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Resource allocation within the replacement clutch: do female European starling (*Sturnus vulgaris* Linneus) adjust their reproductive strategy after a full clutch loss?

Ivna Kocijan[1], Petra Dolenec[2], Zdravko Dolenec[3],* and Andreja Radović[4]

[1]University of Applied Health Studies, Mlinarska St. 38, HR-10000 Zagreb, Croatia
[2]Department of Pharmacology, School of Medicine, University of Rijeka, Bra ć e Branchetta 20, HR-51000, Rijeka, Croatia
[3]Department of Zoology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, HR-10000 Zagreb, Croatia
[4]Group for Terrestrial Biodiversity, Division of Biology, Faculty of Science, University of Zagreb, Marulićev trg 20/II, HR-10000 Zagreb, Croatia

An important factor in the evolution of reproductive strategies in birds is the loss of a clutch or a brood. Many avian species produce a replacement clutch following the loss of the first clutch, but additional breeding effort carries physiological costs and can also reduce female fitness. Thus, egg production in replacement clutches is usually reduced. In contrast, European starling mothers seem to invest equally in their first and replacement clutches. This study investigated whether female starlings use differential allocation of resources to offspring, rather than egg production, to strategically balance investment and

*For correspondence. (e-mail: dolenec@zg.biol.pmf.hr)

returns from the replacement clutch. By removing the first clutch, we induced females to lay a replacement clutch, and focused on covariation of egg size, embryo sex and laying order in both clutches. Results suggest that starling mothers created a pattern of resource allocation with laying order, but not with offspring sex, in the replacement clutch; whereas no pattern of resource allocation existed in the first clutch. This finding indicates that although starlings do not reduce egg production between first and replacement clutches, they may use other mechanisms to fine-tune their investment and maximize their fitness gains from the replacement clutch.

Keywords: Egg size, laying order, reproductive strategy, replacement clutch, sex ratio.

THE loss of a clutch or a brood, which mainly occurs due to depredation, is considered to be a significant factor in the evolution of reproductive strategies in birds[1]. Many bird species produce a replacement clutch after having lost their previous clutch[2–4]. In a number of bird species, maternal investment in egg production (clutch and egg size) in replacement clutches is reduced as compared to first clutches[5,6]. In contrast, European starlings (*Sturnus vulgaris*) seem to invest equally in subsequent breeding attempts. Their replacement clutches were not found to differ in clutch and egg size from the first clutches[3,7]. On the other hand, it is known that egg production is costly[8,9]. Females' fitness in particular may be compromised by an additional breeding effort required for production of a replacement clutch, because she solely pays the metabolic and nutritional price of egg production and usually a higher price of incubation and rearing than her mate. Costs generated by investment in reproduction can negatively affect parents' chances of survival as well as their future reproductive output[10,11].

As theories predict, parents should be able to reduce their reproductive costs and achieve greater fitness returns if they adjust their reproductive strategy to environmental conditions and their own breeding quality, especially when fitness benefits from their offspring are sexspecific[12,13]. In European starlings, sons potentially carry greater fitness returns to their mothers because of male facultative polygyny and hence a higher variance in reproductive success[14]. A primary female starling breeding early in the season may thus be expected to produce more sons or allocate more resources into eggs which bear sons. Nevertheless, if the breeding effort of a starling female is suddenly interrupted by an unpredictable event such as full clutch loss, a mother who decides to produce a replacement clutch would have to re-start breeding in a presumably lower body condition because of the physiological effort already invested in production of the first annual clutch. We hypothesized that in case of such an event, a starling mother producing a replacement clutch shortly after the first clutch had been produced,

would have to adjust her reproductive strategy by modifying the pattern of resource allocation to her offspring or by adjusting the primary sex ratio.

To test our predictions and investigate whether starling mothers would indeed allocate resources differentially or make adjustments to the sex ratio after the full clutch loss, we carried out a clutch removal experiment. By removing first clutches, we experimentally induced the laying of replacement clutches. We compared the clutch sex ratio and the relationship between egg size, laying order and embryo sex in first and replacement clutches, since these mechanisms may be used by avian mothers to differentially allocate resources to offspring[9,15–23].

The European starling is a hole-nesting, semi-colonial passerine bird found throughout temperate Europe. It is resident in the south and the west, whereas populations from other areas usually migrate for wintering to southwestern Europe and northwestern Africa, as does our study population[24]. This is a species with moderate sexual size dimorphism: fledgling and adult males are larger and heavier than females by 7–8% (ref. 25). Neither egg mass nor egg volume has been found to vary with sex in this species[26]. In starlings, sexual size dimorphism begins after hatching because of faster male growth rates during postnatal development[27,28]. Male European starlings are facultatively polygynous[29,30].

Data were collected at Mokrice rural area (46°00′N, 15°55′E), northwestern Croatia, in April and May 2009. The study site consists of open farmland with small, isolated patches of forest dominated by common oak (*Quercus robur*) and European hornbeam (*Carpinus betulus*). Here, the starlings breed in a nest-box colony with 50 nest boxes; majority of the population produces two broods per season (60–80%, Z. Dolenec, unpublished data). Approximately 5% of the colony members breed in natural holes, mainly in oak trees and these were not included in the study.

Incubating females were colour-ringed for identification during the egg-laying period. Nest boxes were visited daily after 12 h to determine the laying date of the first egg in each clutch and the precise laying order of the following eggs by marking each newly laid egg with a permanent marker pen. First eggs in all first clutches included in this study were laid within 4 days, during 7–10 April. Clutch size was recorded upon clutch completion, the clutches considered complete after two consecutive days with no new eggs in the nest.

To minimize differences in the amount of resources invested by females in the production of their first clutches, 20 clutches with six eggs each were chosen for the analyses. Our first assumption was that the mothers of the 20 analysed clutches were of similar quality because they were all primary females (as opposed to secondary females which mate later in the season with polygynous males); the second assumption was that they invested approximately the same amount of energy and nutrients

in their first clutch because of the same clutch size (6 eggs) and incubation period (7 days).

Egg length and breadth were measured to the nearest 0.1 mm with a Vernier calliper. Egg volume was calculated using the formula by Hoyt[31]: Volume = $0.51LB^2$, where L = maximum length and B = maximum breadth. Volume was analysed as it is indicative of a female's investment in an egg[19].

On the seventh day of incubation, we removed the clutch and transported the eggs to our laboratory for molecular DNA sexing. Nine to eleven days after the removal of eggs, 17 females started laying a replacement clutch within five days (between 27 April and 2 May). Again, eggs were numbered sequentially as they were laid, measured, and after 7 days of incubation removed for sex determination. All 17 replacement clutches were included in the analyses, regardless of their size (9 with 6 eggs; 5 with 5 eggs; 2 with 7 eggs; 1 with 4 eggs).

Intra-specific parasitism is common in European starlings[32,33]. Parasitically laid eggs were discovered in five nests of the first clutch (four nests with one parasitic egg and one nest with two parasitic eggs) and in three nests of the replacement clutch (one parasitic egg in each). They were recognized based on abnormal laying sequence and unusual shape and pigmentation[34], and were excluded from all analyses.

A total of 217 eggs were collected from 37 clutches: 120 eggs from 20 first clutches and 97 eggs from 17 replacement clutches.

DNA was extracted from embryonic tissue using the Wizard Genomic DNA Purification Kit (Promega, USA). Ten eggs without an embryo inside were presumed to be unfertilized (five in first clutches and five in replacement clutches) and were not sexed. Sex was determined using the polymerase chain reaction (PCR) method with the P2/P8 primer pair[35]. PCR products were separated by electrophoresis in 2% agarose gels stained with SYBR Safe DNA Gel Stain (Invitrogen, USA) and visualized under UV light. Males and females were recognized by the presence of one or two bands respectively. The method was previously verified as reliable[36,37]. Sex ratio was defined as the proportion of male embryos observed.

Egg-laying order was divided into three categories because of the clutch size variations within the replacement clutch: (i) first egg laid, (ii) middle eggs (mean values of all eggs except the first and last were taken) and (iii) last egg laid.

Analyses were performed with SPSS 15.0. SAS v. 9.2 statistical software was used for modelling variation in egg volume in relation to clutch order (first versus replacement clutch), embryo sex and egg-laying categories. We used the generalized linear mixed model (GLIMMIX procedure) with identity link function and Gaussian error variance. In this model, the embryo sex was introduced as a categorical variable, and clutch order and laying order categories were introduced as covariates. Female identity

was introduced to the model as a random factor and as the blocking factor for the variance in the data. The relationship between the embryo sex, clutch order and egg-laying categories was analysed using GLIMMIX procedure with logit link function and binomial error variance, with female identity as a random and blocking factor. The level of significance was set at $P < 0.05$. Means are presented with standard deviations, unless otherwise noted.

The laying order, egg dimensions and sex were determined for 115 eggs from 20 first clutches and 92 eggs from 17 replacement clutches, but three females from the first clutch were excluded from the analyses because they either did not renest, or they renested elsewhere.

Mean size of the replacement clutch was 5.7 ± 0.77 (range 4–7, modal clutch size 6). On average, females reduced their clutch size by 0.3 eggs, but no significant change in clutch size was found when comparing the two clutches for individual females (paired t-test, $t_{16} = 1.571$, $P = 0.136$). Mean egg volume was 6.797 ± 0.469 cm^3 in the first clutch and 6.713 ± 0.369 cm^3 in the replacement clutch, with no significant change in volume between the first and replacement clutches (clutch order: $F_{1,32} = 0.19$, $P = 0.669$). Egg volume was found to vary with laying order categories ($F_{2,158} = 4.12$, $P = 0.018$; Figure 1). Separate analyses testing for contrasts between laying order categories showed that the first eggs were smaller than the middle eggs ($P = 0.004$), whereas no difference in volume was found between the middle and last eggs ($P = 0.277$), or between the first and last eggs ($P = 0.153$). First eggs in the replacement clutch were smaller than the clutch mean (paired t-test: $t_{16} = 2.62$, $P = 0.019$), but not in the first clutch (paired t-test: $t_{19} = 0.03$, $P = 0.974$). No significant difference in volume of male and female eggs was found (embryo sex: $F_{1,158} = 2.58$, $P = 0.110$).

The overall sex ratio in the first clutch was 53.9% males (62/115) and in the replacement clutch it was 51.1% (47/92). In both cases, it did not differ from parity (binomial test, $P = 0.456$ first clutch; $P = 0.917$ replacement clutch). When controlling for female identity and variance blocking, the clutch sex ratio analyses did not reveal difference in sex ratio between the two clutches ($F_{2,32} = 0.78$, $P = 0.468$; SAS statements: MODEL number male embryos/number of male embryos = brood order (/noint); RANDOM brood order/subject = female).

We examined whether female European starlings allocate resources to their offspring differently in first and replacement clutches and if they adjust clutch sex ratio in replacement clutches after the full clutch loss.

We detected a slight difference in the pattern of variation of egg size with laying order between first and replacement clutches. Egg size varied with laying order in the replacement clutch, with the first-laid egg being smaller than the clutch mean, whereas in the first clutch there was no such pattern (Figure 1). Several explanations for this finding are possible. First, the fact that there was no pattern in the first clutch indicates that there was

no constraint on the high quality primary females at the time of their breeding. In the replacement clutch, however, first-laid eggs were smaller than the rest of the eggs in the clutch, which may indicate that resources were distributed along the laying sequence. The covariation of egg size with laying order may serve to maximize offspring's survival chances in a set of circumstances under which the replacement clutch was produced (maternal body condition and the environment). Previous studies have demonstrated that egg size and chick size at hatching are positively correlated, and some studies have found a positive correlation between the egg size and survival of hatchlings within the first week after hatching[38-40]. The fact that the first eggs in the replacement clutches were smaller than the rest of the eggs in the laying sequence indicates that mothers allocated more resources to the later-laid eggs. The adaptive significance of this is not immediately obvious but it might be considered as a strategy to compensate for the negative effects of asynchronous hatching for the late-hatched young. Balancing hatchling size hierarchies and sibling competition may increase brood survival chances in the first few days after hatching[15,39,41].

In this experiment, we detected no decline in clutch size and no difference in egg size between the two clutches of individual females. These findings accord with previous studies which showed that European starling mothers invest the same amount of effort in their first and replacement clutches[3,7]. The lack of decline in clutch size is consistent with the breeding quality hypothesis which states that the clutch size is characteristic of individuals regardless of their timing of breeding[5,42].

We did not detect any changes in primary clutch sex ratio between the first and replacement clutches. Biasing towards the sex with potentially higher reproductive success when mother is in good condition is predicted by the
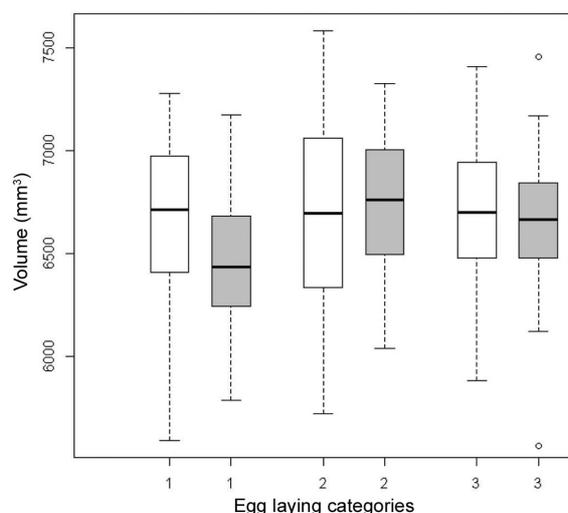
Trivers–Willard hypothesis[12] and has been observed in a number of avian species[43-46]. If a mother gains different fitness benefits from her sons and daughters given her own body condition, then she is expected to produce the more beneficial sex in greater number[12]. Likewise, a primary female starling breeding early in the season would be expected to bias the sex ratio of her clutch towards sons, according to Trivers–Willard hypothesis[12]. We hypothesized that females would adjust the clutch sex ratio following the full clutch loss based on the assumption that production of the replacement clutch carries physiological costs which in turn may affect female quality and may reduce female fitness[9]. Male starlings seem to be costlier to rear: they have faster postnatal growth rates[27,28] and as fledglings they are heavier than females by 7–8% (ref. 25). However, in our study, the ratio of sons to daughters did not deviate from parity in either of the two clutches, nor did it differ between the clutches. Daughters were not overproduced despite being the less costly sex, arguably because in the European starling, they are more sensitive to poor rearing environment than sons[25]. We found no indication that mothers favoured one sex over the other by laying them in a better position in the laying sequence or by better provisioning the eggs of a certain sex in either the first or the replacement clutch.

In conclusion, the results of this study suggest that European starling mothers divide resources along the laying sequence in the replacement clutch, unlike the first clutch, although they do not reduce egg production compared to the first annual clutch, nor do they adjust the clutch sex ratio. The pattern of resource allocation within the replacement clutch may serve as a mechanism to maximize the mother's fitness. However, more solid conclusions are difficult to draw from the current study. The question whether the observed reproductive pattern arises due to timing of breeding or intrinsic quality of females was not addressed here and remains yet to be investigated. An experimental protocol which would include a group of non-manipulated, late breeding females to compare the primary females with would help to distinguish between the effects of date and quality. Therefore, to explain with more precision how females adapt their breeding efforts in response to the full clutch loss, a further study should assess whether late breeders carry out similar strategic decisions as documented here.

Figure 1. Box plot of egg volume (mm³) by laying order categories (1, first eggs; 2, middle eggs; 3, last eggs) in the first clutch (white) and replacement clutch (solid).

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