escasez de alimento. La jerarquía de tamaños existente en las nidadas de abubilla podría permitir que esta estrategia solo reduzca el número de pollos, sin afectar a la condición de los supervivientes.

4. Mientras los machos muestran una estrategia de alimentación fija, independientemente de la disponibilidad de alimento, las hembras son más flexibles a los cambios en esta disponibilidad, en ambas fases del ciclo. En condiciones de escasez, las hembras reducen la proporción de presas consumidas en la etapa temprana de pollos, pero la aumentan en la fase tardía. Estas respuestas diferentes entre sexos serían un reflejo de las diferentes estrategias y roles de los dos sexos en la reproducción.

5. En la fase temprana de estancia de los pollos en el nido, antes de que se produzca la reducción de nidada, las hembras de abubilla mantienen la estrategia de alimentar preferentemente a los pollos de mayor tamaño, independientemente de la

disponibilidad de alimento. Estos resultados no apoyarían la hipótesis de que las especies con reducción de nidada tengan la posibilidad de sacar adelante todos los pollos, si las condiciones de disponibilidad de alimento fuesen favorables. La abubilla invierte preferentemente en los pollos de mayor valor reproductivo incluso en condiciones de disponibilidad de alimento *ad libitum*, por lo que los pollos más pequeños parecen cumplir una función diferente a la de sobrevivir como volantones.

6. En la fase temprana de pollos, el comportamiento de petición de los pollos refleja su nivel de hambre. Cuando la disponibilidad de alimento se ve reducida, es más probable que un pollo sea alimentado cuando un pollo más grande no pide. En cambio, en situaciones de abundancia, hay más probabilidades de que un pollo sea alimentado, incluso si pide un pollo más grande. De esta forma, tanto la disponibilidad de alimento como la petición del pollo más grande, va a influir en el éxito de alimentación de cualquier pollo de la nidada.

7. Las abubillas carecen de mecanismos de reconocimiento de pollos de críalo dentro del nido, siendo éstos alimentados con la misma frecuencia que los pollos de abubilla, incluso en nidadas mixtas, donde la hembra de abubilla tiene la posibilidad de comparar entre los pollos de las dos especies.

8. Las abubillas parecen reconocer a los volantones de críalo, tanto cuando hay pollos de abubilla con los que comparar, como cuando solo hay volantones de críalo. Este comportamiento apunta a que las abubillas han sufrido cierto grado de parasitismo interespecífico, apareciendo las defensas solo en una fase tardía de la reproducción.

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