Nest size affects clutch size and the start of incubation in magpies: an experimental study

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Nest size has been suggested to be a sexually selected trait indicating parental ability of both males and females. To test whether a female's reproductive decisions (e.g., clutch size and starting incubation) change in relation to experimental manipulation of nest size, as would be predicted if nest size is a sexually selected signal reflecting the male's parental quality, we manipulated nest size in a population of monogamous magpies before laying by adding or removing about 20 cm of large sticks in the roof of magpie nests. On the one hand, we found that clutch size of reduced nests was smaller than that of control or enlarged nests. Moreover, clutch size was significantly related to nest size after manipulation, which indicates that females adjust clutch size to the final size of the nest, nest size thereby being a good candidate for a sexually selected trait. On the other hand, number of eggs hatched during the first day is hypothesized to be related to the expected available resources during nestling growth, and subsequent nestlings hatched are likely to die due to brood reduction if resources are not sufficient to raise well-developed nestlings. Nest size is hypothesized to inform females about a male's willingness to invest in reproduction, and we found that in broods of experimentally reduced nests, females started to incubate earlier in the laying sequence than they did in broods of control or enlarged nests. Moreover, in experimentally reduced nests, fewer nestlings hatched during the first day, and the difference in body mass between the first and the fourth nestling hatched increased. This result is in accordance with the hypothesis that the female's decision of when to start incubation in the laying sequence is mediated by nest size, a sexually selected trait signaling parental quality. We discuss alternative explanations for the results such as the possibility that nests of different treatments may differ in their thermoregulation properties or in their protection against predators. *Key words:* clutch size, female decision making, magpies, nest building, parental investment, *Pica pica,* sexual selection. *[Behav Ecol 12:301–307 (2001)]*

Nest size in monogamous passerines has recently been hypothesized to be a sexually selected signal of parental quality. Females may be able to assess male parental quality from their participation in the nest-building process or from nest characteristics and then adjust clutch size according to male parental quality or his willingness to invest in reproduction (Soler et al., 1998b). Empirical data have supported the hypothesis in several species. In the black wheatear (*Oenanthe leucura*), nest size was related to parental quality (Moreno et al., 1994). In the barn swallow (*Hirundo rustica*), nest size was related to male contribution in nest building, and nest size was related to the number of eggs laid by a female during the breeding season (Soler et al., 1998a). In the rufous bush robin (*Cercotrichas galactotes*), nest size was positively related to the size of prey males carried to the nest to feed the young (Palomino et al., 1998). In the magpie (*Pica pica*), nest size was related to laying date (Soler et al., 1995). Moreover, great spotted cuckoos (*Clamator glandarius*) parasitized magpie nests based on nest size (Soler et al., 1995). An experiment demonstrated that magpie pairs selected by the great spotted cuckoo were of better parental quality than those not selected because selected magpies raised more nestlings than did those not selected (Soler et al., 1995). In accordance with cuckoos selecting magpies that build large nests, magpie populations in sympatry with the great spotted cuckoo build smaller nests than allopatric magpies (Soler et al., 1999). The only experimental work testing the hypothesis that nest building is a sexually selected signal was carried out in the black wheatear. In

this species females that paired with males that carried more stones to the nest laid earlier in the breeding season, resulting in a higher reproductive success in these females (Soler et al., 1996b).

In the present study, we experimentally increased or decreased nest size in a population of monogamous magpies before laying to determine whether females' reproductive decisions (e.g., clutch size and starting incubation) are affected by nest size, as would be predicted if nest size is a sexually selected signal (de Lope and Møller, 1993). Specifically, we statistically tested two hypotheses and associated predictions.

Hypothesis 1

The first hypothesis is that nest size is a sexually selected signal showing a male's willingness to invest in reproduction. It is generally accepted that individual birds adjust clutch size to their quality and/or to territory quality and that, within similar environments, greater ability to nourish the offspring should be associated with a larger clutch size (Lack, 1968; Sæther, 1994). Accordingly, we predicted that, if nest size indicates male parental quality, magpie pairs with experimentally reduced nest size should lay a smaller clutch compared to controls or compared to pairs whose nests were experimentally enlarged (prediction 1a). Moreover, if nest size per se is a signal that females use to adjust clutch size, then we should expect a positive relationship between clutch size and nest size after the experiment (prediction 1b) and the same relationship when using only control nests (prediction 1c). An alternative hypothesis is that the number of male trips carrying nest material, rather than nest size per se, is the signal that females use to assess male quality. In this case we should expect no effect of experimental manipulation on clutch size

(prediction 2a) and a positive relationship between clutch size and nest size before the experiment (prediction 2b).

However, clutch size could also be related to other factors such as predation risk or thermoregulatory properties of nest material. It is generally accepted that there is a negative relationship between clutch size and risk of nest predation (e.g., Lima, 1987, and references therein). The roof of the magpie nest could affect the risk of nest predation by making it difficult for predators to enter the nest and prey upon eggs or nestlings (Birkhead, 1991). It could therefore be that the expected larger clutches in experimentally enlarged nests were simply the result of those nests being safer than the reduced ones. If that were the case, nest size after manipulation should explain the probability of a nest being predated (prediction 3). Another alternative hypothesis for the expected increase in clutch size related to nest size is that our manipulation of nest size could affect the thermoregulatory properties of nests and thus differences in the thermoregulatory costs to an incubating female. A large dome would reduce the costs to an incubating female and thus she may be able to lay more eggs. In this scenario, it can be predicted that fertilized eggs that failed to hatch should be more common in small nests (prediction 4).

Hypothesis 2

The second hypothesis is that the male's expression of sexually selected characters signaling parental quality should influence the female's decision on when to start incubating (Gibbons, 1987; Harper et al., 1994; Wiebe and Bortolotti, 1994). For a given clutch size, natural variation in the female decision of when to start incubation may reflect variation in parental quality; ''poor'' parents (or parents in a poor habitat) may start incubation earlier in the laying sequence than ''good'' parents (Gibbons, 1987). This is because hatching time of a nestling in relation to that of its siblings is related to the probability of offspring survival and to offspring physical condition, not only as nestlings (e.g., Bortolotti, 1986; Howe, 1976; Zach, 1982), but also after leaving the nest (Husby, 1986), and hatching time is determined mainly by the amount of food the parents provide to the nestlings (Gibbons, 1987). Pairs with poor parental quality, by starting incubation early in the laying sequence, would waste less energy in producing a nestling hierarchy, allowing early mortality of some of them, which in any case would die later (Gibbons, 1987). Then magpie females could facultatively decide when to start the incubation in relation to male parental quality (which is hypothesized to be reflected by nest size) because males of high parental quality will provide future offspring with better and/or more food.

In this scenario, we predict that experimentally size-reduced nests should start incubation earlier in the laying sequence than enlarged or control nests (prediction 5). However, because the decision of when to start incubation is potentially related to clutch size (Wiebe and Bortolotti, 1994), differences between treatments should appear even after controlling for clutch size. These predicted differences between treatments should produce different degrees of hierarchies in nestling body mass in experimentally reduced, enlarged, or control nests. We predict that, after controlling for clutch size, the largest differences in body mass of nest mates should appear in experimentally reduced nests, whereas the smallest differences should appear in experimentally enlarged nests (prediction 6).

However, a female's decision of when to start incubation could also be related to the eggs' protection from adverse weather or other environmental factors affecting hatchability (the egg viability hypothesis; Arnold et al., 1987; Veiga, 1992).

It has been demonstrated that nest size is related to egg insulation against harmful environmental conditions such as low temperatures and rain (Kern, 1984; Kern and Riper, 1984; Sciurine and Kern, 1980), and thus our experiment would potentially provoke different insulating properties in different treatments. The egg viability hypothesis states that starting incubation early in the laying sequence prevents a reduction in egg hatchability. Thus, it can be predicted that eggs that fail to hatch should be more frequent in nests where the female starts incubation later in the laying sequence (prediction 7). An additional prediction from the egg viability hypothesis is that nest size should predict hatchability after controlling for the effect of start of incubation (prediction 8).

METHODS

Study area

The study was carried out in La Calahorra, a plot of almond trees (*Prunus dulcis*) located in the Hoya de Guadix, southern Spain (37°18′ N, 3°11′ W). La Calahorra is located in a high-altitude plateau, approximately 1050 m above sea level, occupying about 3.5 km² and containing about 100 magpie nests.

Study species

The magpie is a monogamous passerine commonly used as a host by the brood parasitic great spotted cuckoo in this area. However, none of the seven parasitized magpie nests found in La Calahorra plot during the year of the experiment were used in the analyses. Magpies normally build a domed, almost spherical nest with a stick framework. After the framework is finished, a bowl of mud is built inside and lined with fibrous roots, hair, and grass (nest cup; Birkhead, 1991). Both members of the pair participate in nest building, but the male makes significantly more trips to collect mud and large twigs, generally collecting more sticks than the female (Birkhead, 1991). The size of the nest structure has been suggested to be a reliable signal of territory quality and/or pair quality (Soler et al., 1995). Moreover, it has been hypothesized that the number of trips and/or the volume of sticks brought by a male magpie signals his quality and willingness to invest in reproduction, acting as a postmating sexually selected trait (Soler et al., 1995).

Magpies in our study area usually lay six or seven eggs (clutch size varies between 2 and 10 eggs; Soler et al., 1996a). The eggs are incubated exclusively by the female several days after the first egg is laid, but usually before clutch completion, resulting in asynchronous broods (Birkhead, 1991). During incubation the male frequently feeds the female (Birkhead, 1991). Some nestlings usually die from starvation, especially during the first week after hatching (Husby, 1986; Reynolds, 1996; Slagsvold et al., 1992; Tatner, 1982), and the species is considered to adopt the brood reduction strategy (Husby, 1986; Reynolds, 1996; Slagsvold et al., 1992).

Experimental design

At the beginning of the breeding season of 1997, we started to look for magpie nests. The nests were found at different stages of building, and we assigned each nest to one of the following groups: experimentally increased nest volume, decreased nest volume, or control. Nest treatment was assigned before knowing the final nest volume. When the nest framework was finished but some soft materials were still needed to line the nest cup, we performed the experiment. The manipulation consisted of carefully removing sticks from the roof of

the nest, reducing the largest nest diameter by about 20 cm for the experimentally reduced nests; we kept removed sticks and used them to increase the nest volume of experimentally enlarged nests. We also visited control nests at this nest stage during a similar period of time, but did not remove sticks. In none of the experimental nests did we manipulate the nest cup volume (nest capacity or space where the eggs were to be laid). We measured the size of nests before and after manipulation (control nests were measured only once) using a ruler (precision $\pm$ 1 cm), and nest volume was calculated as 4/3 ($\pi \times a \times b^2$)/1000 (in liters), where a is the largest radius of the ellipsoid nest and b is half of the nest width. We considered only nests of first clutches built in almond trees; nests of replacement clutches or nests built on the top of older nests were not included in the study.

The experimental manipulation did not provoke nest abandonment before laying by magpies, as the desertion rate of experimental nests did not differ from that of control nests (experimental, both enlarged and reduced nests, 23.4%, $n = 49$; control nests, 25%, $n = 20$; $\chi^2 = 0.06$, df = 1, $p = .81$). Moreover, we did not find differences in desertion rate of experimentally enlarged or reduced nests (enlarged, 20.8%, $n = 25$; reduced, 25.0%, $n = 24$; $\chi^2 = 0.18$, df = 1, $p = .68$).

We visited the nests twice weekly until recording the laying date (date when the first egg was laid) and clutch size (total number of eggs laid), and three times weekly when the expected hatching date approached (19 days after fourth egg was laid). Because we were interested in whether nest size manipulation affects the female's decision of when to start incubation in the laying sequence, following Clark and Willson (1981), we classified magpies according to which egg a bird began to fully incubate, estimated as the number of eggs hatched during the first day of hatching (number of recently born nestlings [less than 1 day old] plus the number of magpie eggs still in hatching process). This is a good estimation of the number of eggs in the nest when a female started incubation because magpies lay one egg per day, and the incubation period is 21–22 days per egg (Birkhead, 1991). Magpie eggs that do not hatch usually remain in the nest for several days (Brown, 1924; Husby, 1986). Thus, all eggs that had disappeared before the oldest nestling was 5 days old were presumed to have hatched successfully, but the nestling was presumed to have died later. Magpie nestlings, as well as most nidicolous birds, change skin color from red to orange (during the first 24 h in magpies; Soler et al., personal observations). Thus, when we found several nestlings, we were able to estimate their age by color and size.

We also estimated the level of nestling hierarchy. Level of nestling hierarchy depends on brood size and whether or not brood reduction has occurred before the last egg hatches. In magpies, brood reduction frequently occurs before the last egg hatches (see above), and the nest-size experiment is predicted to affect clutch size. To avoid these possible confounding factors, we used the difference in body mass between the heaviest and the fourth nestling in the body mass hierarchy. We decided to use differences in body mass between those nestlings because magpies usually start the incubation upon laying the fourth egg (Birkhead, 1991; Soler et al., unpublished data), and brood reduction frequently occurs with the fifth and subsequent nestlings. When the largest nestling weighed between 20 and 30 g (3–4 days old), using a portable digital balance (Sartorius Portable PT600, precision $\pm$ 0.01 g), we recorded body mass of all nestlings in the nest. We did not use nests with brood size smaller than four, nor those that we were not able to visit at this stage or for which the body mass of the heaviest nestling was not between 20 and 30 g. We hereafter call this variable "difference in body mass." To control for the effect of clutch size, we included clutch size
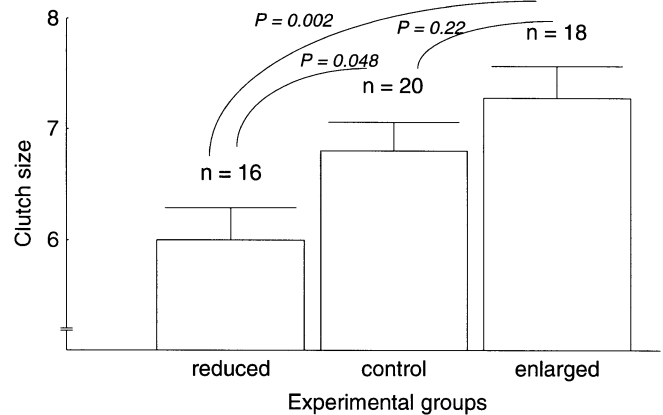

Figure 1
Clutch size of magpies with reduced, control, or enlarged nests. Values are means $\pm$ SE. Least squares difference post-hoc probabilities for difference between experimental and control groups are also shown.

as a covariate in the analyses or calculated residuals of the number of hatched eggs during the same day controlled for clutch size.

There were some nests where some of the eggs failed to hatch. To determine whether those eggs contained embryos, 4 days after the last chick was hatched, we broke the eggs still in the nest and checked for dead embryos or lack of fertilization. Although embryo mortality may take place before development can be seen with the naked eye, in all nests where some of the eggs failed to hatch, at least one contained a dead embryo. Because we classified magpie nests as failed or not in egg incubation, this potential methodological problem does not exist in our data set.

Statistical procedure

Clutch size and the start of incubation in the laying sequence showed an approximately normal distribution (Kolmogorov-Smirnov test for discrete variables, $p > .3$), as well as the laying date and difference in body mass (Kolmogorov-Smirnov test for continuous variables, $p > .2$). Nest volume, both before and after manipulation, did not differ from a normal distribution after natural logarithmic transformation (Kolmogorov-Smirnov test for continuous variables, $p > .2$). Therefore, we used parametric tests following Sokal and Rohlf (1995).

Due to nest predation during the breeding cycle and nest desertion before or during laying, sample sizes varied for different variables. To detect any possible bias in the data, we tested for possible differences in laying date between treatments (reduced, control, and enlarged nests) in all statistical tests performed. All tests were two-tailed. Values presented are means $\pm$ SE.

RESULTS

Is clutch size affected by manipulation of nest size?

In accordance with prediction 1a, but contrary to prediction 2a, experimental manipulation affected clutch size ($F = 5.05$, df = 2,51, $p = .001$; Figure 1; difference in laying date between groups: $F = 0.03$, df = 2,51, $p = .97$), and magpie females with an experimentally reduced nest laid smaller clutches than did control females or females with an experimentally increased nest volume (Figure 1). However, there were no significant differences in clutch size between females
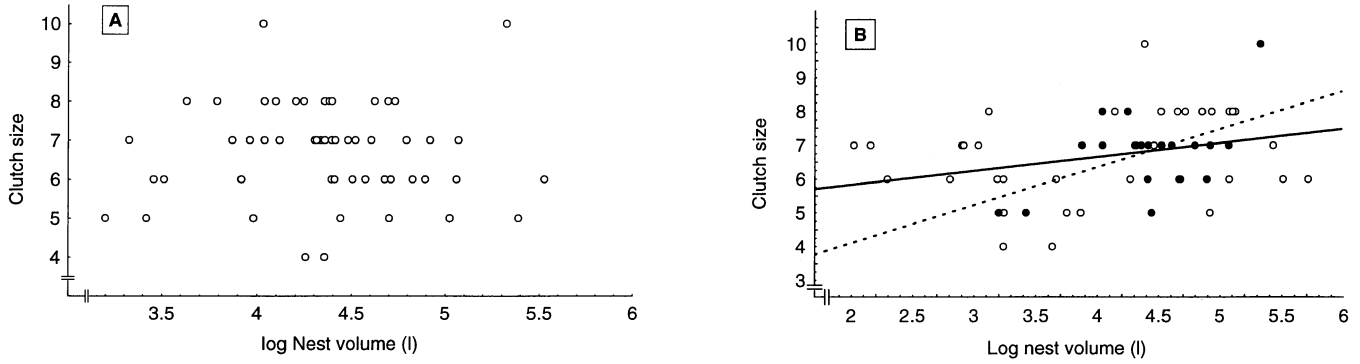
Figure 2
Relationships between clutch size and nest volume (A) before and (B) after experimental manipulation of nest size. The continuous line in (B) is the regression line using both control (filled circles) and experimental (open circles) nests with the equation: $y = 1.86x + 1.25$. The dotted line in (B) is the regression line when using only control nests with the equation: $y = 0.41x + 5.00$.

with control nests and females with experimentally increased nest volume (Figure 1).

Moreover, in agreement with prediction 1b, clutch size was positively related to nest volume after manipulation ($r = .29$, $n = 54$, $p = .033$; Figure 2B), not only for total nests but also among control nests (prediction 1c; $r = .51$, $n = 20$, $p = .023$; Figure 2B). However, contrary to prediction 2b, there was no relationship between clutch size and nest volume before manipulation ($r = .01$, $n = 54$, $p = .97$; Figure 2A). Therefore, it was nest size per se and not the number of trips that the male made to the nest carrying nest materials that affected clutch size.

These results could also be explained by differences in predation risk or thermoregulatory properties of nests of different treatments. However, contrary to prediction 3, nest size after manipulation did not explain the probability of a nest being predated (nest volume of depredated nests = 73.51 ± 13.86, $n = 12$; non-depredated nests = 89.02 ± 10.29, $n = 44$; log-linear regression analyses, maximum-likelihood method, $-2 \log(\text{likelihood}) = 58.09$, $\chi^2 = 0.10$, $p = .75$). In addition, contrary to prediction 4, fertilized eggs that failed to hatch did not occur more often in small nests; nest size after manipulation did not predict hatching failure (volume of nests with one or more fertilized eggs that failed to hatch = 71.26 ± 21.81, $n = 8$; volume of nests where all egg hatched = 92.15 ± 11.72, $n = 33$; log-linear regression analyses, maximum-likelihood method, $-2 \log(\text{likelihood}) = 39.18$, $\chi^2 = 1.29$, $p = .26$).

Does the female's decision on when to start incubation depend on nest size?

In accordance with prediction 5, we found a significant effect of nest volume on the number of nestlings born during the first day of hatching (ANCOVA, clutch size as covariate, $F = 4.59$, df = 2, 35, $p = .038$; Figure 3A; difference in laying date between groups: $F = 0.06$, df = 2,36, $p = .95$). Moreover, post-hoc comparisons revealed significant differences between experimentally reduced and enlarged magpie nests, but no significant differences between control and experimentally reduced nests, nor between control and experimental enlarged nests (Figure 3A).

Following prediction 6, difference in body mass between the largest and the fourth nestling in the body mass hierarchy differed significantly between treatments (ANCOVA, clutch size as covariate, $F = 5.04$, df = 2, 25, $p = .015$; Figure 3B; differences in laying date between groups: $F = 0.52$, df = 2, 26, $p = .60$). Moreover, post-hoc comparisons revealed significant differences between experimentally reduced and controls nests or nests experimentally enlarged (Figure 3B). However, nonsignificant differences appeared when comparing differences in body mass of control magpie nests and that of experimentally increased nests (Figure 3B). Therefore, nest size manipulation affects a female's decision of when to start incubation in the laying sequence, resulting in different levels of nestling hierarchy between the first and the fourth nestling.

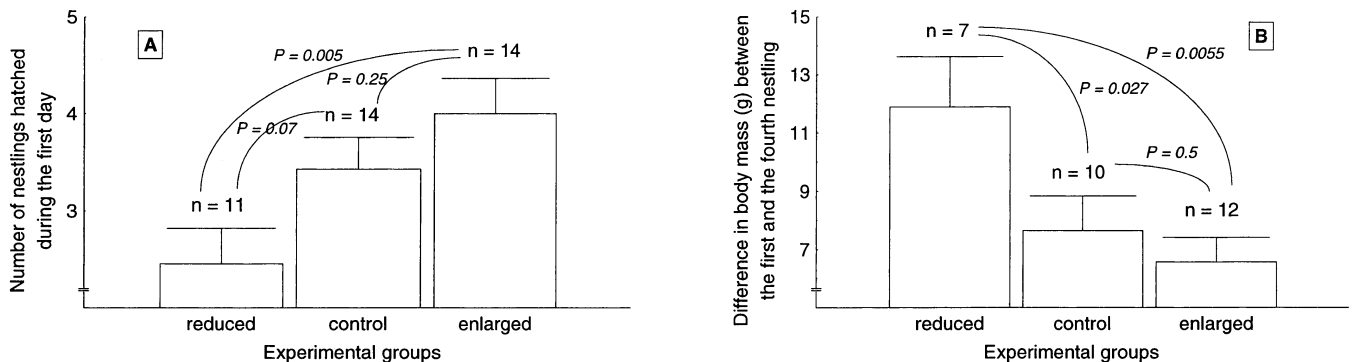This result could also be explained by the egg viability hy-

Figure 3
(A) Number of nestlings hatched during the first day and (B) difference in body mass between the heaviest and the fourth nestling for reduced, control, and enlarged nests. Values are means ± SE. Least squares difference post-hoc probabilities for difference between experimental and control groups from an ANCOVA (clutch size as covariate) are also shown.

pothesis because our experiment could have provoked different insulating properties in different treatments and, in accordance with this hypothesis, magpies may have decided to start incubation earlier in the reduced nests where insulation was poor. However, contrary to the prediction 6, eggs that failed to hatch were more common in nests where the female started incubation earlier in the laying sequence (number of nestlings hatched during the first day; nests where hatching failures occurred = 2.17 ± 0.48, $n = 6$; nests where hatching failures did not occur = 3.65 ± 0.24, $n = 31$; $F = 6.42$, df = 1,35, $p = .016$), although it could be that the eggs that did not hatch were those already laid when the female started to incubate. Moreover, contrary to prediction 7, nest size did not predict hatchability after controlling for the start of incubation in the laying sequence (ANCOVA; dependent variable, nest with eggs that fail to hatch; independent variable, nest volume after manipulation; covariable, number of eggs hatched during the first day; $F = 0.10$, df = 1,34, $p = .92$), as would be predicted by the egg viability hypothesis. Therefore, although the sample size of nests where hatching failures occurred is small, our results suggest that the egg viability hypothesis does not explain variation in the start of incubation provoked by nest volume manipulation.

DISCUSSION

Nest size and sexual selection

Sexual selection theory predicts that, in some species, females are able to detect mates of high parental quality on the basis of male traits that reliably signal parental quality (Grafen, 1990; Heywood, 1989; Hoelzer, 1989; Price et al., 1993). Therefore, such females should adjust clutch size not only to their own ability to nourish the offspring but also to the ability of their mates (Lack, 1968; Sæther, 1994). Nest size has been proposed to be a sexually selected trait signaling parental quality in passerines (Soler et al., 1998b). In magpies, nest size has previously been proposed to be a signal of parental quality, but based on a negative correlation between nest size and laying date (Soler et al., 1995). In accordance with this hypothesis, our experiment demonstrates that female magpies adjusted clutch size to the manipulated nest volume (Figure 2). Moreover, clutch size of individual females with experimentally reduced nests was smaller than that of females with control or enlarged nests (Figure 1). We did not manipulate nest cup volume, which has been hypothesized to determine clutch size because the size of the nest cup constrains the number of nestlings that can fit in the nest without overcrowding (Slagsvold, 1982, 1989; but see Soler et al., 1998b). Thus, our results support the hypothesis that nest size is a sexually selected trait in magpies.

Other explanations for our results could be related to the accepted relationship between clutch size and risk of nest predation and cost of incubation. Nest size could affect both predation risk and incubation costs. But, in contrast with these alternative hypotheses, nest size after manipulation did not explain the probability of a nest being predated nor did it explain hatching failure. However, the low sample sizes of depredated and failed nests do not allow us to completely reject the alternative hypotheses.

If the relationship between nest size and clutch size in magpies was mediated by the thermoregulatory or antipredatory properties of large nests, a positive relationship between clutch size and nest size could be predicted, independent of the studied magpie population. Magpies are the main hosts of the brood parasitic great spotted cuckoo, and the cuckoo selects magpie pairs that build large nests (Soler et al., 1995).

This preferential host selection by cuckoos selects for reduced nest size in magpie populations sympatric with cuckoos (Soler et al., 1999). If nest size is only a result of natural selection (e.g., thermoregulatory properties of nest material and reduced risk of nest predation), it can be predicted that the smaller nest size of sympatric magpie populations caused by the great spotted cuckoo selection pressure should be related to a smaller clutch size (see arguments for alternative explanations above). However, this was not the case in a study of magpie populations in Europe, and, after controlling for the effect of latitude, magpie populations sympatric with the great spotted cuckoo built smaller nests, but laid larger clutches, than allopatric magpie populations (Soler et al., 1999). Thus, natural variation of nest size per se, although it is likely related to the cost of incubation and avoidance of predators, does not constrain clutch size in magpies. Therefore, although alternative explanations cannot be completely rejected, a sexual selection process is likely to mediate the detected effect of our nest size manipulation on clutch size.

Nest size and female decision of when to start incubation

Parental quality has been hypothesized to be related to the female's decision of when to start incubation (Gibbons, 1987; Harper et al., 1994; Wiebe and Bortolotti, 1994). This is because hatching time of a nestling in relation to that of its siblings, as well as parental quality, affect probability of nestling survival (Clutton-Brock, 1991). However, individual quality has scarcely been investigated as a proximate factor during laying that affects female (or pair) decision of when to start incubation (Wiebe and Bortolotti, 1994).

At the beginning of the breeding season, a female may have an uncertain estimate of the quality of the territory in which she breeds, her nest site, her mate, and even her own abilities (Amundsen and Slagsvold, 1996). These conditions could vary among individuals from the same population, but also among years for the same individual, and could explain individual variation in the level of hatching asynchrony (Amundsen and Slagsvold, 1996), which is primarily determined by the decision of when to start incubation in the laying sequence (e.g., Mock and Parker, 1997), but also by clutch size. Nilsson (1993) demonstrated that marsh tits (*Parus palustris*) without experimental food supplementation started to incubate earlier in the laying sequence than with food supplementation. His explanation was that asynchronous broods imply that females have to incubate, but also produce and lay eggs, two activities that are very costly, and, although an early start of incubation may be advantageous during the nestling period, they were forced to delay the onset of incubation (the energy constraint hypothesis). However, Wiebe and Bortolotti (1994) found different results when studying the effect of experimental food supply during the prelaying period in a population of American kestrels (*Falco sparverius*). Wiebe and Bortolotti (1994) hypothesized that some species should facultatively start incubation later in the laying sequence when supplemental food is provided during the prelaying period. This is because one of the main costs of the early start of incubation is that small nestlings may die from starvation or trampling, even when food is abundant (Amundsen and Slagsvold, 1991). Thus, delaying the start of incubation in the laying sequence may be best when food is abundant, and hatching spans should be facultatively adjusted if food availability is predictable (Wiebe, 1995).

Level of hatching asynchrony is usually measured as the difference in hatching time between the first and the last hatched nestling. However, our predictions were not related to hatching asynchrony but to female reproductive decisions (clutch size and incubating time). We hypothesized that sex-

ually selected characters influence a female's estimation of resources mediated by parental feeding investment. Thus, the male's expression of sexually selected characters should influence the female's decision of when to start incubation and thereby the degree of nestling hierarchy (i.e., difference in body mass between the first- and the fourth-hatched nestling). We found experimental support for the hypothesis that nest size is a sexually selected trait in magpies. The magpie is a monogamous bird that builds its nest after pairing, and nest size is thus a good candidate for a postmating sexual selected trait indicating willingness to invest in reproduction (Soler et al., 1998b). Females with experimentally enlarged nests overestimated the quality of their mates and laid an optimistically large clutch (Figure 1). By manipulating nest size, we manipulated female estimation of mate quality. In agreement with this hypothesis, we found that females laying in experimentally enlarged nests started incubation later in the laying sequence and increased the number of eggs that hatched the first day (Figure 3A). Moreover, differences in body mass between the first and the fourth nestling were smaller in enlarged nests (Figure 3B). These results support the hypothesis that sexually selected traits influence a female's decision of when to start incubation. Moreover, these results are in accordance with magpies being a species that is facultatively able to manipulate hatching span, but this decision is not energetically constrained.

The "good parent" sexual selection process favors traits that reliably signal parental quality (see examples in Andersson, 1994; Møller, 1994), which would be related to the amount of food allocated to the nestlings. Thus, females could use such traits to decide when to start to incubate in the laying sequence.

An alternative explanation for the results could be given by the egg viability hypothesis (Arnold et al., 1987; Veiga, 1992). This hypothesis predicts that an early start of incubation in the laying sequence, resulting in asynchronous hatching, protects eggs from adverse weather or other environmental factors affecting hatchability. Because our experiment could have provoked different insulating properties in different treatments, our results could be explained by the egg viability hypothesis. However, contrary to this hypothesis, eggs that failed to hatch were more common in nests where the female started the incubation earlier in the laying sequence and nest size did not predict hatchability after controlling for when the female started to incubate. Therefore, our results suggest that the egg viability hypothesis does not explain variation in hatching asynchrony provoked by our manipulation.

Mate quality has previously been hypothesized to influence a female's decision of when to start incubation. Our experiment provoked an increase in clutch size of enlarged nests and a decrease in the reduced nests that cannot be explained by nest insulation characteristics, but can be explained by nest size being a sexually selected trait signaling male parental quality. Thus, variation in number of nestlings hatched the first day due to the experimental manipulation of nest size can be explained by differences in female estimation of male quality rather than by differences in nest insulation characteristics.

In conclusion, our results demonstrate that nest size affects clutch size and the start of incubation in magpies, and we suggest that these effects are mediated by nest size being a sexually selected trait. Females, by estimating a male's willingness to invest in reproduction from the size of their nest, decide a clutch size and when to start incubation in the laying sequence according to male quality, as predicted by the hypothesis of sexually selected traits being a proximal factor influencing individual variation in such a trait.

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