



Nest-building activity and laying date influence female reproductive investment in magpies: an experimental study

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Nest size or nest-building activity has recently been hypothesized to be a postmating sexually selected signal in monogamous birds: females may assess a male's parental quality and willingness to invest in reproduction by his participation in nest building. Females may thus adjust their reproductive effort (i.e. clutch size) not only to their own abilities but also to those of their mates. We investigated whether female magpies, *Pica pica*, use nest-building activity rather than nest size to adjust their reproductive effort during replacement breeding attempts. After we removed their first clutch, high-quality pairs that built a large nest for the first clutch were more capable of building a replacement nest and females adjusted their clutch size in relation to the time it took to build the nest rather than nest size. We also found support for the hypothesized trade-off between clutch size and egg size in magpies. In replacement clutches females decreased clutch size and increased egg volume, thereby probably improving the survival probability of their offspring in less favourable conditions.

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Nest size or nest-building activity has recently been hypothesized to be a postmating sexually selected signal in monogamous birds (Soler et al. 1998a): females may assess a male's parental quality and willingness to invest in reproduction by his participation in the nest-building process. Females may thus adjust their reproductive effort (i.e. clutch size) not only to their own abilities but also to those of their mate. Comparative (Soler et al. 1998a) and empirical (Lens et al. 1994; Moreno et al. 1994; Soler et al. 1996, 1998b, 2001; Palomino et al. 1998) studies have supported the hypothesis in several species.

Since nest size is the result of nest-building activity, females could use either the male's activity, or the resulting nest size, as a signal of his willingness to invest in reproduction. In the black wheatear, *Oenanthe leucura*, a species in which males carry heavy stones to the nest site (a sexually selected activity), females directly monitor males' nest-building activity to assess their parental and/or phenotypic quality and accordingly to adjust their investment in reproduction (Moreno et al. 1994; Soler et al. 1996). However, in some species, monitoring the male's nest-building activity could take considerable time that could otherwise be used for other activities such as

foraging. Thus, one can predict that females would use traits strongly related to nest-building activity, but more easily detectable, such as nest size. This is the case in magpies, *Pica pica*, since an experimental increase in nest size resulted in an increase in clutch size (Soler et al. 2001). Thus nest size per se is the signal that female magpies use to adjust clutch size.

Ecological or ethological factors may be related to differential costs associated with the use of nest size or nest-building activity as a signal of a male's willingness to invest in reproduction. For instance, in species that usually use nests from previous years, it could be difficult for females to distinguish between old and new material carried to the nest. In this case, nest size would not be a reliable signal of nest-building activity. Furthermore, large nests take time to build (Collias 1997; Soler et al. 1998a; Hansell 2000), which may be a constraint close to the optimal breeding time, especially for migrants or for individuals laying a replacement clutch after losing the first (e.g. Hamilton & Orians 1965). In these cases, females may use their mate's nest-building time to indicate their willingness to invest in reproduction (Soler et al. 1998a).

We examined whether females change their criteria from nest size to nest-building time for assessing the male's interest in investing in a replacement clutch, when faced with time constraints. We tested the hypothesis in the magpie, by experimentally inducing pairs to build a

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new (replacement) nest after clutch completion. In this way we manipulated the time constraint and were able to compare nest size, clutch size and egg size of first and replacement clutches of the same magpie pair.

The magpie is a long-lived monogamous bird that breeds once a year, but, after predation, they are able to lay a replacement clutch. They usually build a new nest for each breeding attempt, but may use the same nest for replacement clutches by adding new material (Birkhead 1991; Sorci et al. 1997). Since nest size is a postmating sexually selected signal in magpies that females use to adjust clutch size during the first breeding attempt (Soler et al. 2001), this is a good species to test our hypothesis.

We predicted that, after losing the first breeding attempt, magpie pairs should build a smaller nest for the replacement clutch because building a large nest would require too much time and delay laying (prediction 1).

Since there may be sexual conflict over the effort put into the second breeding attempt, females should assess the willingness of their mate to invest in that second attempt. Then, following our hypothesis, females should change their criteria for estimating their mate's interest in investing in a replacement clutch and adjust their reproductive effort (i.e. clutch size) to the nest-building activity of males (i.e. total time needed to build a new nest). Thus, differences between first and second clutch sizes of the same female should be explained by the building time of replacement nests (prediction 2a), but not by variation in nest size (prediction 2b) as would be predicted if female criteria did not change from the first to the second breeding attempt.

Our experiment, however, might not necessarily provoke females to reassess the male. Since females have already estimated the quality of their mate from the initial nest size and both male and female share an interest in speeding up a second clutch, females may use that previous estimation to adjust clutch size in replacement clutches. If so, nest size of the first breeding attempt should explain clutch size in replacement clutches (prediction 3a), or should be related to any other variable explaining female investment in reproduction (i.e. nest-building time; prediction 3b).

Furthermore, since some magpies that lose their first clutch may postpone future breeding to the next year, this experimental approach allows us to analyse the probability of magpies having a replacement clutch in relation to the nest size of their first breeding attempt. Therefore, since the probability of renesting should be related to the quality of the magpie pair (Birkhead et al. 1991), we were able to test further predictions of the hypothesis that the nest size of the first breeding attempt in magpies is a reliable signal of pair quality (i.e. the female's reproductive investment; Soler et al. 1995, 2001). We predicted that magpie pairs that built large nests during the first breeding attempt should be more likely to have a replacement clutch than those that built small nests, even after controlling for the effect of laying date (prediction 4).

This experimental approach also allowed us to test predictions about the general hypothesis of a trade-off between the number of eggs and egg size (egg quality). In

general, there is no relationship between clutch size and egg size in magpies (Birkhead 1991). However, since females may vary in the number and size of their eggs, to demonstrate a trade-off between clutch size and egg size, comparisons of clutches of the same females are needed. Clarkson (1984; cited in Birkhead 1991) found a negative relationship between variation in clutch size and egg size from first to second attempt clutches in magpies, suggesting a trade-off between clutch size and egg size. If there is such a trade-off, variation in clutch size between first and replacement clutches of the same female should explain variation in egg size (prediction 5a). In several studies of passerines, egg size had a positive effect on nestling mass, especially during the early posthatching period (Magrath 1992; Smith & Bruun 1998; Reed et al. 1999; Styrsky et al. 1999, 2000). Furthermore, recent studies have suggested a trade-off between clutch size and larger eggs in less favourable conditions, to maximize reproductive success (Smith & Bruun 1998; Styrsky et al. 1999). Smith & Bruun (1998) found in a nonexperimental study in European starlings, *Sturnus vulgaris*, that nestling survival was related to egg mass only in areas with a low proportion of pasture. Styrsky et al. (1999) also showed in a cross-fostering experiment that nestling mass in house wrens, *Troglodytes aedon*, was positively related to egg mass, but only late in the season. According to these studies and to Clarkson's (1984) findings, we should find a reduction in clutch size, but an increase in egg size, from first to replacement clutches of the same magpie female (prediction 5b), because larger eggs would have a positive effect on early growth of nestlings.

METHODS

Study Area

We did the experiment in the spring of 1999 on a magpie population at La Calahorra, Hoya de Guadix (37°18'N, 3°11'W, southern Spain), a high altitude plateau, ca. 1000 m above sea level. The vegetation is sparse, including cultivated cereals (especially barley) and many groves of almond trees, *Prunus dulcis*, in which magpies prefer to breed (for a more detailed description see Soler 1990).

Species

Magpies occur throughout large parts of the Holarctic region. They are territorial and sedentary with a well-described biology (extensively reviewed in Birkhead 1991). A single clutch of 3–10 eggs is laid in spring from March to May in their western European range (Birkhead 1991). If they lose a clutch during egg laying or incubation, they may lay a replacement (Birkhead 1991; Sorci et al. 1997). However, clutches depredated during the late incubation period are rarely replaced (Birkhead 1991).

The magpie normally builds a domed, almost spherical nest with a stick framework. A bowl of mud is built inside the framework and lined with fibrous roots, hair and grass

(nest cup; Birkhead 1991). Both sexes build the nest, but the male makes significantly more trips to collect mud and large twigs, generally collecting more sticks than the female (Birkhead 1991). Therefore, nest size and nest-building time should depend largely upon male investment.

Replacement clutches are significantly less successful than first attempts, owing to less favourable environmental factors, such as reduced food availability (Birkhead 1991) or nestling immunocompetence (Sorci et al. 1997). Replacement nests and clutches are usually smaller than those in first attempts, but replacement eggs are larger (Clarkson 1984).

In our study area, great spotted cuckoos, *Clamator glandarius*, frequently parasitize magpie nests (e.g. Soler 1990; Soler et al. 1995, 1999), but we did not use parasitized nests in the present study.

Experimental Procedure

At the beginning of the breeding season we started to look for magpie nests in the study area. We visited each nest at least twice a week to detect the beginning of egg laying (laying date). After the fifth egg was laid, we visited the nest every 2 days to determine when the clutch was completed (clutch size). We recorded egg size and nest size 2–3 days after clutch completion, and we removed the eggs from the nest, simulating predation and inducing the magpies to build a new nest and lay a replacement clutch. About a week after removal of the eggs, we started looking for replacement nests. Although some magpie pairs may use the same nest for replacement clutches, in 1999 we found only one, and we used only pairs that built a new nest. Although the majority of magpies in our population are not colour ringed, we know from those that are (15–20%), that pairs usually defend a territory throughout the breeding season, and replacement nests are built in the same territory, close to first nests (Birkhead 1991; Sorci et al. 1997). Therefore, it is almost certain that each pair built a replacement nest close to the first one. Since the probability of having a replacement clutch decreases as the season progresses (Birkhead 1991), we decided to stop manipulating nests on 12 May, which is close to the mean laying date of magpies in the study area (Soler et al. 1995; Sorci et al. 1997).

We experimentally depredated 32 magpie nests, of which we found 20 (62.5%) finished replacement nests. However, our sample size was reduced because we excluded pairs that built first ($N=5$) or replacement nests ($N=4$) on the top of nests from previous years, or used their nest of the first breeding attempt ($N=1$). In analyses including clutch size and/or egg size we also did not use data from the pair that did not build a new nest for their replacement clutch or nests that suffered predation or parasitism by the great spotted cuckoo during egg laying ($N=5$) or after clutch completion, but before we were able to measure egg size ($N=3$). The great spotted cuckoo usually destroys some magpie eggs during laying and, since magpies usually remove broken eggs from their nest (Soler et al. 1997), we were unable to estimate the magpie's clutch size or egg size in these nests.

We measured nest size with a ruler (precision ± 1 cm), and calculated nest volume as $4/3\pi ab^2 m^3$, a being the largest radius of the ellipsoid nest and b half of the nest width. Egg size (measured with a digital calliper, accuracy 0.01 mm) was also calculated as the volume of an ellipsoid (cm^3). To avoid pseudoreplication, we used mean egg size of each nest in the analyses. We calculated the time to build the replacement nest as the date when the first egg was laid in the replacement clutch minus the date when we removed the first clutch. Although we visited nests frequently, we did not detect the majority of replacement nests until they had eggs, because females lay replacement clutches as soon as the nest is built. Therefore our measurement of nest-building time should be strongly related to the real nest-building time.

Ethical Note

We used the majority of the removed eggs in other experiments, mostly to replace eggs destroyed by the great spotted cuckoo (as in Soler et al. 1997, 1999). Therefore, since many of the experimental magpies were able to lay replacement clutches and magpies live for a long time (see above), we believe that the experiment did not affect the magpie population.

Statistical Methods

Since distributions of clutch size, nest size, egg size and nest-building time did not differ significantly from a normal distribution (Kolmogorov–Smirnov test: NS), we used parametric tests following Sokal & Rohlf (1995).

Nest size, clutch size and egg size of first and replacement clutches were positively related (nest size: $r_{13}=0.78$, $P=0.0007$; clutch size: $r_{12}=0.48$, $P=0.08$; egg size: $r_9=0.88$, $P=0.0003$). As a measure of variation in these variables between first and replacement clutches, we used the residuals of the regression of first and replacement variables, hereafter called residual nest size, residual clutch size and residual egg size, respectively.

Since laying date may affect nest size, clutch size and egg size, we used laying date of the first breeding attempt as a covariable in some of the analyses. As our other analyses were paired, laying date of the first breeding attempt is intrinsically controlled. Manipulation date could also affect nest-building time if later manipulated nests were built faster because of time constraints. However, manipulation date did not significantly affect nest-building time ($r_{16}=-0.29$, $P=0.24$).

All statistical tests were two tailed; values are means \pm SE.

RESULTS

Nest-building Time and Reproductive Effort

In accordance with prediction 1, replacement nests were on average 55.8% smaller than the pair's first nest (paired t test: first nests: $0.20 \pm 0.027 m^3$; replacement nests: $0.09 \pm 0.013 m^3$; $t_{14}=6.23$, $P=0.00002$).

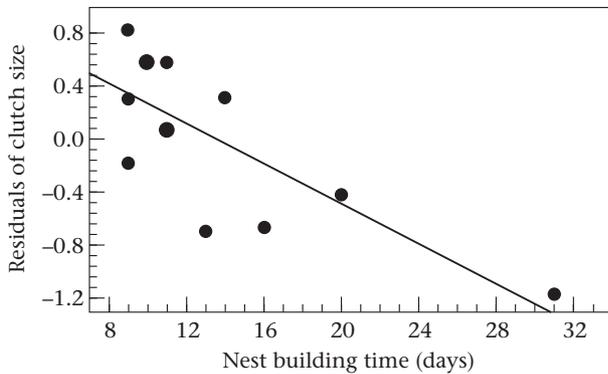


Figure 1. Relationship between residuals of clutch size (replacement clutch size controlled for first clutch size) and time needed to build the replacement nest. Larger circles are two points with the same values. The regression line has the equation: $Y=1.02-0.075X$.

In a stepwise multiple regression analysis, residual clutch size was significantly explained by the nest-building time (Fig. 1; prediction 2a), but not by residual nest size (prediction 2b). However, although not statistically significant, the second variable that entered into the model was residual nest size; residual egg size did not enter the analysis (forward multiple regression: adjusted $R^2=0.79$, $F_{2,6}=16.36$, $P=0.004$; partial regression coefficients: nest-building time: $r=-0.80$, $P=0.003$; residual nest size: $r=-0.31$, $P=0.11$). We also performed a backward multiple regression, including the same variables, with exactly the same results. Furthermore, when nest-building time was removed from the analysis, residual nest size did not explain residual clutch size ($R^2=0.0002$, $F_{1,8}=0.002$, $P=0.97$). In addition, contrary to predictions 3a and 3b, nest size of the first breeding attempt did not explain replacement clutch size ($R^2=0.004$, $F_{1,11}=0.004$, $P=0.85$), nor did it explain nest-building time ($R^2=0.02$, $F_{1,10}=0.18$, $P=0.68$), which is the variable that best explains replacement clutch size. These results suggest that magpie females reassess their mate's interest in investing in reproduction for replacement clutches and change their criteria of assessment from the first to the second breeding attempt.

First Nest Size and Pair Quality

In accordance with prediction 4, a logistic regression analysis showed that first nest size was the main predictor of whether magpies were able to lay replacement clutches (maximum likelihood: $\chi^2_1=11.7$, $P=0.006$), but not laying date (maximum likelihood: $\chi^2_1=1.0$, $P=0.32$). Furthermore, the difference in deviance between models including and excluding laying date was far from significant (difference in deviance: 0.62, $P=0.43$) and, even when we included laying date in the model, nest size of first clutches remained a significant variable explaining the probability of building a replacement clutch (multiple model: maximum likelihood: $\chi^2_2=12.33$, $P=0.002$; partial contribution to the model of nest size: parameter in the model: 0.025, $P=0.02$; partial contribution to the model of laying date: parameter in the model: -0.06 , $P=0.44$).

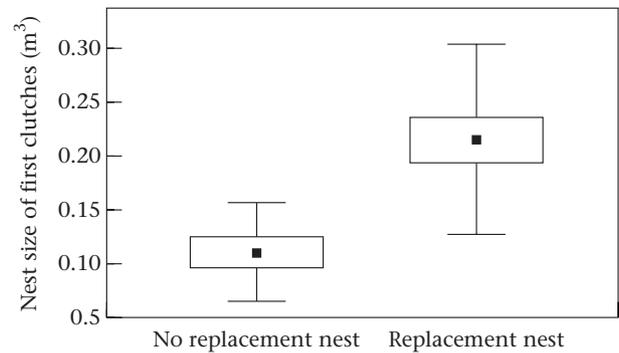


Figure 2. Nest sizes for the first clutch of magpie pairs that either did or did not build a replacement. Means (■) are given with SE (box) and SD (lines). Replacement nest built: $N=10$; no replacement nest built: $N=17$.

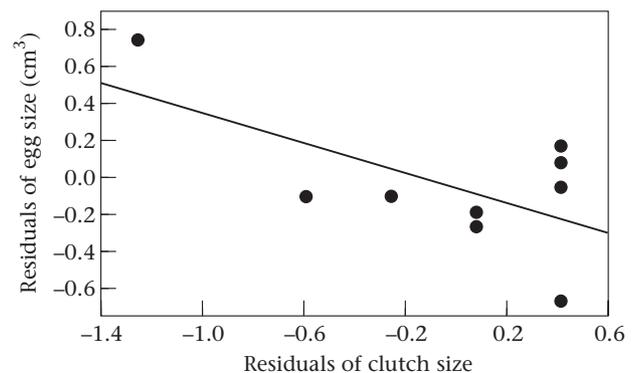


Figure 3. Relation between residuals of egg size (replacement clutch egg size controlled for first clutch egg size) and residuals of clutch size (replacement clutch size for first clutch size). The regression line has the equation: $Y=-55.37-408.9X$.

When we compared nest sizes of magpies that were able to lay a replacement clutch and those that did not, we found that magpies able to lay a replacement clutch were those that built larger nests in the first breeding attempt (Fig. 2), even after controlling for the effect of laying date of the first clutch (ANCOVA, covariate: laying date: $F_{1,31}=7.53$, $P=0.01$).

Trade-Off between Clutch and Egg Size

In accordance with prediction 5b, replacement clutches were smaller than first clutches (paired t test: first clutch: 6.9 ± 0.3 ; replacement clutch: 6.1 ± 0.2 ; $t_{13}=2.35$, $P=0.035$) while egg size increased (paired t test: first clutch: 9.4 ± 0.8 cm³; replacement clutch: 9.8 ± 0.9 cm³; $t_{10}=2.54$, $P=0.03$).

As predicted from the possible trade-off between clutch size and egg size (prediction 5a), the only variable that marginally explained variation in egg size from first to replacement clutches, although not significantly, was residual clutch size (forward multiple regression: R^2 adjusted=0.30, $F_{1,7}=4.41$, $P=0.07$; Fig. 3), and no other variables (e.g. residual nest size or nest-building time) entered into the multiple regression model. Although our

sample size is small, we believe that all these results together provide further evidence of the trade-off between egg size and clutch size in magpies.

DISCUSSION

Magpie females use nest size for first broods to assess the male's quality and willingness to invest in reproduction and adjust their clutch size accordingly (Soler et al. 2001). Since laying date is negatively related to reproductive success (Birkhead 1991), pairs that lose their first clutch need to start a replacement clutch as soon as possible. Exaggeration of nest size should then no longer be a selective behaviour or a sexually selected signal. Instead selection should favour those individuals able to build a new nest in a short period, and replacement nests should be smaller than the first nests, built without this time constraint. In accordance with these hypotheses, we found that replacement nests were significantly smaller than first nests (prediction 1).

Females did not use their assessment of mate quality from the first nest size to adjust clutch size in replacement nests. First nest size did not explain clutch size in replacement nests, and females adjusted replacement clutch size to the nest-building time of the new nest but not to the variation in nest size between first and replacement nests. Furthermore, nest size did not show any relationship with nest-building time for replacement clutches. An alternative explanation for these results could be that a change in maternal condition rather than a delay in the timing of breeding changed the way experimental females adjusted reproductive effort to nest-building behaviour. Even if that were the case, however, females changed the trait used to adjust reproductive effort, from nest size for first clutches (Soler et al. 2001) to nest-building activity for replacement clutches, and this change is of selective advantage because of the delay in optimal laying date provoked by the experimental predation.

We further tested whether nest size in the first attempt is an indicator of pair quality (Soler et al. 1998a). If nest building is costly (in terms of energy and predation), only individuals in good condition should be able to build large nests (Zahavi 1987; Lens et al. 1994). Since male magpies make more trips and carry more large sticks to the nest (Birkhead 1991), and in the first attempt the nest-building period is not constrained by time, nest size can be exaggerated depending on the condition and nest-building ability of the male. The degree of exaggeration of nest size then functions as a postmating sexually selected signal for the female to assess male quality (Soler et al. 1998a, 2001). Therefore nest size in the first attempt should indicate pair quality and should predict the probability of the pair building a replacement nest. In this study pairs that built a large first nest were significantly more likely to build a replacement nest (prediction 4). In addition, first and replacement nest sizes of a pair were strongly positively related: magpies building a large first nest also made a relatively large replacement nest, independently of the time they needed to build it. These results further support the idea that nest size in magpies is an indicator of pair quality.

We also found evidence for a possible trade-off between egg size and clutch size in magpies. Variation in egg size between first and replacement clutches of the same female was marginally, although not significantly, explained by variation in clutch size. The lack of significance was probably due to the small sample size. Furthermore, in accordance with the predictions, magpie females reduced clutch size but had larger eggs in replacement clutches. We believe that these results indicate that, in this species, a trade-off exists between larger eggs and smaller clutch size in less favourable conditions (replacement clutches), thereby maximizing offspring survival (Smith & Bruun 1998; Styrsky et al. 1999). However, recently, Nager et al. (2000) indicated important changes in egg composition during the laying sequence in black-backed gulls, *Larus fuscus*, and egg quality had a significant effect on the survival of chicks. Their study suggests an important trade-off between egg quality and number of eggs laid in this species. The importance of egg size and quality for fitness-related traits and survival of nestlings in magpies has not yet been investigated, and further research is necessary to clarify this issue.

In conclusion, we suggest that when time is a limiting factor for nest building in magpies (in this study after depredation of the first clutch), high-quality pairs, which build a large first nest, are more capable of building a replacement nest; and in this case time taken to build the replacement nest becomes an important signal for the female to adjust her future reproductive effort (i.e. clutch size). Rapid builders also reduce their delay in laying date: the sooner they start incubating their replacement clutch, the higher their reproductive success will be. Although our conclusions are cautious owing to the small sample size, this study also gives further support for the hypothesized trade-off between clutch size and egg size in magpies.

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