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ORIGINAL PAPER

Egg-spot pattern rather than egg colour affects conspecific egg rejection in the house sparrow (*Passer domesticus*)

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Abstract Brood parasitism could be a selective pressure on each female to have a type of egg that permits recognition. House sparrows (*Passer domesticus*) undergo conspecific brood parasitism and can recognise parasitic eggs. In this study, we analyse the effect of relative size in experimental parasitic eggs compared to the host eggs. We modified egg colour and the spot pattern to determine the influence of these characteristics on egg rejection. Furthermore, we examine whether egg rejection increases with "stimulus summation". Our results show that egg rejection is not affected by relative egg size. However, changes in the spot pattern proved to exert the highest influence on egg rejection (32.4% of trials), significantly higher than when only egg colour is changed (3.8%). Therefore, our results suggest that parasitism may be a pressure favouring the maintenance of spotted eggs in house sparrow.

Keywords Egg rejection · Conspecific brood parasitism · House sparrow · *Passer domesticus*

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Introduction

Bird eggs vary considerably among females within a species in terms of size, colour and spot patterns, and various hypotheses attempt to explain this variability (reviewed in Underwood and Sealy 2002; Kilner 2006). A function of variability in egg colour and spot pattern may be to facilitate egg recognition of foreign eggs in species with interspecific or conspecific brood parasitism (Victoria 1972; Freeman 1988; Davies and Brooke 1989a, b). Sexual selection has been also invoked to explain intra-specific variation in egg colour (Moreno and Osorno 2003; Soler et al. 2005). Spotted eggs have been related to crypsis against depredation in open nests, with eggs from hole-nesting birds being frequently spotless (Kilner 2006). Independently of functional hypotheses, egg colour and spot patterns are also affected by environmental and female conditions (Gosler et al. 2005; Avilés et al. 2007; Martínez-de la Puente et al. 2007). Egg size, although highly repeatable within females, also varies among females of the same species (reviews in Williams 1994; Christians 2002).

Conspecific brood parasitism (CBP) is a reproductive tactic by which a female lays eggs in nests of conspecific individuals, which then care for the eggs and young (Yom-Tov 1980; Andersson 1984; Rohwer and Freeman 1989; Petrie and Møller 1991). CBP imposes costs to hosts such as reduced incubation efficiency, increased mortality of own young, or increased investment in parental care (Møller 1987; Evans 1988; Hepp et al. 1990). For this reason, hosts are selected to develop antiparasitic defences such as the recognition and rejection of parasitic eggs (Petrie and Møller 1991). Therefore, CBP would favour each female to have an egg type that reduces the intra-clutch egg variability and increases the difference among females in a population (Victoria 1972; Collias 1984;

Freeman 1988). In fact, colour and spot pattern have a genetic component (Wei et al. 1992; Collias 1993; Gosler et al. 2000). This would facilitate the learning of the egg characteristics (Rothstein 1974, 1975, 1978; Lotem et al. 1995; Hauber and Sherman 2001; Petrie et al. 2009), and egg characteristics kept to a lesser variation within the clutch would serve to recognise the presence of parasite eggs (Stokke et al. 1999; Davies 2000; Soler et al. 2000).

The influence that only one feature of the eggs exerts on recognition and rejection may be less important than the summation of several egg features, due to the effect of a "stimulus summation" (Rothstein 1982). Among the characteristics of the eggs that could generate the recognition and rejection of foreign eggs are egg size, ground colour and the colour, size and density of spots. In the village weaver, *Ploceus cucullatus*, which is host to other species as well as conspecifics, each female lays one type of egg different from the others throughout their lives, with different ground colours, both spotted as well as unspotted (Victoria 1972; Collias 1984). Females reject eggs that differ from their own in the ground colour, and when the ground colour of parasite eggs is within the range of host clutch, the presence or absence of spots determines the rejection (Victoria 1972). Parasitic cuckoos lay relatively small eggs for its body size presumably to match the host eggs in size and increase the chance of acceptance (Payne 1974). Recent experiments have confirmed that some hosts can discriminate against foreign eggs based on its size (Marchetti 2000).

The house sparrow, *Passer domesticus*, despite nesting in holes, lays spotted eggs, which vary both in ground colour and in the density of brownish-red spots (Seel 1968; Lowther 1988; Harrison 1991). House sparrow egg colour is determined by female identity, but variability between and within clutches of the same female remains (López de Hierro and De Neve unpublished data). House sparrows suffer CBP at a rate of 0–12% (Manwell and Baker 1975; Kendra et al. 1988; Cordero et al. 1999; Veiga and Boto 2000; López de Hierro and Ryan 2008) and have the ability to recognise and reject eggs at a rate of around 32–35% (Kendra et al. 1988; Moreno-Rueda and Soler 2001; López de Hierro and Ryan 2008). Egg rejection is costly in house sparrow, which loses 44.4% of their eggs, the abandonment of the clutch being usual (Moreno-Rueda and Soler 2001).

The goal of the present study is (1) to analyse the effect of egg characteristics (egg size, colour and spot patterns) on egg rejection; (2) to determine which egg characteristics most influence the egg rejection in the house sparrow; and (3) to examine whether the rejection of experimental eggs increases owing to the "stimulus summation", when more than one egg characteristic is modified. For this, we collected data over a 4-year period from various clutches laid by the same house sparrow females.

Materials and methods

The study species

House sparrows nest in cavities or build closed nests among tree branches (Cramp and Perrins 1994) and are chiefly monogamous, with a low rate of extra-pair copulations (Veiga and Boto 2000). Egg size is highly repeatable for a particular female (Anderson 2006), and it does not seem to be affected by the advance of the breeding season (Veiga 1990; Anderson 1998; although see Lowther 1990) or the clutch size (Lowther 1990; Veiga 1990; Marcos and Monrós 1994). Nevertheless, egg size of the last egg frequently varies within a clutch (Lowther 1990; Marcos and Monrós 1994). The ground colour of house sparrow eggs varies from pure white to bluish, and there are a small percentage of brownish eggs (in our females, 1.4%, n=830 eggs; López de Hierro, unpublished data); the eggs have spots of varying size and brown tones, and the density of spots varies considerably, from a large patch at the blunt end to a uniform spot pattern throughout the entire eggshell (Summers-Smith 1963; Dawson 1964; Harrison 1991; Fig. 1, column 1). The last-laid egg in a clutch tends to be strikingly different from the others in colour features and size (Seel 1968; Lowther 1988; Anderson 2006).

Characteristics of the study captive nesters

The individuals used in the study had been kept in a 45 m^3 indoor aviary in the Science Faculty of the University of Granada since 1999. The number of individuals was more or less constant (mean 75±SD=10 individuals) throughout the study years, with a sex ratio around 1:1. The aviary provided 40 nest boxes, about 50% of which were occupied each season. All the sparrows were individually colour-ringed. The birds were provided ad libitum with water, seed mix, fly maggots, vitamins, powdered calcium, mineral salts, apple, lettuce and nestling food (more details in Moreno-Rueda and Soler 2002). They were also provided with a sand tray for their habitual dust-baths. Cotton wool and plant material were provided for nest construction during the breeding season. The artificial illumination was regulated by a timer which kept the birds at the same photoperiod as the external environment.

Previous studies of the same individuals revealed that egg rejection rate in experimentally parasitized nests was 23–30% (Moreno-Rueda and Soler 2001), a frequency not significantly different from rejection rates found in natural populations (35%, Kendra et al. 1988; 33%, López de Hierro and Ryan 2008). Therefore, it seems that captive conditions do not affect the rejection behaviour in house sparrow.

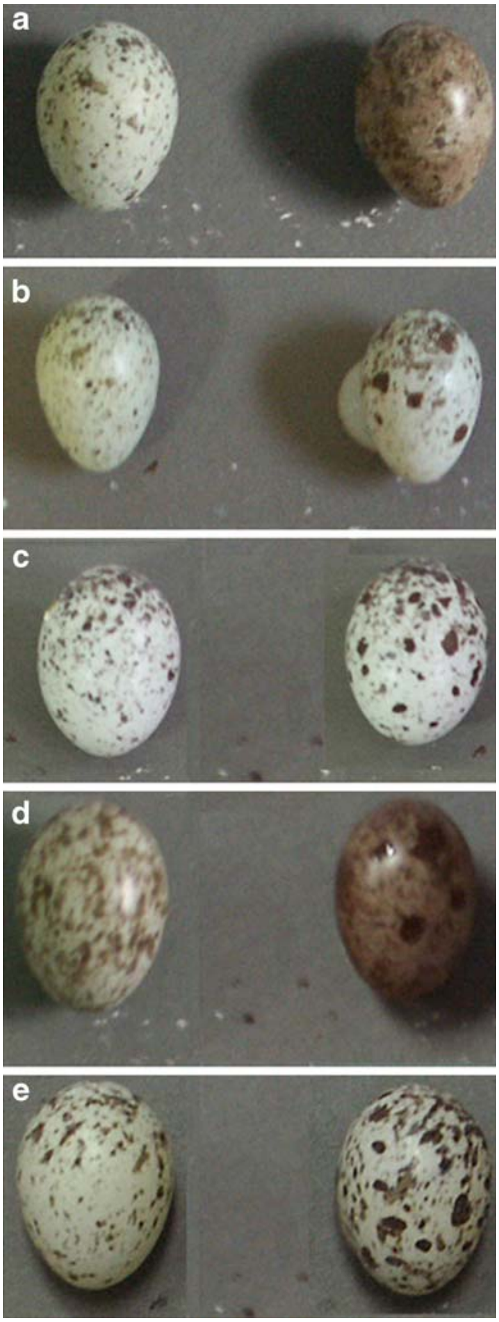

Fig. 1 Experimental modification of egg colour and spot pattern. On the *right* are real house sparrow eggs, and on the *left*, the modifications in egg colour (**a**), spot size (**b**), spot density (**c**), egg colour plus spot size (**d**), and spot size plus spot density (**e**). The real eggs are from the same clutch where the experimental eggs were modified

General methods

The study was carried out during the breeding seasons of 2003–2006 inclusive. Daily observations were made from the start of each breeding season to identify pair members and their nest boxes as well as possible changes in pair composition or of nest box use. The nest boxes were examined daily to gather information on the nest-building process, laying date, laying order, clutch size, clutch number per season and instances of CBP. We inferred brood parasitism if two new eggs were laid on the same day (Yom-Tov 1980), given that this species lays one egg every 24 h (Cramp and Perrins 1994), but throughout the study, there were no instances of two eggs being laid on the same day.

Experimental design

Egg size

A conspecific egg was placed in different clutches (n=21) of eight females during 2003, 2004 and 2005 breeding season to determine whether egg size influences parasitic-egg rejection (there is no significant difference in egg rejection among clutches and years; Moreno-Rueda and Soler 2001 and unpublished data). The experimental egg was added to the host's nest when the second or third host egg was laid and before the onset of incubation. Fresh natural eggs were used in our experiments since it has been shown that artificial eggs increase the costs of rejection and so may influence the decision to accept or reject the experimental egg (Martín-Vivaldi et al. 2002). All experimental eggs used in this study were supplied by other nests of the captive nesters who did not participate in this experiment. Eggs were collected the day they were laid and transferred to another nest or kept fresh in a refrigerator for almost a day. The experimental eggs were photographed with the complete host clutch using a Minolta Dimage 7 digital camera. For each photo, we placed the eggs on a Kodak neutral-grey card that included a ruler to correct the egg-size measurements in order to examine differences in egg size among the female's own eggs and the foreign egg. Egg maximal length (L) and maximal width (W) were assessed for eggs from the photographs using the ruler tool of the Photoshop program. With the same tool, we evaluated the result measured for a centimetre in the ruler on the Kodak neutral-grey card. With the value obtained when measuring this real centimetre, the egg measurements were corrected. Afterwards, the egg length and width were used in the volume formula $V= 0.498\times W^2\times L$ (Spaw and Rohwer 1987).

Repeatability of the observer's assessments was estimated by measuring these characteristics twice in 81 eggs (Lessells and Boag 1987). The second measures took place 15 days after the first. Repeatability of the observer's assessments was significant for the all variables (R=0.9, P<0.0001). There was no significant difference when egg size was measured with calliper or with photos (Wilcoxon matched pairs: Z=1.26, P=0.21, n=20).

Modification of egg features

For 21 females, we modified the colour and spot pattern of their own egg features in successive clutches (n=59) to determine whether such modifications influence egg rejection. The features modified were (a) egg colour (n=12), (b) spot size (n=14), (c) spot density (n=14) and (d) a+b (n=10), and (e) b+c (n=9) to determine how the modification of more than one factor influenced egg rejection. All modifications were made to five females.

The egg features were modified with plastic paint (Titanlux © brown tobacco n° 544) as follows: (a) for the egg colour, the plastic paint was diluted so as not to hide the pattern of the spots and without affecting the hatching of the experimental eggs. The tone produced was darker than the original ground colour but similar to the original colour of the spots in order not to change this factor (see Fig. 1). (b) The size of ten spots chosen randomly was increased by 25% with a no. 7 brush. These spots were distributed throughout the egg so that the female could notice the change in the spots despite the constant rotation of eggs during incubation. The painting was consistent with the original colour of the spots (Fig. 1). (c) Spot density was increased, painting 30 spots evenly distributed with the same colour and size as the rest of the spots on the egg (Fig. 1). (d) Change in egg colour and size of spots; and (e) size and density of spots on the same egg were changed following the methods described above.

Egg rejection

The following responses to experimental eggs were noted during the daily inspections: (1) acceptance, the experimental egg remained in the nest until at least one egg hatched; (2) ejection, the experimental egg disappeared or was found crushed inside the nest; (3) egg burial, when the experimental egg was found buried in the nest lining; (4) clutch desertion, the entire clutch was found cold after incubation began. Responses 2, 3, and 4 were considered egg rejection.

Statistical analyses

To determine whether the size of the experimental egg or the change in the characteristics of the egg influenced rejection, we used a generalized linear mixed model (GLIMMIX; Littell et al. 1996), in which the dependent variable (egg rejection) had a binomial distribution (0=acceptance, 1=egg rejection), associated to a logit function. To value the effect of egg size, the explanatory variables were the size of the female's own eggs, experimental egg size and the difference between the mean size of the female's own eggs and the experimental egg size. In experiments on egg-feature modifications, the treatments were included as a fixed factor. To determine whether "stimulus summation" influences egg rejection, we performed an analysis with a variable to differentiate the treatment with one modification or two modifications as a fixed factor. Female and year variables were introduced as random factors in all GLIMMIX analyses. The inclusion of female identity in the analyses precluded pseudoreplication. In the study, we used non-related females and experienced breeders. Hosts may learn to recognise a foreign egg better after a successful rejection (Hauber et al. 2006). Nevertheless, this is not the case in the house sparrow, in which a successful rejection did not affect the future host responses (unpublished data).

After results for the GLIMMIX of egg-feature modification and the large differences in percentages of egg rejection between treatments varying in colour (treatment a) and those varying spot pattern (treatments b, c, d and e), another analysis was performed (GLIMMIX), comparing the two major types of modification (0=egg colour, 1=spot pattern). In this analysis, we included data from an experiment varying egg colour, but not spot patterns, performed on 14 different females in 2001. In this experiment, we varied the egg colour with plastic blue paint (Titanlux © blue no. 347). We included these data to increase the sample size of egg-colour modification because there was no difference in response between the two experiments (chi-square test: χ^2 Yates corrected=0.01, P=0.9). The GLIMMIX analysis was carried out in the same manner as the previous ones, including the two major types of modification (egg colour and spots patterns) as a fixed factor.

The model residuals adjusted to a normal distribution (Kolmogorov–Smirnov: P>0.2; Siegel and Castellan 1998). To decide the best fit model of GLIMMIX, we used the Scale Disperse criterion (Scale Disperse >0.98 in all analyses; Littell et al. 1996).

The degrees of freedom of GLIMMIX models were calculated using the Satterthwaite method, and for this reason the degrees of freedom vary among analyses. This method is recommended for unequal group variances (Fai and Cornelius 1996). The GLIMMIX procedures were performed using the SAS program (SAS 1989-96 Institute Inc., Cary, NC, USA; Littell et al. 1996).

Results

The egg size differed more between females than within females (analysis of variance, $F_{1,13}$=206.3, P<0.001). The experiment of a foreign-egg introduction generated 33.4% of egg rejection (n=21). The female's own egg size did not influence egg rejection (GLIMMIX: $F_{1,3.3}$=0.1, P=0.9) nor the experimental egg size ($F_{1,3}$=0.3, P=0.6). Egg rejection was not affected by the difference between the female's own egg size and experimental egg size ($F_{1,14}$=0.1, P=0.8).

In experiments modifying the features of female's own egg, 27.1% of the modified eggs were rejected (n=59), but there were no significant differences in the response to the treatments (GLIMMIX: $F_{4,27}$=0.8, P=0.5), although the change in the colour generated the lowest percentage of rejection, and the size of spots resulted in the highest (Fig. 2). The change of more than one feature in the same egg did not influence the egg rejection more than in the treatments with only one modification (GLIMMIX, $F_{1,48}$=0.2, P=0.6; Fig. 2). However, significant differences were found in the response on egg colour vs. spot-pattern modification (GLIMMIX, $F_{1,37}$=6.0, P=0.02), with egg-colour modification resulting in a lower egg rejection rate (3.8%, n=26) than spot-pattern modification (32.4%, n=37).

Frequencies of egg rejection in this study (27–33%) did not significantly differ from those found in previous studies in the same captive nesters (23–30%, Moreno-Rueda and Soler 2001) neither in wild populations (35%, Kendra et al. 1988; 33%, López de Hierro and Ryan 2008; Fisher exact test, always P>0.5). The frequency of egg rejection did not vary with own host spots colouration (r=0.01, P=0.96), spots distribution (r=0.18, P=0.63) or spots size (r=0.16, P=0.66, n=20 in all cases).

Discussion

Results show that egg rejection is not affected by host-egg size, experimental-egg size or the difference between the size of the female's own eggs and that of the experimental egg. Nevertheless, the modification of spot patterns generated significantly more egg rejection when compared with egg-colour modification. That is, the results suggest that foreign egg rejection is caused by variation in spot patterning but is not significantly influenced by egg size or egg colour.

Hosts may recognise foreign eggs on the grounds of discordance (a relatively crude rule by which the egg type in the minority is rejected) or by "true recognition" of their own eggs (Rothstein 1975; see also Hauber and Sherman 2001). True recognition may take the following two forms: hosts may learn to identify their own eggs by imprinting on them (Rothstein 1974; Lotem et al. 1995) and can thus reject from memory (Petrie et al. 2009). Alternatively, they could reject on the basis of direct comparison (Lahti and Lahti 2002).

In this study, we found no effect of egg size on rejection despite the high repeatability in egg size within females and the significant difference between females (Anderson 2006; this study), which could facilitate foreign-egg rejection. Other studies that have considered this factor in egg recognition have concluded that egg size has little or no influence on the rejection of conspecific eggs because of the high variability among the eggs laid by an individual female (Victoria 1972) or because the egg size is very similar among females of the same species (Jackson 1998; Lahti and Lahti 2002). To our knowledge, only Marchetti (2000) found an effect exerted by the conspecific egg size on rejection, this being in the yellow-browed leaf warbler (*Phylloscopus humei*). That study demonstrated that rejection decisions are based on the relative size of eggs in the host clutch, with individuals accepting eggs of similar size

Fig. 2 Egg rejection percentages of modified eggs for colour and/or spot traits

as their own. By contrast, in the house sparrow, the difference between the female's own eggs and foreign eggs did not influence the rejection decision.

According to López de Hierro and De Neve (unpublished data), house sparrow egg colour and spot pattern are significantly determined by female identity. This may indicate a genetic component that maintains egg-colour patterns in this species within a relatively narrow range of environmental variation. Because of this variability in egg characteristics (colour and spots pattern) between females and clutches in the house sparrow, we should expect the variation in any of them to facilitate the recognition and rejection of foreign egg (e.g. Victoria 1972; Rothstein 1982; Moksnes et al. 1993; Stokke et al. 2002, 2004; Moskat et al. 2008a). However, only the spot pattern, but not egg colour, significantly affected egg rejection in the present study. Moreover, none of the treatments that changed two features in a single egg presented a greater effect on egg rejection, suggesting that there is no “stimulus summation” in the rejection of foreign eggs in the house sparrow. Even in the treatment of modifying colour and spot size in the same egg, the percentage of rejection was very similar to that caused by changing only the spots size and much higher than that from altering only the egg colour (Fig. 2). The probability of rejection in the blackcap (*Sylvia atricapilla*) is significantly influenced by the colouration of the blunt egg part, egg rejection being more probable when the blunt egg part of the host clutch is darker (Polaciková et al. 2007). This may be connected with the spot concentration in the blackcap's eggshell. Similar to our results, the warbling vireo (*Vireo gilvus*) hosts reject brown-headed cowbird's eggs only based on eggshell spot pattern (Underwood and Sealy 2006). In the great reed warbler (*Acrocephalus arundinaceus*), egg rejection increases gradually with the increase in spot density (Hauber et al. 2006; Moskat et al. 2008a).

Intra-clutch variation affects egg rejection in other species (Avilés et al. 2004; Cherry et al. 2007; Moskat et al. 2008b). However, in the house sparrow, intra-clutch variability does not affect egg rejection (López de Hierro and Soler 2006). On the other hand, more spotted eggs could indicate lower quality (Martínez-de la Puente et al. 2007), and egg rejection could be more probable in low-quality clutches, given the high costs of egg rejection in this species (Moreno-Rueda and Soler 2001). However, spotting characteristics of own eggs did not affected the probability to egg rejection in this study.

Long ago, it was noticed that birds nesting in cavities tended to lay white eggs, whereas spotted eggs were related to open nests, as confirmed by recent comparative analyses (Kilner 2006). About 80% of birds that build nests in exposed sites lay eggs that have red or brown spots (Lack 1958), which is interpreted as an adaptation for concealment from predators (Tinbergen et al. 1962; Solís and de Lope 1995; Lloyd et al. 2000; Sánchez et al. 2004; Kilner 2006). The question arises why the house sparrow, a hole-nesting bird, has eggs that are conspicuously spotted. Cavity nester species which presently lay spotted eggs might have changed their nesting habit from open nesting to cavity nesting and retained spottiness from their open-nesting time. However, the primitive nest type in the house sparrow is a more or less spherical structure (Kulczycki and Mazur-Gierasinska 1968; Heij 1986), therefore, being a closed nest.

Protoporphyrins are the principal pigments responsible for egg-spot patterns in birds (Kennedy and Vevers 1976; Miksik et al. 1996). Due to the pro-oxidant properties of protoporphyrins (Afonso et al. 1999; Shan et al. 2000), it has been proposed that they could either signal female quality because increased pigmentation would indicate oxidative tolerance (Moreno and Osorno 2003) or, alternatively, be an indicator of poor condition, since high levels of protoporphyrins produce physiological stress that may be reflected in females' physiological condition (Martínez-de la Puente et al. 2007). Protoporphyrins may also be used to compensate for localised shell thinness arising from a lack of calcium in the environment (Gosler et al. 2005), thereby reducing permeability and water loss during incubation (Higham and Gosler 2006).

Besides these explanations, brood parasitism explains the presence of spot patterns as a means of facilitating egg recognition (Swynnerton 1918; Stokke et al. 1999, 2002; Davies 2000; Soler et al. 2000; Lahti 2005, 2006; but see Moskat et al. 2008a). In another study (López de Hierro and De Neve, unpublished data), egg-colour variance explained by female identity was very low (5–10%), while the spot pattern was the feature that presented the least variability, and its variation was explained in 40.5% by the female identity. This implies that spot pattern, least variant within females, is better than egg colour to egg rejection. In addition, in hole-nesting birds, low light in the nest could hamper the reliable recognition of colours but allow recognition of contrasts in light and dark, i.e. spot patterns. In summary, our results suggest that spot patterns in the house sparrow may be maintained for the recognition and rejection of foreign eggs, an explanation that does not exclude other functions (signalling or structural).

Ethical Note

The capture and retention of sparrows was authorised by the Andalusian government (Consejería de Medio Ambiente). This research adhered to the legal requirements of Spain and all institutional guidelines. The paint used in the egg-feature modifications (Titanlux © brown tobacco no.

544 and Titanlux © blue no. 347) is not toxic for animals nor the environment, which follows the Directive 1999/45/EC (RD.255/2003). The manipulation did not have adverse effects on the embryos, as experimental eggs were accepted (*n*=43); 25 eggs hatched successfully (58.14%). This hatching success did not differ significantly (chi-square test, $\chi_{1,253}{}^{2}=0.11$, $P=0.7$) from the hatching rate of non-manipulated clutches in this captive nesters in 2000 (58.4%, *n*=206 eggs, Moreno-Rueda and Soler 2002).

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