

FUNCTIONAL SIGNIFICANCE OF NEST SIZE VARIATION IN THE RUFIOUS BUSH ROBIN *CERCOTRICHAS GALACTOTES*

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Avian nest building behaviour has generally been viewed as a result of natural selection, and several functional hypotheses have been suggested to explain variance in nest size. These include responses to predation and parasitism risk, and aspects of nest stability, clutch size, insulation and sexual display. We studied variation in nest size in the Rufous Bush Robin *Cercotrichas galactotes*, a songbird in which both sexes contribute in nest building. Nest size was marginally negatively associated with the probability of brood parasitism, but no relationship was found with nest predation. Four additional hypotheses of the function of nest size variance were considered. The nest support hypothesis, the clutch size hypothesis and the thermoregulation hypothesis did not explain the nest size variation found, but the sexual display hypothesis was partially supported because clutch size was positively correlated with the amount of nest material, and this nest feature also tended to be positively correlated with size of prey provided to chicks by males. Nest building behaviour in the Rufous Bush Robin can be considered a post-mating sexual display that reflects the willingness of males to invest in parental care and allows females to adjust their reproductive effort accordingly.

Key words: *Cercotrichas galactotes* - nest building - nest size variation hypotheses - sexual selection

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INTRODUCTION

Avian nests are special constructions which primarily have the function to provide insulation and protection to developing eggs and young. However, nests or nest sites are used by males in some species to attract a mate, and so nest-building behaviour can be associated with courtship and pair formation. This male behaviour varies from simple advertizing of a potential nest site to the building of an entire nest (Collias & Collias 1984).

If males contribute to nest building, females can benefit from choosing a male with a high quality nest, because good thermal insulation of such a nest may increase time available for foraging

while leaving eggs or chicks unattended (White & Kinney 1974; Hoi *et al.* 1994) and reduce energy demands for incubation (Walsberg & King 1978; Kern 1984; Kern & Riper 1984; Weathers 1985). For instance, in the hole-nesting Pied Flycatcher *Ficedula hypoleuca*, females shorten their sitting spells when the nest box is artificially warmed (Von Haartman 1956). Nest size may also be important, because this is related to nest conspicuousness and hence to the probability of nest predation (Lack 1954; Löhrl 1980; Slagsvold 1982, 1989a, 1989b; Møller 1987). Thus, females can benefit from choosing safe (i.e. small) nests because this will reduce predation risk (Martin 1988). Furthermore, male nest-building may af-

fect breeding duration because male contribution may reduce the period between the start of nest-building and the onset of egg-laying (Lens *et al.* 1994).

Female mate choice has in several studies been found to be related to male nest building ability. In some species the females prefer the male with the largest number of completed nests (Collias & Victoria 1978; Garson 1980; Evans & Burn 1996). In others, female choice is based on the quality of the nest constructed by the male. For instance, in the Penduline Tit *Remiz pendulinus*, large nests with good thermal insulation and, therefore, fledging success are preferred (Hoi *et al.* 1994).

Recently, several studies have focused on nest size as a sexually selected trait, with individuals of better parental quality building larger nests in the Black Weathar *Oenanthe leucura* (Moreno *et al.* 1994), the barn swallow (Soler *et al.* in press) and the Magpie *Pica pica* (Soler *et al.* 1995). Nest building behaviour might predict the quality and/or condition of a potential partner. This pre-nesting sexual display may allow females to adjust their reproductive effort to the quality of the partner (Moreno *et al.* 1994). Nest building is costly (in terms of energy and risk of predation) and only individuals in good condition should be able to build large nests. In that scenario, nest-building behaviour would provide information about the quality of the potential partner, allowing individuals to choose a mate in non-monogamous species, while in monogamous species assessment of willingness to invest in reproduction may also allow partners to invest differentially in reproduction relative to the quality of the mate. Soler *et al.* (1998) demonstrated (1) that species in which both sexes contribute to nest building have larger nests than those in which only the female builds, and (2) a positive relationship exists between nest size (relative to body size) and parental investment (measured as the nestling period), thereby concluding that a sexual selection component is involved in nest-building activity.

The aim of this paper is to consider six non-exclusive functional hypotheses for nest size variation in a songbird, the Rufous Bush Robin *Cer-*

cotrichas galactotes. Nest size is subject to several, sometimes conflicting, evolutionary pressures: two selection pressures favour small nests (1 and 2) and four favour large nests (3-6). These selection pressures are:

(1) Nest size may be related to the probability of the nest becoming depredated both due to nest conspicuousness and the detectability of the bird while building. According to this hypothesis, depredated nests should be larger than successful ones;

(2) If nest size reflects parental quality of the builders, cuckoos should preferentially parasitize larger nests (Soler *et al.* 1995). Nest conspicuousness may also contribute to this relationship. This predicts that pairs building larger nests will have a higher probability of being parasitized than pairs building smaller nests;

(3) The clutch size hypothesis suggests that nest cup volume can be adjusted to the future clutch size (Snow 1978; Møller 1982). This hypothesis would be supported if nest cup volume was positively related to the number of eggs laid;

(4) The nest support hypothesis posits that nest material may be used to form a solid base for the nest, increasing its stability (Collias & Collias 1984). This hypothesis predicts that the amount of nest material is negatively correlated to site stability;

(5) The thermoregulatory hypothesis suggests that nest material may help to maintain egg temperature and buffer temperature fluctuations (White & Kinney 1974; Whittow & Berger 1977; Kern 1984; Hoi *et al.* 1994). Thus, thickness and/or density of the nest wall should be positively related to thermoregulatory capacity of the nest and therefore to hatching success;

(6) The sexual display hypothesis posits that nest size may allow the pair members to adjust reproductive effort to parental and/or phenotypic quality of partners (Moreno *et al.* 1994; Soler *et al.* 1998). As the Rufous Bush Robin is a monogamous species, a post-mating sexual selection in relation to nest-building is predicted. We might expect that an increasing amount of nest material should result in (a) an earlier laying date, (b) a lar-

ger clutch size, and (c) better parental care and/or a larger number of fledged young. These predictions are based on the hypothesis that nest building effort is a reliable signal of parental investment in reproduction and thereby in feeding rate and fledging success.

METHODS

Study species

The Rufous Bush Robin is a small passerine that breeds in dry areas, around the Mediterranean Sea, south of the 25°C July isotherm, mainly in lowlands (Voous 1960). Most recent studies have focused on its relationship with the Common Cuckoo *Cuculus canorus* (e.g. Alvarez 1994a, 1994b, 1996) and its breeding ecology (López-Iborra 1983; López & Gil-Delgado 1988; Palomino *et al.* 1998). As far as we know, no sexual selected trait has previously been detected in this species. Nest are commonly parasitized by Common Cuckoos in our study area (Alvarez 1994a; pers. obs.). The Rufous Bush Robin is attracted to man-made habitats such as parks, orange and grape groves, gardens and groups of prickly pear *Opuntia maxima* (Cramp 1988). Although it occasionally uses old nests of other species (Cramp 1988), Rufous Bush Robins usually build their own, open nests which are loosely-constructed (López-Iborra 1983). Nests are built, after pairing by both sexes, in a thick bush or a low tree, often near the trunk (López-Iborra 1983; Cramp 1988; pers. obs.). Common nest material is fine twigs and roots, and the nest cup is commonly lined with sheep and rabbit hair (López-Iborra 1983).

Study area

The study area comprised vineyards with scattered fruit trees, and with small patches used for vegetable production. It is located 20 km south-east of Sevilla, Spain (37°9'N, 2°14'W), at 12 m altitude. The region is characterized by a Mediterranean climate, with rainy springs and autumns, and dry, hot summers (noon temperatures above 40°C in July and August). The study was carried

out during 1995-1996, except for measurements of nest height above ground, which were made only during 1993-1994.

General field procedures

Rufous Bush Robins were captured in net traps or mist nets early in the breeding season, and they were fixed with numbered aluminium rings (Spanish Institute for Nature Conservation-ICONA) as well as plastic colour rings, which allowed individual identification during the breeding season and in successive years. We only used first clutches in order to avoid confounding factors such as nest predation and parasitism in previous breeding attempts in the same year. We recorded first clutches of each pair by following the breeding activities of pairs and looking for nests in possible nest locations. All nests were checked twice a week during incubation and every two days during the nestling period in order to collect data on laying date, clutch size, number of hatched eggs and number of fledglings. Clutch size was defined as the total number of eggs in a complete clutch, and laying date as the day when the first egg was laid, assuming that one egg was laid daily.

Nest measurements

In order to avoid distress in adults and/or nestlings, and because we needed to weigh the nests by removing them from their base, nests measurements were taken after fledging or nest predation. These measurements could be biased because nestling activity provokes nest expansion (Slagsvold 1989b). Therefore, although a low degree of nest degradation appeared, nest volume, but not nest mass, could have differed between depredated and non-depredated nests. Several variables of nest size, namely depth of the cup, inner diameter, external diameter and nest height above ground were measured using a tape measure (accurate to the nearest 0.5 cm). Both nest diameters were taken as the mean value of two perpendicular measures for each variable. Thickness of the nest bottom was measured by inserting a wire through the center of the egg-chamber. Nest mass

was measured with a Pesola balance (accurate to 2 g). Nest height was defined as depth of the cup plus thickness of the nest bottom. We calculated nest volume and nest cup volume as 1/2 of an ellipsoid for which:

$$\text{Volume} = 4/3 \pi a^2 b x$$

where a is the smallest radius of the ellipsoid, b is the largest radius and x is the fraction of the ellipsoid (1/2). The difference between nest volume and nest cup volume was the volume of nest material. Density of the nest wall was calculated as the ratio between nest mass and volume of nest material. After removing the nest from the tree, we estimated nest support as the percentage of the area of the base of the nest in contact with branches. Nest height above ground was defined as the distance between the edge of the nest cup and the ground.

Parental investment measurements

Seven nests were recorded with a video camera during 2 hours when nestlings were 3 or 4 days old. We measured the number of male and female feedings and estimated prey size relative to adult bill size. Prey size was considered 3, 2 or 1 when it was larger, similar to or smaller than adult bill size, respectively. Mean prey size was calculated as the ratio of the sum of all prey sizes to number of feedings.

Statistical procedures

In order to avoid pseudo-replication, pairs from the 1996 breeding season were included in the analyses for testing the sixth hypothesis only if individuals were not mated in the years before, because each pair member could know the parental ability of its mate from previous experience. We were unable to obtain estimates of all variables for all individuals, and, therefore, sample sizes differ among some analyses.

Logistic regression was used to study the relationship between nest size (independent variable) and probability of being parasitized and the nest being depredated (dependent variables) using the maximum-likelihood method (Cox 1970). We used non-parametric statistics due to the small sample sizes (Siegel & Castellan 1988). Kendall t correlations were used when partial correlations were necessary. First-order Kendall partial correlations were calculated according to Siegel & Castellan (1988) and second-order Kendall partial correlations according to Sokal & Rohlf (1981). Because the predictions raised in the hypotheses are 'a priori' and they had been supported previously in other species, we used one-tailed tests. Values reported are means \pm SD.

RESULTS

Rufous Bush Robin nests were mainly placed in vines *Vitis vinifera* (95.5% of 176 nests) in our

Table 1. Nest size measurements, nest mass and percentage of nest support for Rufous Bush Robin first clutch nests.

	Mean	SD	n	Min	Max
Large diameter (cm)	13.43	1.57	37	9.0	17.5
Small diameter (cm)	7.24	0.69	37	6.3	9.5
Nest mass (g)	104.81	48.46	37	34.0	226.0
Depth of the cup (cm)	4.42	0.73	36	2.5	5.8
Thickness of the bottom (cm)	3.61	1.67	36	0.3	8.1
Nest cup volume (cm ³)	120.36	19.43	36	83.5	165.4
Nest volume (cm ³)	763.81	237.08	36	383.1	1382.7
Volume of nest material (cm ³)	643.45	230.12	36	265.1	1225.5
Percentage of nest support (%)	67.66	24.97	37	10.0	100.0

study area, although other sites such as in fruit trees (1.1%) and directly on the ground (3.4%) were also used. The mean height above ground was 53.0 ± 14.6 cm ($n = 176$) for all nest locations, and 51.2 ± 8.9 cm ($n = 168$) for nests built in vines. Summary statistics of the other nest parameters are given in Table 1.

Testing the hypotheses

1. Nest predation. The probability of nest predation was not significantly related to nest volume (depredated: 829.1 ± 248.5 cm³ ($n = 14$); successful: 722.2 ± 225.4 cm³ ($n = 22$); Logistic regression analysis, maximum likelihood $\chi^2_1 = 2.47$, $P = 0.06$). Since predation often has a seasonal pattern, we also tested the model including nest volume and laying date as independent variables, but the relationship remained non-significant ($\chi^2_2 = 3.31$, $P = 0.1$).

2. Nest parasitism. The probability of being parasitized was significantly but positively associated with nest volume (i.e. parasitized nests were smaller, not larger as predicted, than unparasitized nests; parasitized 673.9 ± 215.5 cm³ ($n = 8$); non-parasitized 789.5 cm³ \pm 240.3 ($n = 24$); Logistic regression analysis, maximum likelihood $\chi^2_1 = 3.53$, $P = 0.03$). However, the probability of being parasitized is known to decrease with laying date in the Rufous Bush Robin (Palomino *et al.* 1998), and the association between probability of being parasitized and nest size disappeared after including laying date in the model ($\chi^2_2 = 2.17$, $P = 0.17$).

3. Clutch size. Nest cup volume was not significantly associated with clutch size (Kendall $\tau = 0.04$, $n = 27$, $P = 0.39$), even after controlling for laying date (Kendall partial $\tau = 0.01$, $n = 25$, $P = 0.45$). Nest cup volume increased with depth of the cup, but this did not increase the base of the cup. Analysis of residuals of nest cup volume on depth of the cup resulted in a non-significant correlation between those residuals and clutch size (Kendall $\tau = -0.02$, $n = 27$, $P = 0.45$), even after controlling for laying date (Kendall partial $\tau = -0.03$, $n = 25$, $P = 0.4$).

4. Nest support. There was no significant cor-

relation between nest support and quantity of nest material, both considering nest volume ($r_s = 0.07$, $n = 34$, $P = 0.34$) and nest mass ($r_s = 0.02$, $n = 35$, $P = 0.47$). Furthermore, we did not record any cases of nest failure as a result of a nest falling. Thus, variation in nest size is not explained by this hypothesis.

5. Thermoregulation. The percentage of hatched eggs was neither significantly correlated with thickness of the nest bottom (Kendall $\tau = 0.09$, $n = 18$, $P = 0.3$) nor with density of nest wall (Kendall $\tau = 0.20$, $n = 18$, $P = 0.2$), and the relationships remained non-significant after controlling for clutch size (thickness of the nest bottom: Kendall partial $\tau = 0.09$, $n = 18$, $P = 0.3$; density of the nest wall: Kendall partial $\tau = 0.20$, $n = 18$, $P = 0.1$) and clutch size and laying date (thickness of the nest bottom: Kendall partial $\tau = 0.11$, $n = 18$, $P = 0.26$; density of the nest wall: Kendall partial $\tau = 0.19$, $n = 18$, $P = 0.14$).

6. Sexual display. Laying date was not significantly related to the amount of nest material measured as volume of nest material ($r_s = -0.21$, $n = 31$, $P = 0.13$) but it was significantly related to nest mass ($r_s = -0.32$, $n = 32$, $P = 0.035$). Clutch size was significantly larger as the amount of nest material, measured as nest mass, increased (Kendall $\tau = 0.44$, $n = 32$, $P < 0.001$; Fig. 1) even after

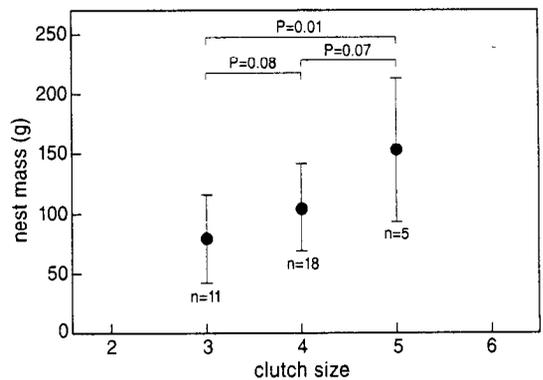


Fig. 1. Mean nest mass values \pm SD for the three clutch sizes recorded. Sample sizes and differences in nest mass for different clutch sizes (Mann-Whitney U -test) are indicated.

controlling for laying date (Kendall partial $\tau = 0.38$, $n = 29$, $P = 0.002$). This relationship was not found however, when the amount of nest material was estimated as the volume of nest material (Kendall $\tau = 0.18$, $n = 31$, $P = 0.07$).

The number of fledged young was not related significantly to the quantity of nest material, either measured as nest mass ($r_s = -0.39$, $n = 13$, $P = 0.095$) or volume of nest material ($r_s = -0.44$, $n = 13$, $P = 0.065$). The number of male feedings was not significantly associated with mass of the nest material (Kendall $\tau = -0.05$, $n = 7$, $P = 0.44$). The amount of nest material, measured as nest mass, was not significantly related to the number of female feedings (Kendall $\tau = -0.24$, $n = 7$, $P = 0.23$) or with female mean prey size (Kendall $\tau = 0.14$, $n = 7$, $P = 0.33$). However, mean prey size delivered by males tended to be positively related to the mass of the nest material (Kendall $\tau = 0.52$, $n = 7$, $P = 0.045$). The relationship remained significant when controlling for number of nestlings (Kendall partial $\tau = 0.59$, $n = 7$, $P = 0.033$) and number of nestlings and laying date (Kendall partial $\tau = 0.65$, $n = 6$, $P = 0.033$).

In summary, none of the first five hypotheses explained variance in nest size in the Rufous Bush Robin. Our results partially support the hypothesis that nest size variance arose as a result of sexual display, because (1) females increased their investment (clutch size) in reproduction as nest mass increased (Fig. 1), and (2) nest size was a predictor of male future parental care (measured as size of prey given to the chicks).

DISCUSSION

Nest size can be viewed as a result of a trade-off between selection pressures which favour small nests and those favouring large nests. Costs of nest predation and parasitism, which are related to nest conspicuousness are included in the first group, while building large nests is beneficial, because the eggs/chicks are better protected against cold and/or falling. It has been demonstrated that laying date affects nest predation (e.g. Nice 1957;

Thompson & Nolan 1973; Byrkjedal 1980) and the probability of being parasitized (Palomino *et al.* 1998). However, after considering the effect of laying date, nest predation and parasitism did not explain nest size variation in the Rufous Bush Robin. Cuckoos, which also have been suggested to be the most likely predators of Rufous Bush Robin nests (Alvarez 1994b; Palomino *et al.* 1998), search for host nests by monitoring the host's nest building activity from a nearby tree (Chance 1940; Wyllie 1981). Thus, hosts constructing larger nests would have a higher probability of being discovered than those building smaller nests. Nevertheless, if large-nest builders are able to carry greater amounts of nest material per trip than small-nest builders, number of trips are kept low, and large-nest builders would then not increase the probability of being parasitized and/or depredated. An alternative explanation for the absence of a relationship between nest size and parasitism and/or nest predation could be that nest size variation was related to nest site, with smaller nests built at more accessible or better visible places. However, most Rufous Bush Robins build their nests in vines (see Results) and nests are covered completely by the canopy plant and are invisible for Cuckoos sitting in a nearby tree. Thus, there is no reason to think that nest size per se is related to visibility or accessibility for Cuckoos.

Several functional hypotheses which favour large nests have been proposed to explain nest size variation. However, the clutch size, the nest support and the thermoregulation hypotheses were not supported by our data. Although, in general, microclimate of nest site can be important in nest structure (being related to thermoregulation), most Rufous Bush Robins build their nests in vines which are growing in extensive groves, and thereby, nest sites probably show similar microclimates, not affecting nest structure. As mentioned in the introduction, the functional hypotheses are non-exclusive, and we can not completely reject any one of them, because (1) sample size may not have been large enough to reveal small effects, (2) in one case, statistical test results were

close to significance (predation hypothesis), (3) nests were measured after breeding, so that there could have been differences between nest-volume variables where nestlings had been reared and those depredated with eggs or small nestlings (see Methods). If that was the case, predation and clutch size hypotheses (which were tested using nest-volume variables) would be weakly tested, and data on nest volume at the beginning of breeding are needed to further test these hypotheses.

Nest building behaviour may be a sexually selected trait, with nest size being a signal of the willingness of the builder to invest in reproduction (Moreno *et al.* 1994; Soler *et al.* 1995, 1998). In monogamous species in which both sexes build the nest, nest building behaviour may allow partners to invest differentially in reproduction relative to the quality of the mate (Burley 1986; Andersson 1994; Møller 1994). In the Rufous Bush Robin, females may assess the willingness of the male to invest in parental care through nest building behaviour. This was supported since the relationship between the amount of nest material (nest mass) and size of prey provided by males to the chicks was significant. On the other hand, female Rufous Bush Robins may invest relatively more in reproduction in response to male sexual display, as supported by our finding that clutch size increased with nest mass (Fig. 1). Moreover, nest size could provide information about the ability of that individual to avoid predation, and also the risk taken by that individual bird in the nest building process (in terms of time spent building; Soler *et al.* 1998). Therefore, although risk of nest predation could limit nest size, the result of the trade-off between nest size and risk of predation could be used as a signal of individual quality in sexual selection (Soler *et al.* 1998). However, an alternative hypothesis is that nest size expansion, and thereby nest cup volume, is proportional to the number of chicks reared (Slagsvold 1989b). So, a relationship between nest mass and number of eggs or chicks could be due to the relationship between brood size and nest cup expansion. However, nest mass was not

significantly related to variation in nest cup volume ($r_s = 0.12$, $n = 36$, $P = 0.5$), which implies that an increase in the amount of nest material does not reduce the stability of the nest expansion.

The sexual display hypothesis predicts that females would base their decisions of how many eggs to lay on their mate's contribution to nest building. However, nest building could function as a signal for both male and female, with the male contribution indicating to females their parental care in the future and the female contribution indicating to males how much they will invest in reproduction. Accordingly, nest size will reflect not only male, but also female willingness to invest in reproduction. Although better knowledge of the relative contribution by each sex to nest size may clarify the influence of male nest-building behaviour on female reproductive decisions, the predictions raised from the sexual display hypothesis will be the same regardless if one or both sexes are responsible for nest building.

In conclusion, nest building behaviour in the Rufous Bush Robin may be considered a post-mating sexual display which allows females to assess the willingness of males to invest in parental care, and to adjust their reproductive investment according to the parental quality of their partner.

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SAMENVATTING

Vogels hebben bij het bouwen van hun nest de keuze om een groot of klein nest te maken. Het bouwen van een groot nest kost meer energie, en vergt bovendien een langere bouwtijd waarin predatoren of broedparasieten de nestplaats kunnen opmerken. Aan de andere kant geeft een groter nest wellicht een betere bescherming aan eieren en jongen, omdat een dikkere nestwand betere isolatie biedt tegen afkoeling en een groter nest stabiel kan worden gebouwd. Ook kan een groter nest meer eieren bevatten, zodat een beter broedresultaat kan worden verkregen. Los hiervan dient de nestgrootte bij sommige soorten als een indicatie voor de kwaliteit van de bouwer. Mannetjes die zich met een groot nest presenteren of die veel bijdragen aan de gezamenlijke bouw, zouden de voorkeur van vrouwtjes kunnen genieten.

Het aldus onstane dilemma om een groot dan wel een klein nest te bouwen, is onderzocht bij Rosse Waai-erstaarten *Cercotrichas galactotes* in een Spaans wijngaardengebied. De vogels broeden hier meest in dichte wijnstruiken, goed afgeschermd tegen de spiedende ogen van hun voornaamste belager, de Koekoek *Cuculus canorus*. Beide partners bouwen aan het nest. De variatie in nestgrootte werd onderzocht in relatie tot het aantal eieren, de kans op verloren gaan van het broedsel door predatie, broedparasitisme of instabiliteit van het nest. In het broedseizoen werd het aanbrengen van prooien vastgelegd op video. Na het uitvliegen van de jongen of predatie van de nestinhoud werd de dikte van de nestwanden en de hoeveelheid gebruikt nestmateriaal gemeten. Nestgrootte en -massa en dikte van de nestwanden hadden alle weinig of geen invloed op het broedsucces: er werd alleen een negatief verband gevonden tussen nestgrootte en de kans op broedparasitisme, een onverwacht resultaat. Sexuele selectie lijkt meer bepalend voor de nestgrootte. Vrouwtjes investeerden meer in grotere nesten, door er meer eieren in te leggen. Ook mannetjes investeerden meer in grotere nesten, door het aanbrengen van grotere prooien naar grotere nesten. Ook al leidden deze inspanningen niet tot een meetbaar beter broedresultaat, toch lijken beide ouders in te spelen op informatie die ze over hun partner verkrijgen tijdens de gezamenlijke nestbouw.

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