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Extra Nestlings That Are Condemned to Die Increase Reproductive Success in Hoopoes

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ABSTRACT: The adaptive value of routinely laying more eggs than can be successfully fledged has intrigued evolutionary biologists for decades. Extra eggs could, for instance, be adaptive as insurance against hatching failures. Moreover, because recent literature demonstrates that sibling cannibalism is frequent in the Eurasian hoopoe (*Upupa epops*), producing extra offspring that may be cannibalized by older siblings might also be adaptive in birds. Here, directed to explore this possibility in hoopoes, we performed a food supplementation experiment during the laying period and a clutch size manipulation during the hatching stage. We found that females with the food supplement laid on average one more egg than control females and that the addition of a close-to-hatch egg at the end of the hatching period increased the intensity of sibling cannibalism and enhanced fledging success in hoopoe nests. Because none of the extra nestlings from the experimental extra eggs survived until fledging, these results strongly suggest that hoopoes obtain fitness advantages by using temporarily abundant resources to produce additional nestlings that will be cannibalized. These results therefore suppose the first experimental demonstration of the nutritive adaptive function of laying extra eggs in vertebrates with parental care.

Keywords: clutch size, food availability, hatching asynchrony, icebox hypothesis, sibling cannibalism, *Upupa epops*.

Introduction

Most oviparous animals lay eggs in clutches that, after the embryonic period, produce juveniles that develop to the adult stage. These animals might reproduce one or several times per year, with clutch sizes that vary greatly between and within species. Among other factors, clutch size variation depends on (i) phylogeny (i.e., evolutionary ancestor; Murphy 1989); (ii) ecological factors, including predation (Slagsvold 1984; Lima 1987; Martin et al. 2000; Dillon and Conway 2018) and other aspects of habitat quality (e.g., food availability; Grüebler et al. 2018; Michel et al. 2022); (iii) breeding strategies (e.g., laying one or several clutches per year; Geupel and DeSante 1990; O'Brien and Dawson 2013; Cornell and Williams 2016); and (iv) physical environmental conditions related to weather or latitude (Cooper et al. 2005; Høye et al. 2020; Meiri et al. 2020; Lundblad and Conway 2021). Thus, because clutch size is an important determinant of the fecundity component of animal fitness, exploring the factors explaining inter- and intraspecific variability in clutch size has attracted the attention of ecologists and evolutionary biologists for a long time (Cody 1966; Klomp 1970; Godfray et al. 1991; Stearns 2000). Selection favors laying clutches of sizes that optimize lifetime reproductive success of animals in the environment in which they are reproducing, an evolutionary framework that allows testing robust predictions of life history theory (Stearns 1992).

The application of the life history theory to clutch size variation was mainly developed for birds (Moreau 1944; Ricklefs 1980; Jetz et al. 2008), but the same principles have been broadly applied to explain fecundity in other animals, including invertebrates, and even plants (Johnson and Cook 1968; Wilson and Lessells 1994). One of the most relevant hypotheses explaining intraspecific variation in clutch size was proposed by Lack (1947) and suggests that clutch size should adjust to the number of nestlings that parents are able to rear in optimal environmental conditions. This hypothesis, on the one hand, implies that the availability of resources, not only those available at the time of laying but also the expected abundance at the peak of nestlings' food demands, should determine clutch size. On the other hand,

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the hypothesis implies that in cases of suboptimal food availability during the nestling period, broods with an excess of nestlings will be common. Because in suboptimal situations parents would not be able to raise the complete brood, adjusting brood size to environmental conditions soon after hatching would be of selective advantage. Thus, natural selection should have promoted the evolution of strategies facilitating brood reduction—the so-called brood reduction hypothesis, also proposed by Lack (1947, 1954) and revised elsewhere (Stoleson and Beissinger 1995; Stenning 1996). Hatching asynchrony, which is a consequence of starting incubation before the end of egg laying, results in a brood of nestlings of different ages that would allow parents to adaptively invest in those with higher fitness prospects (i.e., those that hatched first; Magrath 1990). Thus, although hatching asynchrony might have multiple adaptive functions (see Stoleson and Beissinger 1995), the brood reduction hypothesis nicely connects optimistic or large clutch sizes to brood sizes that have to be adjusted to the availability of resources at the peak of food demands.

Laying optimistic clutch sizes that hatch asynchronously may have functions other than facilitating brood size adjustment. For instance, it might serve as insurance against possible hatching failures or the early death of first-hatched offspring (the insurance hypothesis; Forbes 1990, 1991; Hardy 1992). Furthermore, last-hatched nestlings might also increase the probability of survival of their older siblings by, for instance, helping to increase the signals of need of the whole brood, eliciting parents to work harder, while older nestlings would be the recipients of the extra work (Caro et al. 2016; Soler et al. 2022*b*). Another possibility of last-hatched nestlings facilitating the survival prospect of their older siblings is that they are used as food to feed their older siblings (the icebox hypothesis; Alexander 1974). A female who experiences a surplus of resources during laying but faces uncertain food resources after hatching might invest those surplus resources into a "larder" that can be used to feed siblings later. Thus, the icebox (or larder) hypothesis suggests that when the resources are abundant at the time of laying, females might pack them as extra eggs to feed older siblings during periods of food shortage. The use of extra eggs as packed food for first-hatched offspring has been described in invertebrates (Crespi 1992; Perry and Roitberg 2006; Osawa 2022) and vertebrate animals, including fishes and amphibians (Crump 1992; Fitzgerald and Whoriskey 1992). However, its application had been considered unlikely to be relevant for birds (Stoleson and Beissinger 1995) because of physical constraints impeding sibling cannibalism (e.g., nestling birds are unable to tear apart or swallow smaller siblings whole) and the apparent relatively low cost of obtaining food during offspring peak demands for species with parental care (Mock 1984; Magrath 1990; Stanback and Koenig 1992). Thus, apart from species that are able to tear apart prey items, avian sibling cannibalism should be restricted to species with extreme nestling size hierarchy (i.e., hatching asynchrony). Yet some recently published evidence suggests that sibling cannibalism occurs among different groups of birds (Ben-Dov et al. 2006; Chan et al. 2007; Ng et al. 2011), with the clearest evidence obtained in the Eurasian hoopoe (*Upupa epops*; Soler et al. 2022*a*). Testing the icebox hypothesis requires validating several key assumptions by (1) providing evidence that the largest nestlings consume the smallest ones, (2) demonstrating that females are able to lay extra eggs as a response to sporadic increases in resource availability (i.e., during the laying stage; Alexander 1974; Soler et al. 2022*a*), and (3) detecting a positive fitness effect. Condemned-to-die extra nestlings that are used as food for older siblings should increase the number of fledglings.

Here, we experimentally test three key predictions of the icebox hypothesis in the Eurasian hoopoe (*U. epops*; hereafter, "hoopoe"). This species shows extreme hatching asynchrony and, soon after hatching, typically experiences intense brood reduction (Martín-Vivaldi et al. 1999; Ryser et al. 2016). Moreover, females frequently use last-hatched nestlings to feed older siblings (Soler et al. 2022*a*). All of these characteristics make hoopoes the ideal species for testing this hypothesis in birds. By experimentally increasing food availability for hoopoe females during the laying stage, we study the possibility that the females were able to convert extra food during short time periods into extra eggs that would increase clutch size and hatching span. Moreover, by removing the last-laid eggs a few days before hatching in one group of nests and adding these eggs to nests where they will hatch last, we test the prediction that sibling cannibalism should occur more frequently in hoopoe nests with an experimental extra egg. This is because our experimental approach assumes that the experimental egg will be the last to hatch, and thus our manipulation should affect not only brood size but also hatching span, which is one of the main predictors of sibling cannibalism in hoopoes (Soler et al. 2022*a*). Finally, although the added eggs are never expected to produce fledglings, we also test the expected positive effect of adding one of those extra eggs on reproductive success. Finding support for these three predictions will provide the first experimental demonstration of the nutritive adaptive function of laying extra eggs in vertebrates with parental care.

Material and Methods

Study Area and Species

This study was carried out during the breeding season of 2021 in a European population of hoopoes breeding in nest boxes in the Hoya de Guadix (37°18′N, 38°11′W), a semiarid, high-altitude plateau in southern Spain. The landscape is dominated by intensively cultivated habitats, mainly with cereal crops as well as olive and almond trees, with patches of pine forests and few holm oaks (Martín-Vivaldi et al. 2006; Soler et al. 2015). The area includes three different habitats: (1) irrigated cropland, where olives, fruit trees, and vegetables and greens are grown; (2) oak savannah with scattered pine plantations; and (3) steppe with very scarce trees and small plots of pine plantations (see Tomás et al. 2020). Approximately 400 nest boxes (35 cm height × 18 cm width × 21 cm depth, 24 cm from the bottom to hole entrance, and 5.5 cm hole diameter) are placed in trees, old cottages, piled stones, and walls throughout the three habitat types.

The hoopoe is a medium-sized, cavity-nesting, insectivorous bird with breeding seasons that extend from March to July when each female raises up to two broods per year (Martín-Vivaldi et al. 2014; Plard et al. 2018; Díaz-Lora et al. 2021). Females lay one egg per day until reaching a typical clutch size of six to eight eggs (range from 4 to 12 eggs; Martín-Vivaldi et al. 1999, 2006). They normally start incubation with the first or second egg, generating asynchronous hatching that usually spans 6 or 7 days. Females stay in the nest during the incubation period and are fed by the male (Díaz-Lora et al. 2020). The first nestlings typically hatch 17–18 days after the first egg was laid (Martín-Vivaldi et al. 1999), and when the last nestlings hatch, the first one is usually one order of magnitude heavier than the last one (Soler et al. 2022*a*). Brood reduction mainly takes place during the first 10 days after the hatching of the first egg and occurs in more than 70% of hoopoe broods (Ryser et al. 2016; Soler et al. 2022*a*). During this period, the female stays in the nest with the brood, feeding the chicks with prey items that the male carries to the nest (Martín-Vivaldi et al. 1999, 2009; Díaz-Lora et al. 2021). Then, during the main period of brood reduction, females are responsible for the food allocation patterns among nestlings of different ages (i.e., size) and therefore for the possible use of the last-hatched nestlings to feed older siblings (Soler et al. 2022*a*). Nestlings typically fledge 24–30 days after hatching (Martín-Vivaldi et al. 2014).

Fieldwork and Performed Experiments

At the beginning of the breeding season, nest boxes were visited every 4 days until hoopoe eggs were detected. Nest boxes detected with signs of hoopoes starting to reproduce (females close to the nest box or presence of small hollows in the nest materials) were visited every 3 days, maximizing the probability of detecting the start of the laying period. The hoopoe nests detected with four or fewer eggs were alternately assigned to one of the two experimental treatments of the food supplementation experiment. Each day, experimental nests ($N = 27$) received approximately 20–25 dead crickets (genus *Gryllus* or *Acheta*), a common prey of hoopoes (Fournier and Arlettaz 2001; Hoffmann et al. 2015; Guillod et al. 2016; Ryser et al. 2016). The food supplementation treatment consisted of emptying a Falcon tube (15-mL tube filled with crickets) through the nest box entrance. Control nests ($N = 22$) were also visited daily, and an empty Falcon tube was partially introduced through the nest entrance. Hoopoe nests that were found with more than four eggs ($N = 23$) were considered "natural nests" and were visited only on days 3, 10, and 19 after the hatching of the first chick.

During the laying period, we observed the inside of both experimental and control nests daily by using a portable endoscope that allowed us to inspect the breeding activity and the number of eggs laid per female (clutch size). On the day when no new egg was detected, we marked the last-laid egg, which is easily distinguished by its coloration (Soler et al. 2014), and stopped the food supplementation treatment. An interaction between habitat type and experimental treatment explaining clutch size was not statistically significant (see electronic supplementary material [ESM] 1; fig. S1; ESM 1–3 and figs. S1, S2 are available online) and was not considered in subsequent analyses. The experimental food supply did not affect hatching failure, and its expected effect on brood size did not reach statistical significance, possibly because of the reduced sample size caused by nest predation or desertion (see ESM 1). Importantly, natural and control nests did not differ in reproductive parameters, such as clutch size, hatching failures, and brood size, suggesting that our daily visits during the laying period did not affect hoopoes' reproduction (see ESM 2; table S2; tables S1, S2 are available online).

Hoopoe nests were visited again 3 days after the expected hatching date (i.e., 18 days after laying the first egg). At this visit, we weighed all of the hatchlings in the nests with a digital scale (Ascher; accuracy, 0.01 g), which, based on previous experience on nestlings' growth, helped us to infer nestling age and thus hatching date of the oldest, heaviest one (hereafter, "hatching date"). Moreover, we inferred egg viability by detecting embryo movements with a digital egg monitor (Buddy, Avitronics; see McClelland et al. 2021). The viability of the eggs, the laying sequence, and the weight of the hatchlings allowed us to estimate the hatching date of the last-laid viable eggs. During this visit, we also performed the clutch size manipulation experiment, which consisted of adding or removing the last-laid eggs from experimental hoopoe nests. Knowing the expected hatching date of last-laid eggs in different hoopoe nests, we removed the experimental egg from one nest and added it to another hoopoe nest where the expected hatching date of the last natural eggs was 1 day before that of the candidate experimental added egg. Therefore, the execution of the clutch size experiment depended on the availability of pairs of nests that matched in hatching dates, while the experimental treatment was unrelated to the treatment groups assigned for the food supplementation experiment. We effectively removed one close-to-hatch egg (i.e., experimental egg) from 11 nests and added the experimental eggs to 11 other nests that matched their expected hatching dates. Hoopoe nests with hatching dates that did not allow experimental egg exchange were considered control nests in this second experiment ($N = 45$).

Hoopoe nests were visited again 1 or 2 days after the expected end of the hatching period. At this visit, considering that hoopoes lay one egg per day and that they do not remove dead nestlings or eggs that failed to hatch (Martín-Vivaldi et al. 1999), we collected information on several reproductive variables. We recorded hatching span as the number of days elapsed from hatching dates of the first to the last egg, hatching failures as the number of detected unhatched eggs, and brood size as the difference between clutch size and the number of unhatched eggs. The intensity of sibling cannibalism was estimated as the difference between brood size and the number of alive or dead nestlings that were detected in the nests (i.e., number of disappeared nestlings; Soler et al. 2022*a*), and the intensity of brood reduction was estimated as the total number of cannibalized and dead nestlings in the nest. Confirming the assumption of our experimental approach, the addition of extra offspring increased brood sizes and hatching span (see ESM 3). On day 18 after the hatching of the first eggs, hoopoe nests were visited again to record reproductive success as the number of nestlings that survived to fledge in nests that were not depredated or abandoned.

Statistical Analyses

The effect of food supply on clutch size was explored by means of general linear models that included experimental treatment and habitat identity as categorical independent factors and laying date (March $1 = 1$) as a covariable. The effects of clutch size manipulation on the intensity of cannibalism, brood reduction during the first 10 days after hatching date, and reproductive success were explored in separate general linear models using information from nests with brood size larger than three nestlings. The model that explored the effects on the intensity of sibling cannibalism included natural brood sizes and laying date as covariables. Finally, factors affecting reproductive success were also explored in general linear models that included experimental treatment as the categorical independent factor and laying date, natural brood size (i.e., brood size without considering the removed or added experimental egg), and intensity of sibling cannibalism as continuous predictors. Including natural brood size in the model allowed us to control the number of fledglings for the original brood size. Including information from the food supplementation experiment during the laying stage in models exploring the effects of clutch size manipulation does not affect statistical inferences (i.e., statistical significance) or explain additional significant proportion of variance of intensity of cannibalism ($F = 1.55$, $\text{df} = 2, 33$, $P = .227$), brood reduction ($F = 1.34$, $\text{df} = 2, 33$, $P = .275$), or breeding success ($F = 0.47$, $\text{df} = 2, 26$, $P = .628$). Furthermore, the interaction between the two performed experiments did not associate with the intensity of cannibalism ($P = .822$), brood reduction ($P = .921$), or breeding success ($P = .704$). Thus, we present results from models that did not include the treatment of the food supplementation experiment as an additional independent factor. To show the experimental effects, we used least squares (LS) means ± standard error, which by definition controlled for the effect of all other independent factors.

All analyses were performed in R (ver. 4.1.1; R Core Team 2021) and RStudio environment (ver. 1.4.1717; RStudio Team 2021). For general linear models, we used the lm function from the R package stats (ver. 3.6.2; R Core Team 2021). LS means were calculated using the R package emmeans (ver. 1.7.3). The assumptions of normality and homoscedasticity were checked with the functions shapiro.test and leveneTest, respectively.

Results

In accordance with the predictions of the icebox hypothesis, we found significant effects of the food supply experiment on clutch size ($F = 4.70$, $\text{df} = 1, 33$, $P = .038$). On average, females provided with extra food laid approximately one more egg (LS mean ± SE = 7.45 ± 0.30) than control females (LS mean ± SE = 6.58 ± 0.31). That was the case after controlling for the nonsignificant negative effect of the laying date ($\beta \pm \text{SE} = -0.19 \pm 0.15$, $F = 1.58$, $\text{df} = 1, 33$, $P = .217$) and habitat identity ($F = 3.06$, $\text{df} = 2, 33$, $P = .060$).

The clutch size manipulation experiment did not significantly affect the intensity of brood reduction, but it did affect the intensity of cannibalism (table 1; fig. 1). This was the case after controlling for the significant positive effects of laying dates and natural brood sizes (table 1). In hoopoe nests that received one egg that hatched last, the number of cannibalized nestlings was higher than in control nests or in nests with a reduced clutch size (fig. 1*C*). The clutch size manipulation experiment also affected the reproductive success of hoopoes (table 1; fig. 2). On average, nests with an extra hatchling fledged almost two chicks more than nests with experimentally reduced clutch size (fig. 2*C*). That was the case after controlling for the nonsignificant negative effects of laying date, the significant positive effects of brood size, and the significant negative effects of the intensity of sibling cannibalism (table 1). Finally, none of the nestlings

Table 1: Results from general linear models exploring the effects of the clutch size manipulation experiment on intensity of cannibalism (number of cannibalized chicks), brood reduction, and reproductive success

Model variable	β (SE)	F	df	P
Intensity of cannibalism:				
Laying date	.34 (.15)	5.40	1, 35	**.026**
Natural brood size	.52 (.16)	10.29	1, 35	**.003**
Clutch size experiment	...	3.78	2, 35	**.033**
Brood reduction:				
Laying date	.40 (.15)	6.60	1, 35	**.015**
Natural brood size	.47 (.17)	7.55	1, 35	**.009**
Clutch size experiment	...	1.47	2, 35	.243
Reproductive success:				
Laying date	−.21 (.15)	1.99	1, 28	.169
Natural brood size	.57 (.19)	9.13	1, 28	**.005**
Intensity of cannibalism	−.70 (.17)	16.27	1, 28	**<.001**
Clutch size experiment	...	4.08	2, 28	**.028**

Note: Results from general linear models exploring the effects of the clutch size manipulation experiment, laying date (March 1 = 1), and natural brood size on intensity of cannibalism, brood reduction during the first 10 days after hatching, and reproductive success. The intensity of cannibalism was also included as a continuous independent factor in the general linear model trying to explain variation in reproductive success. *P* values less than .05 are shown in bold.

from experimentally added eggs fledged, but all of them died a few days after hatching.

Discussion

In a wide range of animal taxa, females can use resources that are abundant during the laying period to lay extra eggs as food packed to be used during peak food demands of their offspring (Polis 1981). Although Alexander (1974) suggested that this strategy could also be adaptive in birds, it was later discarded for animals with parental care and rapid growth rate (Mock 1984; Magrath 1990; Stanback and Koenig 1992). However, our results support three main predictions of the hypothesis: (i) the experimental food supplementation

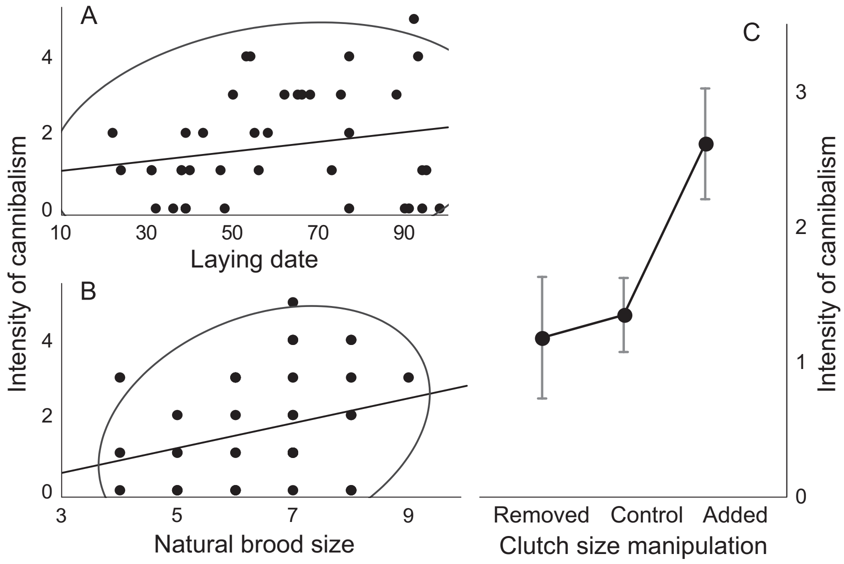

Figure 1: Associations between intensity of cannibalism (number of cannibalized chicks) and laying date (March 1 = 1; *A*) and natural brood size (number of nestlings without considering experimental removed or added egg; *B*). Ellipses indicate 90% confidence intervals, and lines are regression lines. We also show the effect of the clutch size manipulation experiment on intensity of cannibalism and associated standard errors, after controlling for the effects of laying date and brood size (i.e., least squares means; *C*). Data are from control ($N = 21$) and experimental (egg-removed nests = 9, egg-added nests = 10) nests in the Eurasian hoopoe (*Upupa epops*) in southern Spain.

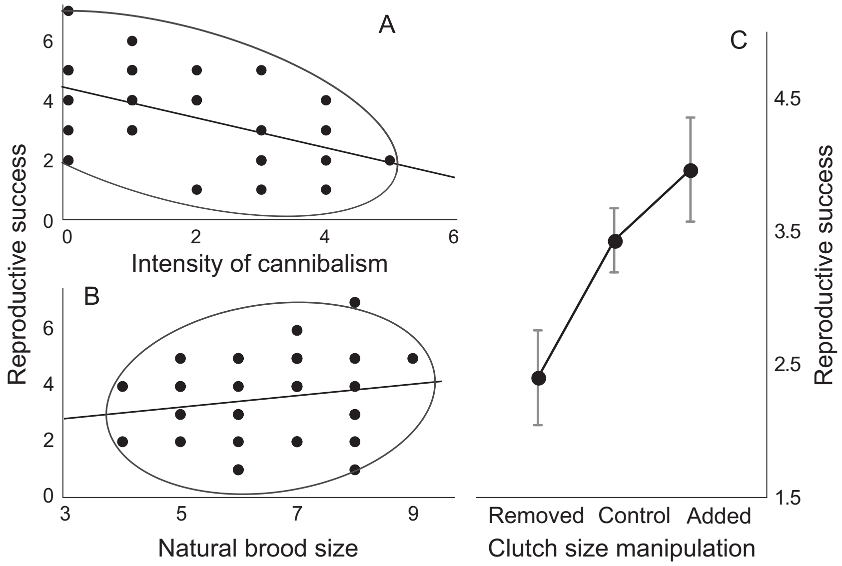

Figure 2: Significant association between reproductive success and intensity of cannibalism (*A*) or natural brood size (*B*). Ellipses indicate 90% confidence intervals. We also show the effect of the clutch size manipulation experiment (control $N = 16$, removed $N = 9$, added $N = 9$; *C*). For this analysis, we considered natural brood sizes larger than three nestlings and nests with reproductive success higher than zero in the European population of Eurasian hoopoes (*Upupa epops*) breeding in Hoya de Guadix (southern Spain).

of hoopoe nests during egg laying resulted in larger clutches, while the experimental addition of eggs that will hatch last (ii) increased the intensity of sibling cannibalism and (iii) increased the reproductive success of broods. The positive effects on breeding success were detected after correcting for the negative effect of the intensity of cannibalism and the positive effect of brood size, which suggests that having an extra hatchling to cannibalize has a positive fitness effect. Below, we discuss these results within the framework of life history theory (optimization of clutch and brood size) and of different hypothetical functions of extra eggs that could result in surplus hatchlings with nil probability of survival under the icebox hypothesis.

Mainly for species that hatch asynchronously, clutch sizes are the upper limit of reproductive success, and therefore those birds usually lay optimistic clutches that produce optimistic broods that should be adjusted to environmental conditions (Lack 1947). This hypothesis predicts that clutch size should mainly be limited by resource availability (Lack 1947, 1954; Slagsvold and Lifjeld 1988). However, although some previous studies have demonstrated the expected effect of food supplementation on clutch size, this is not the general tendency, as shown by meta-analyses (Vanderwerf 1992). Our food supplementation experiment produced larger clutches, which adds to the evidence supporting Lack's hypothesis. Among several functionalities, the extra eggs might have an insurance function (Forbes 1990, 1991; Hardy 1992). However, once this insurance function is no longer necessary (i.e., fewer eggs than expected failed to hatch), the extra eggs resulting from food supplementation may serve other functions. In these cases, the extra eggs that will produce hatchlings with no opportunity of survival might increase the probability of survival of their older siblings (Lack 1954; Stoleson and Beissinger 1995; Soler et al. 2022*b*). That would be the case if the extra nestlings are used as packed food to nourish older siblings (Alexander 1974) or if they enhance parental investment in the brood (Soler et al. 2022*b*).

After hatching, hoopoes should adjust brood size to resource availability (Hildebrandt and Schaub 2018). Extra eggs beyond the number of nestlings that can typically be fledged could have three different functions: (i) to maximize breeding success, (ii) to serve an insurance purpose, or (iii) to maximize the probability of survival of older siblings. Focusing on the possible functions of the last-hatched nestlings rather than on the last-laid eggs, we performed a second experiment that consisted of including or removing one close-to-hatch extra egg that affected not only brood size but also hatching span. The experimental addition of an extra egg increased the intensity of cannibalism and, at a nonsignificant lower rate, brood reduction. Since sibling cannibalism is part of brood reduction, the somewhat mismatching experimental effects on intensity of brood reduction and on sibling cannibalism might be interpreted as cannibalizing extra nestlings having the consequence of increasing the probability of survival of older siblings, thereby diminishing the strength of reduction of the original brood size. According to this interpretation, hoopoe nests that received one experimental egg experienced higher reproductive success than nests where the last-laid egg was removed or control nests. It is worth mentioning here that shortly after the experiment, all of the experimental nestlings were cannibalized or starved, which suggests that the beneficial effects of added hatchlings on their older nestmates mediated their influence on reproductive success. Moreover, cannibalism of the experimental nestlings is unlikely the result of kin recognition due to differences in odors or visual cues between cross-fostered and natural hoopoe nestlings. This is mainly because the experiment was not performed with hatchlings but with eggs close to hatch. All experimental eggs hatched some days after the experiment, and thus the odors of fostered and natural nestlings would be similar. Furthermore, there is strong evidence suggesting that hoopoes do not recognize foreign nestlings in their nest, as they fed great spotted cuckoos (*Clamator glandarius*) that were experimentally introduced into nest boxes with reproducing hoopoes (Arco et al. 2023).

The beneficial effects of adding extra nestlings condemned to die may be due not only to the nutritive effect of cannibalizing experimental nestlings but also to the possible role of extra nestlings influencing parental feeding effort on the entire brood. The experimental nestlings would imply a larger number of nestlings begging for food to which parents should respond by increasing feeding rates (Soler et al. 2022*b*). However, as occurs in blackbirds (*Turdus merula*), these effects on parents can be sex specific and result in similar feeding rates of nests that did or did not harbor extra nestlings (Soler et al. 2022*b*). Although preliminary results in hoopoes suggest that extra last-hatched nestlings do not influence the provisioning rates of males (M. Martín-Vivaldi and J. J. Soler, personal observations), further experimental effort is necessary to completely rule out that possible function.

Depending on the ecological context, particular eggs might have different functions (Mock and Parker 1986), and thus cannibalized nestlings do not necessarily have to be from eggs laid with the exclusive function of packed food. Nestlings that are no longer useful as insurance of hatching failures or early death, or that have reduced probability of survival, could also be used by parents to feed older siblings. Similarly, in the case that hatching failures exceeded the number of eggs laid as insurance, those laid to increase the probability of survival of siblings could function as insurance to reach the adaptive brood size. Thus, although clutch size should be close to the sum of the optimal number of eggs with different functionalities, assigning a particular function to each of the extra eggs that produced extra nestlings (i.e., those with null probability of survival) is simply not possible. Here, we experimentally demonstrated that hoopoes could use extra food during the short period of egg laying to produce extra eggs. However, although the use of last-hatched nestlings as nutrients to feed older siblings occurs very frequently in hoopoes (Soler et al. 2022*a*), the possible multiple functions of last-laid eggs prevent assigning a single function to each of them. In any case, our results clearly showed that the intensity of cannibalism increased by one nestling in nests with one extra egg added, which further demonstrates that hoopoes are able to use extra nestlings as food to feed older offspring. Previous work (Soler et al. 2022*a*) experimentally demonstrated that the intensity of cannibalism decreased in nests with supplemental food, and thus the use of the smallest nestlings to feed older siblings mainly occurs when food is lean after hatching.

Finally, we demonstrated that the experimental addition of one extra hatchling that will be the subject of sibling cannibalism increased reproductive success and thus has an apparent fitness benefit. This result demonstrated the importance of the nutritive adaptive function of last-laid eggs in hoopoes. Consequently, even though the final functionality of last-laid eggs by female hoopoes cannot be a priori assigned, our experimental results indicate that when food is abundant at the time of laying, producing extra eggs that result in extra hatchlings to cannibalize is of selective advantage. The importance of these findings not only deals with detecting fitness advantages of laying extra eggs that will be cannibalized after hatching, which might also occur in some other taxa that, like hoopoes, lay a large number of eggs with extreme hatching asynchrony, but also adds vertebrates with parental care to the large list of taxa producing offspring with nutritional function (Polis 1981; Elgar and Crespi 1992).

From an evolutionary point of view, we speculate that sibling cannibalism should have preceded the evolution of packing eggs as extra food to be used after hatching. As we mentioned above, extra nestlings that are no longer useful as insurance could also be used as food, which might have favored the evolution of sibling cannibalism. Once sibling cannibalism has evolved, the costs of laying extra eggs with different functionalities would be partially counteracted if hatchlings from those eggs could be used as food for siblings during the peak of nestling food demand. We consider this the most parsimonious explanation for the evolution of laying extra eggs to feed older nestlings in hoopoes.

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Statement of Authorship

J.J.S. and M.M.-V. conceived of and designed the experiments and acquired funding and scientific permits. M.D.B., E.M.-R., M.M.-V., and J.J.S. conducted fieldwork. M.D.B. and J.J.S. analyzed the data. M.D.B. wrote the first draft with supervision from J.J.S. All authors substantially contributed to the final version of the manuscript.

Data and Code Availability

All data and code have been deposited in DIGITAL.CSIC (https://doi.org/10.20350/digitalCSIC/15458; Barón et al. 2023).

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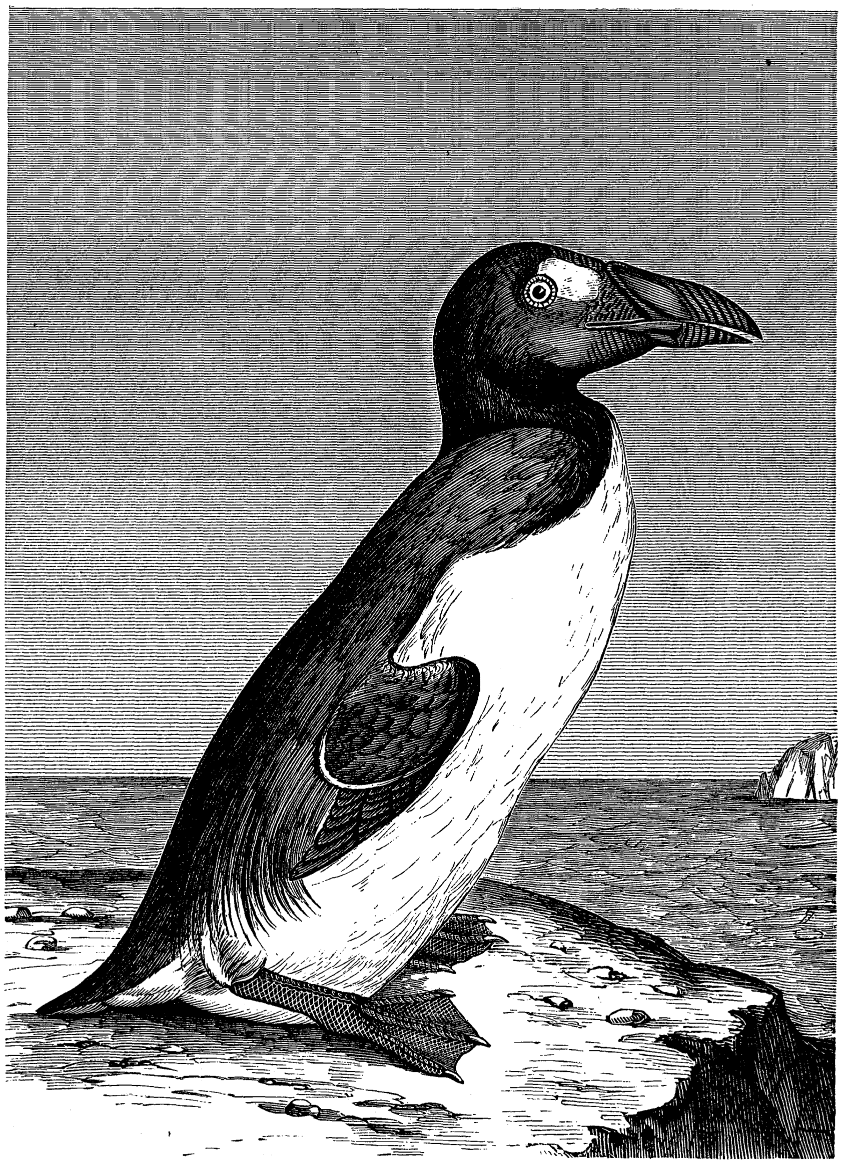

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