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Avian sibling cannibalism: Hoopoe mothers regularly use their last hatched nestlings to feed older siblings

Juan José Soler^{1,2,#,*}, Manuel Martín-Vivaldi^{2,3,#,*}, Soňa Nuhlíčková⁴, Cristina Ruiz-Castellano¹, Mónica Mazorra-Alonso¹, Ester Martínez-Renau¹, Manfred Eckenfellner⁵, Ján Svetlík⁴, Herbert Hoi^{5,*}

¹ Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas (EEZA-CSIC), Almería E-04120, Spain

² Unidad Asociada Coevolución: Cucos, Hospedadores y Bacterias Simbiontes, Universidad de Granada, Granada E-18003, Spain

³ Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, Granada E-18003, Spain

⁴ Department of Ecology, Faculty of Natural Sciences, Comenius University, Bratislava SK-84215, Slovakia

⁵ Konrad Lorenz Institute of Ethology, Department of Interdisciplinary Life Sciences, University of Veterinary Medicine, Vienna A-1160, Austria

ABSTRACT

Sibling cannibalism is relatively common in nature, but its evolution in birds and certain other vertebrates with extended parental care had been discarded. Here, however, we demonstrate its regular occurrence in two European populations of the Eurasian hoopoe (*Upupa epops*) and explore possible adaptive and non-adaptive explanations. Results showed that sibling cannibalism was more frequently detected in Spain (51.7%) than in Austria (5.9%). In these two populations, the hoopoes laid similar clutch sizes, resulting in similar fledging production, but hatching failures were more frequent in the northern population. Consequently, having more nestlings condemned to die in the southern population may explain the higher incidence of sibling cannibalism. In accordance with this interpretation, hatching span and failure, but not breeding date, explained the probability of sibling cannibalism in the Spanish hoopoes, while all three variables predicted brood reduction intensity.

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Furthermore, experimental food supply reduced the probability of sibling cannibalism, but not the intensity of brood reduction. Finally, females allocated fewer resources to the smallest nestlings when they were going to starve, but not necessarily when they were going to be used as food for their siblings. These results suggest that hoopoes produce extra eggs that, in the case of reduced hatching failure and food scarcity, produce nestlings that are used to feed older siblings. These findings provide the first evidence that sibling cannibalism occurs regularly in a bird species, thus expanding our evolutionary understanding of clutch size, hatching asynchrony, parent-offspring conflict, infanticide, and sibling cannibalism in the animal kingdom.

Keywords: Brood reduction; Clutch size; Hatching asynchrony; Ice-box hypothesis; Infanticide; Siblicide; Sibling hierarchy; *Upupa epops*

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*Authors contributed equally to this work

*Corresponding authors, E-mail: jsoler@eeza.csic.es; mmv@ugr.es; Herbert.Hoi@vetmeduni.ac.at

INTRODUCTION

Cannibalism was originally deemed as an abnormal or unnatural behavior in the animal kingdom (Dawkins, 1976; Maynard Smith & Price, 1973). However, this view has changed dramatically over the past few decades, and it is now recognized to be adaptive, phylogenetically widespread, and relatively common in nature (Elgar & Crespi, 1992; Hausfater & Hrdy, 1984; Hrdy & Hausfater, 1984; Polis, 1981).

Sibling cannibalism has been described in a wide range of animal taxa. In most cases, siblings are cannibalized to provide energy and resources during periods of low food abundance (Polis, 1981, 1984; Polis & Myers, 1985). Some invertebrate and arthropod females produce eggs that serve as the first source of postnatal nutrition (Crespi, 1992). In certain vertebrates, such as salamanders, sharks, and fish (Crump, 1992; Fitzgerald & Whoriskey, 1992), sibling cannibalism occurs during the embryonic phase within the mother's body. Sibling cannibalism of newborn offspring is also phylogenetically widespread (Elgar & Crespi, 1992). Typically, the smallest individuals of a brood are at a greater risk of being eaten by the largest ones, and sibling cannibalism is related to within-brood birth and body size asynchrony (Baur & Baur, 1986; Eickwort, 1973; Polis, 1981). Thus, inducing birth asynchrony can be seen not only as a maternal strategy facilitating brood-size adjustment to environmental conditions, as suggested by the brood reduction hypothesis (Lack, 1954), but also favoring sibling cannibalism of particular offspring (Alexander, 1974), at least in the absence of physical constraints (see below).

Although hatching asynchrony is common in birds, sibling cannibalism is very rare (Bortolotti et al., 1991; Ingram, 1962; Stanback & Koenig, 1992) and, thus, the use of last hatched nestlings as a food resource, as posited by the larder hypothesis (or ice-box hypothesis (Alexander, 1974)), is thought to be irrelevant for such species (Mock & Parker, 1998). In general, it would be far easier for parent birds to increase provisioning efforts than to raise additional nestlings to serve as sibling food, thus the benefits to produce extra eggs as back-up food should hypothetically be restricted to species that do not feed their offspring (Stoleson & Beissinger, 1995). Laying extra eggs to hatch asynchronously may not be due to their future use as food, but may serve several functions, including insurance against hatching failures or facilitation of brood-size adjustment (Lack, 1954; Stoleson & Beissinger, 1995). Then, once an "extra" nestling dies, parents or siblings could take advantage and use the body as food. However, even for avian species with obligate siblicide, such as found in raptors, skuas, and pelicans (Morandini & Ferrer, 2015), where dead offspring could be consumed by surviving offspring (Bortolotti et al., 1991), there is very little evidence of sibling cannibalism (Stanback & Koenig, 1992). Three arguments have been proposed to account for the rare occurrence of sibling cannibalism in birds related to avian-specific anatomical, physiological, behavioral, or social characteristics (Mock, 1984; Stanback & Koenig, 1992). The first argument posits that the rapid developmental rate of most bird species reduces the difference in body size between the oldest and youngest nestlings, preventing the former from

killing and feeding on the latter. The second argument predicts that sibling cannibalism needs parental complicity. Even when species show extreme asymmetries in nestling size, nestlings do not actively take food but are fed by their parents, at least during the hatching period when size asymmetries are greatest. The final argument suggests that most bird species cannot dismember prey with their bills, thus cannibalistic nestlings would have to swallow their siblings whole. These arguments would restrict sibling cannibalism to species with extreme hatching asynchrony, and thus extreme sibling size hierarchy, and with beaks that allow them to tear food apart or with a gape wide enough to swallow a nestling whole. Otherwise, sibling cannibalism during the nesting phase could only occur with the complicity of parents, who would have to commit infanticide to feed their older offspring with younger siblings (Mock, 1984; Stanback & Koenig, 1992).

In this study, we investigated sibling cannibalism in the Eurasian hoopoe (*Upupa epops*) and explored possible influencing factors. Briefly, after quantifying the prevalence of sibling cannibalism in two different populations (Spain and Austria) during different breeding seasons, we explored predictive particularities of the breeding biology of hoopoes that may explain the high rate of sibling cannibalism. For instance, as hoopoes cannot tear prey apart, body size differences between nestlings must be large enough to mechanically allow the oldest to swallow the youngest whole (Stanback & Koenig, 1992). Time elapsed between the first and last hatchings (hatching span) is the main determinant of nestling size asymmetry. As such, we predicted a positive relationship between hatching span and the probability of sibling cannibalism.

As mentioned above, sibling cannibalism in hoopoes may be a consequence of the presence of dead nestlings, or nestlings condemned to die. According to the brood reduction hypothesis (Lack, 1954; Stoleson & Beissinger, 1995), hoopoes adjust brood size to environmental conditions based on food availability (Hildebrandt & Schaub, 2018), thus nestlings that will or have died due to limited food availability could be used by adults to feed older nestlings. In this case, the intensity of brood reduction and occurrence and intensity of sibling cannibalism should be related to each other, and both should depend on variables related to food availability (i.e., latitude, time of breeding, and experimental food supplementation). The availability of food is expected to be higher in northern populations (Lundblad & Conway, 2021; Nuhlíčková et al., 2016; Olson et al., 2009), while a decrease in food availability can be expected over the course of the breeding season (De Neve et al., 2004; Sorci et al., 1997). Consequently, we predicted that both the prevalence of sibling cannibalism and extent of brood reduction would be higher in Spain, particularly at the end of the breeding season. We also tested the effect of food availability on sibling cannibalism and brood reduction experimentally. The food supplementation experiment started one or two days prior to the end of the hatching period and ended two or three days after the last egg hatched, which is the period when sibling cannibalism occurs. Thus, we expected that the prevalence and intensity of sibling cannibalism and brood reduction would be lower in experimentally supplemented nests than in control nests.

The intensity of brood reduction depends not only on food availability, but also on brood size, which, in turn, depends on clutch size and hatching success. This is mainly because large clutches that hatch asynchronously may facilitate brood-size adjustment to environmental conditions (Brood Reduction Hypothesis; Lack, 1954) and ensure an optimistic brood size in case of hatching failure (Insurance Hypothesis; Forbes, 1990, 1991; Hardy, 1992). Hoopoes lay large clutches and experience high rates of hatching failure (Soler et al., 2008). Thus, it is possible that large clutches not only reflect the brood size that adults can raise under unrestricted food availability, but also include some “extra eggs” to prevent suboptimal brood sizes in the event of hatching failure. In this case, the intensity of brood reduction, and consequently sibling cannibalism, should be higher in clutches with lower hatching failures. We explored this possibility as it suggests that some cannibalized nestlings may act as insurance against hatching failure and that, without such failures, they are surplus.

A final prerequisite for the occurrence of sibling cannibalism is that parents facilitate the intake of smaller offspring by their older siblings. In hoopoes, most brood reduction events occur at the end of the hatching period and a few days after (Ryser et al., 2016). During this period, females spend most of their time in the nest and are responsible for feeding the nestlings with food delivered to the nest by their mate (Díaz Lora et al., 2020). Thus, mothers not only determine clutch size and hatching span, but also control food allocation among the brood, including the use of the smallest to feed the older offspring. To distinguish between the above-described scenarios explaining the high rate of sibling cannibalism in hoopoes, it is important to know whether females use the smallest nestlings as offspring food just before or after their death. In addition, if females use live offspring as prey, it would be interesting to know whether cannibalized nestlings are in poor physical condition (i.e., runts) or just recent hatchlings of small size, rather than undernourished. Here, we recorded the behavior of females within 58 hoopoe nests in Spain to identify sibling cannibalism and gather information on the characteristics of nestlings used as prey by their mothers.

MATERIALS AND METHODS

Ethics statement

The study was conducted according to relevant Spanish national (Decreto 105/2011, 19 de abril) and regional guidelines. All necessary permits for hoopoe manipulation were provided by Consejería de Medio Ambiente de la Junta de Andalucía, Spain (Ref: SGYB/FOA/AFR/CFS and SGMN/GyB/JMIF). The study area is not protected, but privately owned, and we obtained permission from the owners to work in the properties. Time spent in each hoopoe nest was the minimum necessary for the experiment. The Austrian research was carried out in accordance with ARRIVE guidelines and the EU Directive 2010/63/EU for animal experiments. The study also adhered to the requirements of Austrian welfare laws. Permission to work with the common hoopoes was provided by the government of Lower Austria (license number RU5-BE-7/010-2011; BD2-N-200/057-2005).

Ethical approval and licenses were obtained under the institutional guidelines of the Austrian Academy of Sciences.

Study species

Hoopoes are migratory birds distributed throughout Europe, Asia, and Africa. They inhabit open woodlands or open steppes, grassland, pasture, semi-deserts, or crops with scattered trees, walls, or buildings providing holes for nesting and soil without tall vegetation for feeding (Barbaro et al., 2008; Rehsteiner, 1996; Schaub et al., 2010). Females usually lay one or two clutches of 6–9 (range=4–12) eggs during February–July, but only rarely do pairs succeed in producing more than six nestlings in a breeding attempt (Martín-Vivaldi et al., 1999; Plard et al., 2018). Asynchronous hatching is a consequence of females incubating from the laying of the first or second egg, which produces a considerable size hierarchy within the brood (Martín-Vivaldi et al., 1999). Only females incubate, but both sexes care for the offspring. Males feed females during incubation and early in the chick rearing phase (Díaz Lora et al., 2020). Once the oldest chick is about 10 days old, both male and female provision the offspring directly until fledging (24–30 days post-hatch) (Martín-Vivaldi et al., 2014).

Study areas and general fieldwork

The Spanish population is located in Guadix (N37°18', W38°11') in the south-eastern Iberian Peninsula, where hoopoes breed in nest boxes (5.5 cm (entrance diameter), 24 cm (bottom-to-hole height), 35 cm×18 cm×21 cm (internal height×width×depth)) made from cork and placed in trees or buildings. From early March to late July during the three study years (2017–2019), nest boxes were visited weekly until hoopoe eggs were detected, and then every third day until the end of egg-laying to detect clutch size. The study years represented typical conditions of the semiarid environment, with low average rainfall in May (0.01 mm in 2017 to 1.6 mm in 2018) (Huéneja Meteorological Station; N37°12'54", W02°57'48"; see <https://www.juntadeandalucia.es/agriculturaypesca/ifapa/riaweb/web/estacion/18/102#hist>). Assuming that hoopoe females lay one egg per day, that incubation is initiated after laying the second egg, and that the incubation period is 18 days (Martín-Vivaldi et al., 1999), we visited the nests again 18–22 days after the day the first egg was laid to determine the hatching date of the first nestling. Once hatchlings were detected in the nest, we visually established nestling age and estimated the expected hatching date of the penultimate or last egg, at which time food supplementation and video recording inside nest boxes commenced (see Supplementary Materials for details on equipment installation) (2019, see below). Nests not subjected to food supplementation (2017–2018) were again visited 8 days after hatching to estimate brood size and hatching failures, and again at the end of the nestling period to estimate brood reduction.

The Austrian population is located in the wine-growing region of Wagram (119 km², 230–350 m a.s.l., N48°45'–48°47'; E15°66'–15°73'), Lower Austria. The region is a traditionally cultivated landscape comprised of southern-exposed slopes covered mostly (80%) with vineyards. The

entire hoopoe population breeds in wooden nest boxes (6 cm entrance diameter and 24 cm bottom-to-hole height, 50 cm×35 cm×25 cm (height×width×depth)) (Nuhlíčková et al., 2016). To simulate natural breeding site conditions, the nest boxes were placed in loess walls or hidden in abandoned wooden cottages (Krištofik et al., 2013). Nests were inspected regularly during April to July (2009–2010) for purposes other than detecting cannibalistic infanticide. As in the Spanish population, we visited nest boxes weekly until hoopoe eggs were detected inside, then inspected the nests after three weeks to detect hatching date, and a few days before fledging. These nest visits allowed us to estimate reproductive variables to compare with the Spanish population. Camera recording (see Supplementary Materials for details on equipment installation) began when the oldest nest-mate was able to move around the nest-box (~10 days old, when all eggs were usually hatched). The two study years (2009–2010) represented different environmental conditions. In the wet year (2010), measurable rainfall was about one and a half times that in 2009 (May 113 mm vs. 79 mm, respectively) (Langenlois Meteorological Station; N48°28' , E15°41' ; see <http://www.zamg.at>). For the purposes of the current study, we followed 67 broods (29 nests in 2009 and 38 nests in 2010).

During the 2017–2018 breeding seasons, we frequently recorded sibling cannibalism in the Spanish population in late hatching (i.e., June–July) hoopoe nests with brood sizes larger than seven nestlings (50.5% ($N=6$) and 54.5% ($N=11$) of the recorded hoopoe nests in 2017 and 2018, respectively). During the 2019 breeding season, we evaluated the intensity and prevalence of sibling cannibalism in the entire Spanish hoopoe population. We recorded videos of all available hoopoe nests during the time period when sibling cannibalism occurred (i.e., at the end and few days after the hatching period) and gathered information to explore the possible influencing factors predicted to affect both the extent of brood reduction during that period and the occurrence of sibling cannibalism (i.e., clutch size, hatching date, hatching failures, brood size, hatching span, and experimentally supplemented food).

In 2019, when food was supplemented and most Spanish hoopoe nests were video recorded ($N=58$), we directly observed sibling cannibalism in 21 out of the 30 nests in which cannibalism was assumed it has occurred. In the nine nests where sibling cannibalism was not physically recorded, we observed females handling small nestlings as prey, with nestlings found to have disappeared from those nests after video recording failure. In Austria, of the 48 hoopoe nests that showed brood reduction, the bodies of small nestlings that died a few days after hatching were found in 42 nests at the end of the nestling period. Of the six nests where dead nestlings were not detected, sibling cannibalism was directly observed in two. Thus, in Austria, indirect inferences of sibling cannibalism were based on the sudden disappearance of nestlings between consecutive nest visits.

Food supplementation experiment

For the food supplementation experiment, we added 20 (approximately 15 mL) crickets (*Gryllus campestris*) to the experimental nests, with the remaining nests maintained as

the control. Fresh crickets were frozen and stored at -20°C for a maximum of 15 days. The head and feet of the frozen crickets were removed, and they were maintained at room temperature for a minimum of 3 h before being introduced into the hoopoe nests. Hoopoe females in the experimental nests rapidly detected experimental crickets in the nest box and used all of them to feed their offspring and themselves (Supplementary Video S1). Supplemented crickets were usually only available for 1–2 h.

Nest boxes under experimental and control treatment were visited daily to add the crickets to the nests and to renew batteries and SD memory cards. The experiment started one or two days before the last hoopoe egg hatched and continued until sibling cannibalism was directly detected or inferred from the disappearance of smaller nestlings, or the second or third day after the end of hatching, when body mass of the small living nestlings was close to 10 g, or dead nestlings in the nest boxes were decaying. On the last day of recording, we weighed all nestlings in the nests with a digital balance (Ascher, China; accuracy 0.01 g) and established body-mass hierarchy (body mass of largest nestling divided by body mass of smallest sibling). When sibling cannibalism occurred, we conservatively assumed 4 g (weight of healthy one-day-old nestling) for those nestlings that disappeared when estimating the level of brood hierarchy. Based on daily nest visits and video recordings, we determined the hatching date of the last egg and estimated hatching span (number of days elapsed from hatching of first to last egg), hatching failure (number of eggs that failed to hatch), and brood reduction (number of nestlings that died during the experiment, i.e., approximately 10 days after the older nestlings hatched).

We assigned hoopoe nests to experimental treatments sequentially depending on hatching date and brood size, i.e., we concentrated on nests with more than four successfully hatched eggs. We did so because broods smaller than five rarely occurred in nests of the Spanish population (data from non-experimental hoopoe nests followed in 2017–2018: 2.86%, $N=105$), where we observed brood reduction only sporadically (one out of three nests with brood size lower than five). Thus, 22 and 26 hoopoe nests with a brood size larger than four were assigned to the experimental and control groups, respectively. It should be noted that the experimental effects did not vary qualitatively (i.e., statistical significance) when including the nine nests with brood sizes less than four in analyses, nor when restricting analyses to nests where sibling cannibalism was directly observed (results not shown). Moreover, we included first and second breeding attempts in 10 nest boxes. In four of these, brood size was lower than five in one of the breeding attempts, and thus was excluded from one set of analyses. In the remaining six nest boxes, the first and second breeding attempts received different experimental treatment, with four showing different experimental outcomes between the first and second reproductive events. Thus, nest-box identity did not predict experimental outcome, and therefore first and second experimental events were considered statistically independent. Finally, we did not detect any bias associated with clutch size, hatching date, hatching failure, hatching span, and brood size of experimental and control nests (all $F_{1,46} < 1.11$, all $P > 0.29$).

Video recordings during the 2019 breeding season were also used to study female provisioning behavior and evaluate whether they neglected the small last-hatched chicks in the nest (as previously suggested by direct observations (Martín-Vivaldi et al., 1999)). Whenever possible, we used recordings from the day when the last eggs hatched, and when experimental crickets were not available in the nests. Evaluation of female provisioning behavior started 1 h after the recording equipment was recharged. Briefly, we divided the brood into small-, medium-, and large-sized nestlings that could be visually differentiated, and then counted the number of feeds that the different-sized nestlings received over a 2 h and 15 min period. We then assessed the average number of feeds for each group of nestlings by considering the number of nestlings within each group and estimated the feeding rates of the different-sized nestlings as the average value of each group divided by the sum of the averages of all three groups. Due to recording problems, we were unable to visualize female feeding behavior in 10 of the 58 filmed nests.

Statistical analyses

To explore changes in variables describing hoopoe breeding biology based on study year and population, we used information collected from the Spanish population during the 2017–2018 breeding seasons and Austrian population during the 2009–2010 breeding seasons. Factors affecting the probability of sibling cannibalism, including those related to the experimental food supply, were explored using data collected from the Spanish population in 2019, when we focused on frequency of sibling cannibalism in the population.

Between-population comparisons were carried out using univariate analysis of variance (ANOVA) and Chi-square statistical tests. The effects of food supplementation on the probability of cannibalism and brood reduction were explored using generalized linear models with binomial distribution and logit link function (GLZ). The models included laying date and hatching span as additional continuous independent factors. Likelihood type 3 tests were used to estimate two-tailed *P*-values. The general linear models were used to explore the effects of experimental treatment, hatching date, and hatching span on the intensity of brood reduction and sibling cannibalism in the experimental hoopoe nests. Pearson correlation was employed to explore the associations between preference for feeding smaller nestlings and magnitude of brood reduction, hatching date, and hatching span. Statistical analyses were performed using Statistica (v13, Dell-Inc, 2015).

RESULTS

Breeding biology and sibling cannibalism: between-population and year comparisons

The Austrian and Spanish hoopoes laid clutches of similar size, and although significant among-year variation was detected in both populations, hatching failure (i.e., number of eggs that failed to hatch) was more frequent and intense in the Austrian nests than in the Spanish nests (Table 1). Consequently, at the end of the hatching period, the Austrian broods were significantly smaller than the Spanish broods.

Although significant annual variation in brood reduction intensity was detected in both populations, it was significantly higher in the Spanish population (Table 1). Interestingly, the prevalence of brood reduction in the Spanish and Austrian populations did not differ significantly (Table 1). We also detected between-population differences in brood size (number of hatched chicks) and brood-reduction intensity (number of nestlings that died during nestling period), but not in fledgling production (Table 1).

In the Austrian population, sibling cannibalism (Supplementary Video S2) was slightly, but non-significantly, more frequent in 2010 (13.16%, *N*=38) than in 2009 (3.33%, *N*=30) ($\chi^2_1=2.01$, *P*=0.156). Moreover, independent of the study year, the prevalence of sibling cannibalism was consistently higher in the Spanish (51.72%, *N*=58, data from 2019 breeding season) than in the Austrian population (2009: $\chi^2_1=20.29$, *P*<0.0001; 2010: $\chi^2_1=14.74$, *P*=0.0001). Interestingly, when sibling cannibalism occurred in the Spanish population (8–10 days after the first egg hatched), and as a consequence of the extreme hatching span (mean (CI 95%)=5.62 (5.18–6.06) days), the body mass of the oldest nestling (mean (CI 95%)=37.5 g (34.9–40.2) g, min-max=16.0–63.0 g, *N*=54) was almost an order of magnitude greater than that of the youngest nestling (mean (CI 95%)=5.5 (4.5–6.6) g, min-max=1.7–23.4 g, *N*=54).

Factors affecting sibling cannibalism and brood reduction in Spain

Hatching span was the factor most closely associated with the prevalence and intensity of sibling cannibalism and brood reduction that occurred during the first 10 days after the first egg hatched (Table 2). Supplementation of food at the end of the hatching period significantly reduced the probability of sibling cannibalism (Figure 1), but not its intensity (Table 2). Experimental food did not affect the prevalence (Figure 1) or intensity of brood reduction (Table 2). Finally, brood reduction intensity, but not sibling cannibalism, increased as the season progressed (Table 2).

In addition to the 30 (*N*=58) nests in which sibling cannibalism was detected in Spain during the 2019 breeding season, females themselves were observed cannibalizing offspring in three nests (Supplementary Video S3), and one male was recorded entering another nest and picking up a small nestling as if it was prey (Supplementary Video S4). The intensity of cannibalism by either sibling or adult increased with clutch size (*Beta* (*SE*)=0.36 (0.12), $F_{1,55}=9.41$, *P*=0.003) and decreased as hatching failures increased (*Beta* (*SE*)=−0.29 (0.12), $F_{1,55}=6.09$, *P*=0.017, Figure 2). The same patterns were detected when trying to explain brood reduction intensity (Clutch size: *Beta* (*SE*)=0.43 (0.12), $F_{1,55}=13.70$, *P*<0.001; hatching failures: *Beta* (*SE*)=−0.25 (0.12), $F_{1,55}=4.73$, *P*=0.034, Figure 2). Moreover, clutch size did not predict hatching failures (*R*=−0.06, *N*=58, *P*=0.64), and thus brood reduction intensity was closely related to cannibalism intensity (*R*=0.77, *N*=58, *P*<0.0001) (Figure 2).

Female provisioning behavior, infanticide, brood reduction, and cannibalism

Only 10.4% (CI 95%=8.7–13.0%, *N*=50 nests) of feeding

Table 1 Life history traits of Spanish and Austrian hoopoes in two different study years

Between-year comparisons			Comparisons		
	Mean (CI 95%)	Mean (CI 95%)	Stat.	df	P
Spanish population	2017 (N=61)	2018 (N=44)			
Clutch size	7.23 (6.93–7.53)	7.57 (7.16–7.97)	F=1.92	1,103	0.169
Hatching failures	0.70 (0.45–0.96)	1.14 (0.83–1.44)	F=4.81	1,103	0.031
Hatching failure prevalence	44.26%	70.45%	χ²=7.09	1	0.008
Brood size	6.56 (6.27–6.84)	6.43 (6.02–6.84)	F=0.27	1,103	0.602
Fledgling production	3.78 (3.39–4.17)	4.45 (3.98–4.92)	F=5.62	1,103	0.020
Brood reduction	2.82 (2.37–3.26)	1.98 (1.50–2.45)	F=6.53	1,103	0.012
Brood reduction (Day 8)	1.23 (0.89–1.57)	1.61 (1.18–2.04)	F=1.94	1,104	0.166
Brood reduction prevalence	86.9%	75.0%	χ ² =2.44	1	0.119
Austrian population	2009 (N=29)	2010 (N=38)			
Clutch size	7.59 (7.04–8.13)	6.58 (6.08–7.08)	F=7.62	1,65	0.007
Hatching failures	2.17 (1.51–2.83)	1.32 (0.88–1.75)	F=5.29	1,65	0.025
Hatching failure prevalence	82.76%	68.42%	χ ² =1.79	1	0.181
Brood size	5.41 (5.03–5.80)	5.26 (4.84–5.69)	F=0.27	1,65	0.606
Fledgling production	4.66 (4.09–5.22)	3.68 (3.16–4.21)	F=6.43	1,65	0.014
Brood reduction	0.76 (0.40–1.12)	1.58 (1.22–1.93)	F=10.5	1,65	0.002
Brood reduction prevalence	51.7%	86.84%	χ²=9.98	1	0.002
Between-population comparisons					
	Spain (2017–18)(N=105)	Austria (2009–10)(N=67)			
	Mean (CI 95%)	Mean (CI 95%)			
Clutch size	7.37 (7.13–7.61)	7.01 (6.64–7.39)	F=2.77	1,170	0.098
Hatching failures	0.89 (0.69–1.08)	1.69 (1.31–2.07)	F=16.7	1,170	<0.001
Hatching failure prevalence	55.24%	74.63%	χ²=6.58	1	0.010
Brood size	6.50 (6.27–6.74)	5.33 (5.04–5.61)	F=39.6	1,170	<0.001
Fledgling production	4.04 (3.74–4.34)	4.10 (3.71–4.50)	F=0.07	1,170	0.789
Brood reduction	2.47 (2.14–2.80)	1.22 (0.96–1.49)	F=28.0	1,170	<0.001
Brood reduction prevalence	81.90%	71.64%	χ ² =2.50	1	0.114

Averages, confidence intervals (CI 95%), and sample sizes of life history characteristics, including clutch size, hatching failure, brood size, fledgling production, and intensity and prevalence of brood reduction in breeding hoopoes of Spanish and Austrian populations. Sample sizes and results from between-year and between-population comparisons are also shown. Statistically significant ($P < 0.05$) differences are shown in bold. Stat.: Statistics.

Table 2 Factors affecting sibling cannibalism and brood reduction

	Sibling cannibalism						Brood reduction					
	Prevalence				Intensity		Prevalence			Intensity		
	Estimate (SE)	χ ² ₁	P	Beta (SE)	F _{1,44}	P	Estimate (SE)	χ ² ₁	P	Beta (SE)	F _{1,44}	P
Hatching date	0.017 (0.014)	1.46	0.226	0.212 (0.133)	2.53	0.119	-0.009 (0.025)	0.12	0.726	0.386 (0.109)	12.43	0.001
Hatching span	0.695 (0.299)	7.03	0.008	0.393 (0.134)	8.54	0.005	2.628 (0.820)	37.51	<0.001	0.530 (0.111)	22.98	<0.001
Exp. treatment	0.889 (0.369)	6.65	0.010	0.220 (0.133)	2.73	0.105	0.683 (0.676)	1.31	0.287	0.132 (0.109)	1.45	0.234

Results from generalized linear model (binomial distribution and logit link function) and general linear model exploring effects of experimental food supply, hatching date (1: 1 April), and hatching span (independent factors) on prevalence and intensity of sibling cannibalism and brood reduction, respectively. Statistically significant ($P < 0.05$) differences are shown in bold.

events were directed towards the third of the brood that included the smallest nestlings. Moreover, the rate of feeding the smallest nestlings was negatively correlated with the subsequently observed brood reduction intensity ($R = -0.32$, $t_{46} = 2.31$, $P = 0.025$), but not with the probability of sibling cannibalism (logistic regression, $\chi^2_1 = 1.45$, $P = 0.228$). These results suggest that females allocate fewer resources to the smallest nestlings when they are going to starve, not necessarily because they are going to use them as prey to

feed older siblings.

In all hoopoe nests with evidence of sibling cannibalism, females were recorded handling some of the smallest offspring as prey, even when they were begging for food and did not display outward signs of poor physical condition, i.e., when not fed for several hours. Moreover, in several recorded cannibalism events, a female was observed directly removing a hatchling from an eggshell to feed to an older offspring (Supplementary Video S5). Thus, hoopoe mothers are

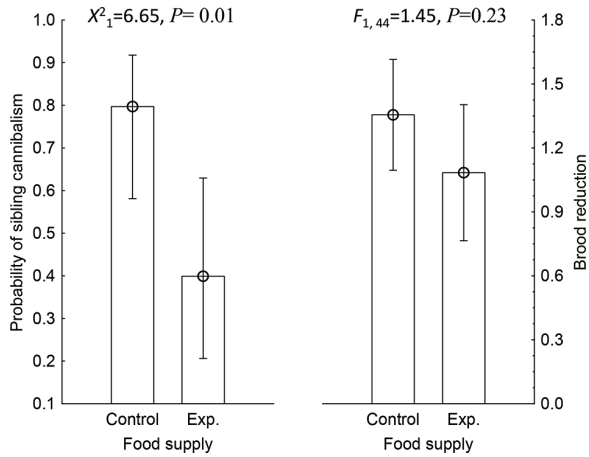


Figure 1 Sibling cannibalism and experimental food supply
 Probability of sibling cannibalism ($\pm 95\%$ CI) and number of nestling deaths in first 10 days after hatching (brood reduction) ($\pm 95\%$ CI) in hoopoe nests with experimental food supply (Exp.) or in control nests.

obviously responsible for brood reduction, including sibling cannibalism events, but the presence of nestlings in poor condition does not necessarily trigger this behavior, i.e., a high likelihood of starving does not necessarily precede sibling cannibalism.

DISCUSSION

Hoopoes lay large clutches, start incubation with the first eggs, and produce large and asynchronously hatched broods, with the last hatched chicks almost invariably dying soon after hatching. In the current study, video recordings confirmed that mothers were responsible for nestling death, either indirectly by discarding the smallest nestlings when provisioning, or directly by treating them as prey items to feed older offspring, which occurred before the nestling died and independent of its physical condition. Moreover, as expected for species that are unable to dismember prey and for which sibling cannibalism is constrained by the relative size of consumed and consumer nestlings, our results showed that hatching span was the main

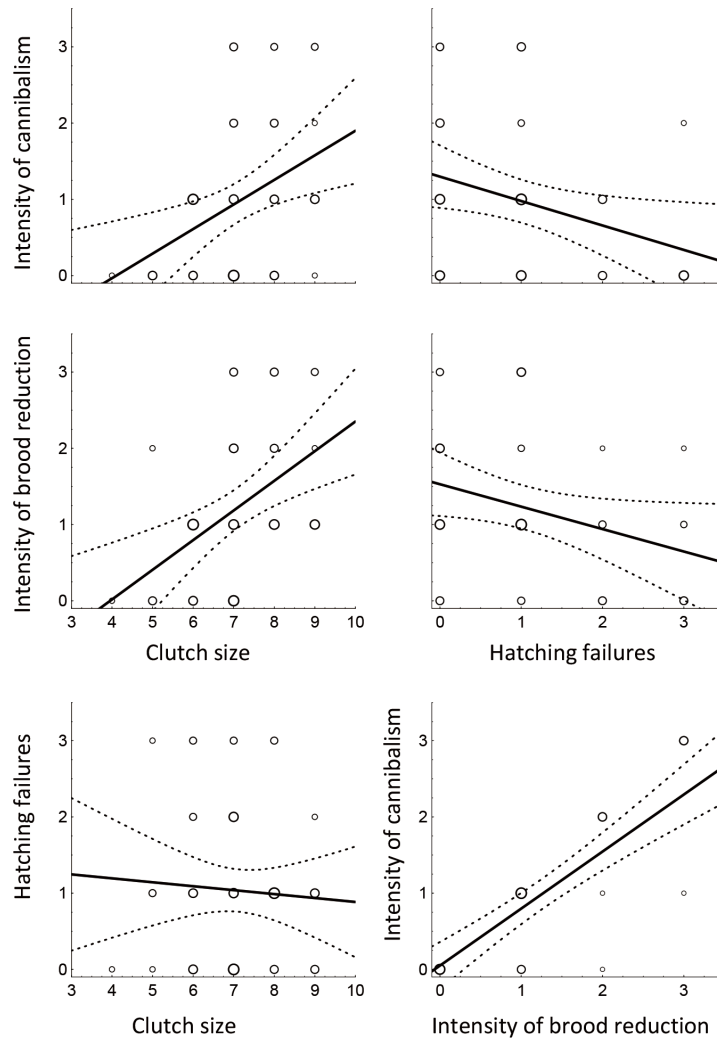


Figure 2 Cannibalism and life history traits
 Associations between intensity of cannibalism and brood reduction, clutch size, and hatching failure. Lines are regression lines and 95% CI, and point size is proportional to log-transformed number of nests with such values.

predictor of the probability and intensity of sibling cannibalism. However, many other species, such as owls (e.g., *Athene noctua* and *Otus scops*) and rollers (*Coracias garrulus*), experience longer hatching spans, but, as far as we know, do not exhibit sibling cannibalism.

Most observations of sibling cannibalism in birds occur after episodes of siblicide due to intra-brood competition under restricted nutritional conditions (Bortolotti et al., 1991; Mock, 1984; Morandini & Ferrer, 2015; Stanback & Koenig, 1992). However, this was not the case for hoopoe nestlings, as they did not show any noticeable within-brood aggression and infanticide was entirely dependent on female behavior. Killing one's own nestlings is an extreme form of parental favoritism (Caro et al., 2016; Mock, 2004; Moreno, 2012). Our results clearly showed that sibling cannibalism is a general strategy in the European hoopoe orchestrated by females, who are responsible for feeding offspring during the hatching period and for a few days afterwards. On the one hand, we detected a negative relationship between the rate of feeding the smallest nestlings and subsequently observed intensity of brood reduction, but no correlation with the probability of sibling cannibalism. This implies that sibling cannibalism, as part of the brood reduction strategy, depends less on females feeding the smallest, last-hatched nestlings than whole brood reduction. On the other hand, all recorded cases of sibling cannibalism were preceded by females treating the to-be-cannibalized nestling as prey, even when it was alive and still begging for food. In a few cases, mothers even fed older siblings with offspring just after hatching. Thus, sibling cannibalism events are not necessarily the consequence of females using nestlings in poor condition to feed older siblings, but rather the consequence of females using extra nestlings condemned to die as food to satiate largest siblings. Whether these extra nestlings are the consequence of laying extra eggs as a way to store food reserves for bad times (i.e., Larder Hypothesis (Alexander, 1974)) is a matter of debate (see below).

The intensity and prevalence of hatching failure, brood reduction, and fledging production, but not brood size, varied among study years. Austrian and Spanish hoopoes laid similar clutch sizes, resulting in similar fledging production. However, while hatching failure occurred more frequently in the northern population, brood reduction was more intense in the southern population. Sibling cannibalism, as part of brood reduction, was also more frequent in the south than in the north. Thus, it is possible that the lower rate of hatching failure makes insurance less necessary in the south, where the relatively large number of extra-nestlings are most times used as a resource to feed older nestlings. Below, we discuss the experimental and empirical results from the Spanish population concerning factors that may explain sibling cannibalism, brood reduction, and hatching failure to determine whether the first two are at least partly the result of the latter.

The supplementation of hoopoe nests with crickets (preferred hoopoe prey in the study area (Martín-Vivaldi et al., 2014)) at the end of the nestling period resulted in a reduction in the use of the smallest nestlings as food, strongly suggesting a link between food availability and sibling

cannibalism. However, the supplementation experiment did not affect the prevalence or magnitude of brood reduction during the days of food supply. The experiment only manipulated food availability for a few days during the period when most sibling cannibalism and brood reduction occurs. Moreover, the daily added crickets were consumed rapidly, and thus manipulation may not be strong enough to induce females to misinterpret environmental conditions to adjust brood size. In accordance with this possibility, hatching date, which is commonly used as a proxy of environmental conditions in general and of food availability in particular (De Neve et al., 2004; Sorci et al., 1997), showed a negative relationship with brood reduction intensity, but not with sibling cannibalism. This evidence suggests that the smallest nestlings subject to brood reduction would die anyway, and that only in the case of food scarcity would they be consumed by older siblings.

The cannibalized nestlings were mainly consumed by siblings, but also occasionally by the adult females and males. As cannibalizing results in death, not surprisingly, the intensity of cannibalism was strongly positively related to the intensity of brood reduction. In his pioneering work (1954), David Lack noted that inter- and intra-specific variations in clutch size and hatching asynchrony are adaptive, allowing birds to adjust brood size to the availability of resources at the time of peak nestling demand. Accordingly, brood reduction resulted in a positive relationship with clutch size and hatching span. In addition, large and asynchronous clutches may also function as insurance against hatching failure (Forbes, 1990, 1991; Hardy, 1992), while variation in hatching failure influences brood size and the level of brood reduction necessary to adjust the number of nestlings to environmental conditions. In agreement with this scenario, brood reduction was negatively related to the number of eggs that failed to hatch. Interestingly, clutch size did not predict hatching failure, but showed a positive relationship with intensity of cannibalism. These last two results could be interpreted as hoopoes laying extra eggs to be used as food resources after hatching, the key point of the larder hypothesis (Alexander, 1974). Producing extra eggs may be relatively cheap for hoopoes, given that females lay relatively small eggs at times of relatively high resource availability, and when they are additionally fed by their males (Díaz Lora et al., 2020). The relatively high proportion of clutches with more than six eggs, in comparison to the rare occurrence of broods with more than six fledglings in Palearctic hoopoes (Arlettaz et al., 2000; Fournier & Arlettaz, 2001; Martín-Vivaldi et al., 1999; Rieder & Schulze, 2010), could be at least partially explained by investment in the last eggs as a food cache. However, our data cannot distinguish this interpretation from the possibility that hoopoes are just using condemned-to-die nestlings as a food resource.

In cases of reduced hatching failure, the cannibalized extra nestlings may be the consequence of surplus hatchlings from “insurance” eggs. In accordance, we found that lower hatching failure was associated with a greater number of cannibalized nestlings. Thus, it is possible that hoopoe sibling cannibalism may just be the consequence of taking advantage of resources that were adaptively employed but not used as

“insurance”. However, this interpretation assumes that, at the population level, clutch size should be adjusted to the expected hatching failure level, which is not supported in the Spanish population, nor when comparing clutch size and hatching failure in hoopoes breeding in Austria and Spain. Since Spanish hoopoes laid similar clutch sizes as Austrian hoopoes, but hatching failures were more frequent in the latter, selection pressures for clutch size adjustment to environmental conditions (Sanz & Moreno, 1995) should have reduced clutch size in the Spanish population, but this did not occur. Considering that some extra-nestlings are consumed by older offspring, it is possible that selection for a smaller brood size in Spain is partially counteracted by the advantages of eating last hatchlings.

Whatever the evolutionary explanation, the most parsimonious argument for cannibalistic behavior in hoopoes is that they take advantage of nestlings that are condemned to die, because older nestlings can consume their smallest siblings. Contrary to what has been assumed in the literature, our results showed that cannibalism of last-hatched nestlings occurs frequently in hoopoes. It may also occur at similar rates in species with similar life history characteristics or in phylogenetically close species, such as the Bucerotiformes, for which anecdotal evidence of sibling cannibalism exists (Chan et al., 2007; Engelbrecht, 2013; Ng et al., 2011). Our findings may encourage research on this behavior in other bird species, while providing the opportunity to test exclusive predictions of the larder hypothesis in hoopoes. Experimental manipulations of food availability during the laying stage, together with removing or adding last-hatched nestlings to hoopoe nests, may serve this purpose. If extra eggs are laid as food caches, food-supplemented nests should contain larger clutches, while cannibalizing experimentally added nestlings should influence fledging success.

DATA AVAILABILITY

Data used in this paper can be found at <https://figshare.com/s/55775bd4f5e31a464fd2>.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

M.M.-V. detected the first recorded evidence of cannibalism in Spain in 2017 and, together with J.J.S., designed the study of the Spanish population, including the experimental approach in 2019. J.J.S., M.M.-V., M.M.-A., C.R.-C., and E.M.-R. carried out fieldwork in the Spanish population and visualized videos. J.J.S. performed statistical analyses and wrote a first version of the manuscript with great help from M.M.-V., S.N., and H.H. S.N. designed the study of the Austrian population and, together with M.E. and J.S., performed the fieldwork and wrote a first draft based on results from the Austrian population. All authors read and approved the final version of the manuscript.

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