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Nest building is a sexually selected behaviour in the barn swallow

JUAN JOSÉ SOLER*, JOSÉ JAVIER CUERVO†, ANDERS PAPE MØLLER‡ & FLORENTINO DE LOPE§
*Departamento de Biología Animal y Ecología, Universidad de Granada
†Estación Biológica de Doñana, C.S.I.C.
‡Laboratoire d'Ecologie, CNRS URA 258, Université Pierre et Marie Curie
§Departamento de Zoología, Universidad de Extremadura

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ABSTRACT

Females may use male nest building to assess male parental quality, and nest size would then be a sexually selected trait. In the barn swallow, *Hirundo rustica*, females select their partner by his tail length, a character believed to signal good genes. Both sexes participate in nest building, although male participation is negatively related to his attractiveness as reflected by tail length. We tested the hypothesis that nest building is a sexually selected trait: females paired with males of high parental quality (as shown by the male during nest building) may obtain a mate providing large amounts of parental investment, while, as has been shown previously, females mated to attractive (long-tailed) males will acquire mates with good genetic quality. Therefore, since nest building in barn swallows occurs after mating, we predicted a postmating sexual selection process by which the female invests differentially in reproduction depending on the male's nest-building effort (reflecting his willingness to invest in reproduction). The volume of material in a nest was related to the male's contribution to nest building and, in agreement with our hypothesis, in a multiple regression analysis, male tail length and nest material volume were negatively related to laying date and positively to female investment in reproduction (total number of eggs laid during the breeding season). Moreover, females paired with long-tailed males (which contribute very little to nest building), but using the same amount of nest material as females paired with short-tailed males, reduced the thickness of the nest and hence increased its capacity. Therefore, in the barn swallow two different traits appear to be sexually selected: tail length of males owing to the good genes process and nest-building ability owing to the good parent process.

Nest-building behaviour is often associated with courtship and pair formation in birds. The degree to which this behaviour is used in courtship varies from mere manipulation of a piece of nest material or display of a potential nest site to the building of an entire nest by the male (Collias & Collias 1984). Nest-building behaviour is also used in sexual display by both polygynous and monogamous bird species (see examples in Collias & Collias 1984) in a postmating sexual selection process (Møller et al. 1995).

Nest-building behaviour may signal the reproductive condition of individuals and physiologically stimulate a partner (Collias 1964), but there is very little information on the importance of the nest itself and its role in mate choice (Hoi et al. 1994). The nest may indicate parental quality, experience or genetic quality, and females could therefore benefit from mating with a superior nest builder. Nest-building behaviour could provide information to pair members about the quality of the potential partner, and such assessment of mate quality may allow individuals to choose a mate in nonmonogamous species, while in monogamous species assessment may also allow partners to invest differentially in reproduction relative to the quality of the mate (Burley 1986; Møller 1994).

In a comparative study of nest size in relation to parental effort in birds, Soler et al. (1998) showed that bird species in which both sexes build the nest have larger nests than those in which only the female builds. Nest size (relative to body size) was positively correlated with

Correspondence: J. J. Soler, Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain (email: jsolerc@goliat.ugr.es). J. J. Cuervo is at the Estación Biologica de Doñana, C.S.I.C., Apartado 1056, E-41080 Sevilla, Spain. A. P. Møller is at the Laboratoire d'Ecologie, CNRS URA 258, Université Pierre et Marie Curie, Bâtiment A, 7éme étage, 7 quai St Bernard, Case 237, F-75252 Paris cedex 05, France. F. de Lope is at the Departamento de Zoología, Facultad de Ciencias, Universidad de Extremadura, E-06071 Badajoz, Spain.

the amount of parental investment (estimated as the relative duration of the nestling period) among passerines. Thus, Soler et al. (1998) concluded that nest size could indicate the willingness of males to invest in reproduction and it could therefore be a postmating sexually selected trait.

Several studies have shown that the nest-building ability of males is related to female mate choice and the reproductive success of the pair. For example, Hoi et al. (1994, 1996) showed that female penduline tits, *Remiz pendulinus*, choose their partner based on nest quality. Evans & Burn (1996) showed that female wrens, *Troglodytes troglodytes*, select their mates depending on the number of nests a male builds. Hoi et al. (1996) also showed a positive relationship between song rate of male penduline tits, a generally accepted sexually selected trait in passerines, and nest quality. Perhaps the species in which it has been most clearly shown that nest size is a sexually selected trait is the black wheatear, *Oenanthe leucura*: individual males of better parental quality build larger nests (Moreno et al. 1994), and morphological adaptations for stone carrying (stones are used in the nest structure) result in an extreme display used in postmating sexual selection (Møller et al. 1995). An experimental increase in the number of stones carried resulted in increased reproductive success owing to differential female investment in reproduction (Soler et al. 1996).

We decided to investigate the relationship between nest building and sexual selection in the barn swallow, *Hirundo rustica*, because sexual selection has been particularly well studied in this species (Møller 1994). The barn swallow is a migratory, insectivorous, monogamous and sexually dimorphic passerine rearing one to three broods per year. Males have considerably longer tails than females (Møller 1994) and tail length is a sexually selected trait (Møller 1988, 1990) that indicates relative quality of the male (Møller & de Lope 1994). However, tail length is negatively related to parental quality: long-tailed males feed the nestlings less often and with poorer quality food than short-tailed males (de Lope & Møller 1993; Møller 1994). Tail length signals genetically based parasite resistance and offspring viability, and it is therefore maintained by sexual selection (Møller 1994).

Barn swallows build cup-shaped nests out of mud, normally mixed with straw, and they line the nest with soft materials such as feathers, hair or straw. Both sexes participate in nest building but there is considerable variation in the male's contribution, which is negatively related to male tail length. Short-tailed males invest more in nest building than long-tailed males (Møller 1994), and female nest-building activity is therefore greater when their partners have long tails.

Both nest size and male tail length in the barn swallow are positively related to clutch size (Møller 1982, 1994). Since egg production is costly, females have to determine the number of eggs to lay relative to their own phenotypic quality and that of their mate (Møller 1992; de Lope & Møller 1993). Therefore, they may lay more eggs when mated to an attractive partner (owing to differential parental investment). Alternatively, a female may lay more eggs if large nests reflect high parental quality of the partner contributing to building the nest. If this is the case, in pairs that use the same nest for all clutches, total number of eggs laid during the breeding season should be positively related to nest size after controlling for the effect of male tail length.

Nest size could also be a consequence of clutch size, because brood size may be constrained by nest size in passerines (Slagsvold 1989). Thus fieldfare, *Turdus pilaris*, with experimentally increased nest cup volumes produced more fledglings. In swallows, females paired with long-tailed males lay large clutches, but suffer most of the cost of reproduction and get little help in nest building. We predict that these females should increase the nest capacity (nest cup volume) while still using the same amount of nest material as other females paired with short-tailed males. In other words, for a given amount of nest material and a given clutch size, females put the same effort into building, whether their mates have long or short tails, resulting in thinner nest walls when it is only or mainly the female that builds. On the other hand, short-tailed males show their good parental quality by their nest-building behaviour, and their females will also lay large clutches. Hence, they need nests with a nest cup volume to fit this clutch size. However, their nests will contain more material than those of long-tailed males owing to the contribution to nest building of males of good parental quality. Therefore, nest cup volume, after controlling for the amount of nest material and clutch size, should be larger when males are long-tailed. Moreover, the amount of nest material should explain variation in total number of eggs laid during the breeding season, after controlling for male tail length, better than nest cup volume does.

In this paper we tested the hypothesis that nest building is a postmating sexually selected trait signalling parental effort. We first analysed the relationship between the male's contribution to nest building and final nest material volume. Second, we analysed the relationship between female quality (estimated by laying date) and investment in reproduction (estimated by the total number of eggs laid during the breeding season) and male sexual attractiveness as reflected by his tail length. We also determined the relationship between amount of nest material, which we hypothesized to be a sexually selected trait indicating future investment in reproduction by the male, and (1) nest cup volume, which is related to the number of eggs the female is going to lay (Slagsvold 1982; independent variable) and (2) female quality and reproductive investment (dependent variables). Finally, we distinguished between the effect of male tail length and amount of nest material on female quality and her investment in reproduction. We predicted that, in addition to the effect of male tail length, amount of nest material would explain variation in both laying date and total number of eggs laid in the barn swallow, the partial correlation coefficients being negative for laying date and positive for the total number of eggs.

MATERIALS AND METHODS

We carried out field work at Badajoz, southwest Spain, during the breeding season of 1995. The study area consisted of agricultural land with scattered groups of trees (de Lope 1983), and the barn swallows bred in rooms in farm houses. In 1997 we studied the relationship between the male's contribution to nest building and final amount of nest material at Seville, southern Spain. Nest size variables (nest material amount and nest cup volume) did not differ significantly between these two areas.

Early during the breeding season we captured adults by using mist nets placed across windows and doors of their breeding rooms. When a new bird was seen in the area, we caught it 1 or 2 days later. We measured tail length to the nearest mm and ringed each bird with a metal ring and a combination of coloured plastic rings.

Barn swallow nests may persist for many years and high-quality nests from previous years may be refurbished and reused (Møller 1994). In this study we only considered pairs that built a new nest in 1995 or 1997 and that used the same nest during the whole breeding season. These pairs should be representative of the population because, for example, in the Badajoz population (1995) we have not found significant differences between the pairs included in this study and the rest of the pairs for laying date (nests in this study: $\bar{X} \pm \mathrm{SE}=49.86 \pm 3.34$, $N=14$; other nests: 43.95 ± 1.52, $N=97$ (date 1 corresponding to 15 February), t test after $\log_{10}$ transformation of variables: $t_{109}=1.69$, $P=0.09$) or male tail length (males in this study: $\bar{X} \pm \mathrm{SE}=96.48 \pm 2.88$, $N=14$; other males: 99.87 ± 0.73, $N=96$, t test after $\log_{10}$ transformation of variables: $t_{108}=1.71$, $P=0.09$). We measured inner diameter, external diameter and height and depth of the nests to the nearest 0.5 cm. We calculated nest volume and nest cup volume as a quarter of the ellipsoid determined by the measured radii by the equation

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

where a is the smallest and b the largest radius of the ellipsoid and x is a fraction of an ellipsoid (1/4). We estimated the volume of nest material as the difference between nest volume and nest cup volume.

We followed 14 monogamous pairs. We visited their nests twice a week in order to collect data on breeding variables such as laying date, clutch size, hatching date and number of fledglings for all nesting attempts.

We studied the relationship between the male's contribution to nest building and final nest material volume by watching male and female behaviour for 1 h per pair in the morning, during similar weather conditions (dry and warm), during the nest-building period. This is enough time to detect the percentage of times that males carried nest material from the total (male and female) visits to the nest with nest material since differences in the male's contribution between cumulative 5-min intervals stabilized at zero with greatly reduced confidence intervals after 30 min of observation (Fig. 1). We recorded the number of visits with nest material by the male and female, and later we measured the nests and calculated the final nest material volume (see above).

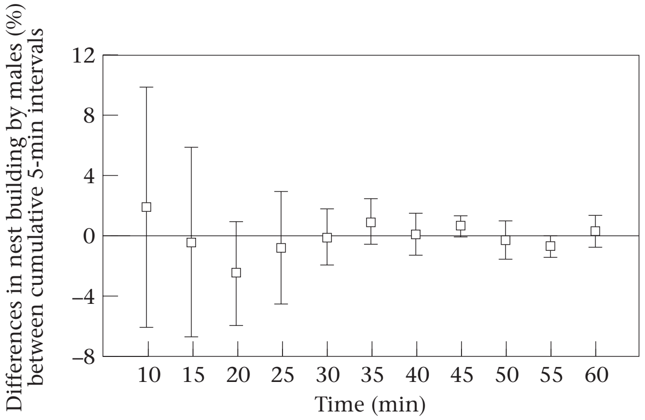

Figure 1. Differences in nest-building contribution by males (%) between cumulative 5-min intervals of observations. Values are means ± 95% confidence intervals.

We used the total number of eggs laid during the breeding season as an indicator of female investment in reproduction because all the pairs studied stayed with the same nest throughout the breeding season. Laying date was used as a measure of female quality because this is known to be negatively related to female condition (Møller 1994).

To distinguish between the effects of male tail length and nest material volume on female investment in reproduction, and following Sokal & Rohlf (1995), we ran multiple regression analyses between female laying date and total number of eggs laid during the breeding season (dependent variables) and male tail length and nest size (independent variables). Since the total number of eggs and nest size could have a phenological component, we controlled for this effect by introducing into the multiple regression analysis the date when the bird was captured (which is close to the arrival date to the breeding area, see above).

Nest volume variables (after natural log transformation), tail length, the male's contribution to nest building and final nest material volume (pairs from Seville) did not differ significantly from a normal distribution (Kolmogorov–Smirnov test for continuous variables: $P>0.2$). Total number of eggs, chicks and fledglings in the reproductive season, which are discrete variables, did not differ significantly from normal distributions (Kolmogorov–Smirnov test for categorized variables: $P>0.2$). Therefore, we used parametric tests in the analyses. All tests are two-tailed. Values reported are means ± SE.

RESULTS

Male Contribution to Nest Building and Nest Size

An increase in the percentage of male visits to the nest with nest material (male contribution to nest building)

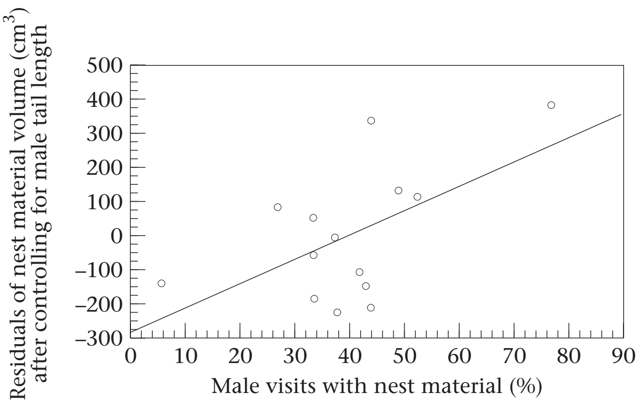

Figure 2. Relationship between final volume of nest material after controlling for male tail length and male contribution to nest building (percentage of male visits to the nest carrying material in 1 h of observation); 100% corresponds to total (male and female) visits to the nest carrying material.

relative to the total (male and female) visits with nest material resulted in nests with more nest material (r=0.49, t_{13}=1.95, P=0.07; after controlling for male tail length: partial r=0.62, t_{12}=2.62, P=0.023, Fig. 2), but not in a larger nest cup volume (r=0.11, t_{13}=0.37, P=0.72).

Laying Date and Male Tail Length

As shown by previous studies (see Møller 1994; Møller et al. 1998), male barn swallows with long tails bred earlier than males with short tails ($r=-0.51$, t_{13}=2.06, P=0.06), but this relationship was far from significant for females ($r=-0.02$, t_{13}=0.07, P=0.94).

Female Investment and Male Tail Length

The total number of eggs laid in the nest during the breeding season was positively related to male tail length (r=0.62, t_{13}=2.75, P=0.02), but not to female tail length (r=0.19, t_{13}=0.67, P=0.51).

Laying Date and Nest Parameters

Nest material volume did not explain nest cup volume ($r=-0.15$, t_{13}=0.53, P=0.61). Pairs with higher values for nest parameters bred earlier than pairs with lower ones (multiple r=0.81, r^2 adjusted=0.59, $F_{2,11}$=10.2, P=0.003; nest cup volume partial $r=-0.65$, t_{12}=2.83, P=0.015; nest material volume partial $r=-0.76$, t_{12}=3.91, P=0.002).

Female Investment and Nest Size

The total number of eggs laid during the breeding season was positively related to the nest parameters (multiple r=0.80, r^2 adjusted=0.57, $F_{2,11}$=9.46, P=0.004; nest cup volume partial r=0.68, t_{12}=3.11, P=0.009; nest material volume partial r=0.72, t_{12}=3.47, P=0.005).

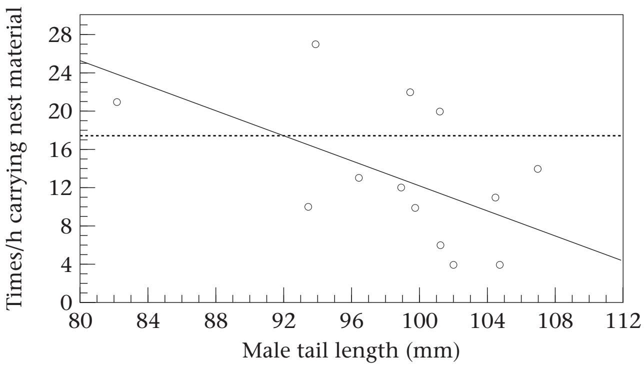

Figure 3. Relationship between number of visits to the nest by males carrying nest material during 1 h of observation and male tail length. ——: Regression line; · · ·: the mean value of the number of times females carried material to the nest.

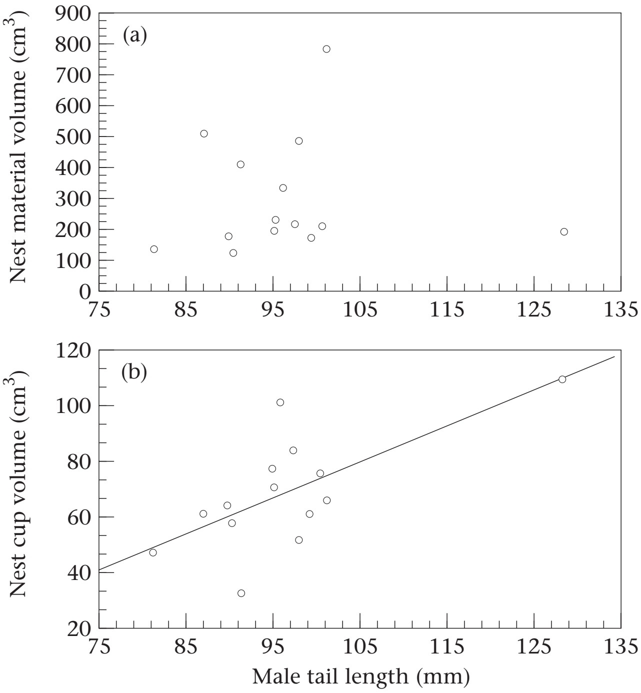

Figure 4. Relationships between male tail length and (a) nest material volume and (b) nest cup volume. The regression line is shown.

Male Tail Length and Nest Size

During the 1-h observations of nest-building behaviour, short-tailed males visited the nests carrying nest material more often than long-tailed males did ($r=-0.58$, t_{13}=2.46, P=0.03; Fig. 3).

Male tail length was not significantly related to the nest size parameters (multiple r=0.63, r^2 adjusted=0.28, $F_{2,11}$=3.53, P=0.065), but while nest material volume did not explain a significant proportion of variance in male tail length (partial r=0.14, t_{12}=0.57, P=0.58; Fig. 4) nest cup volume did (partial r=0.62, t_{12}=2.65, P=0.02; Fig. 4). Therefore, nests of long-tailed males have a larger nest cup volume but not more nest material than nests of short-tailed males.

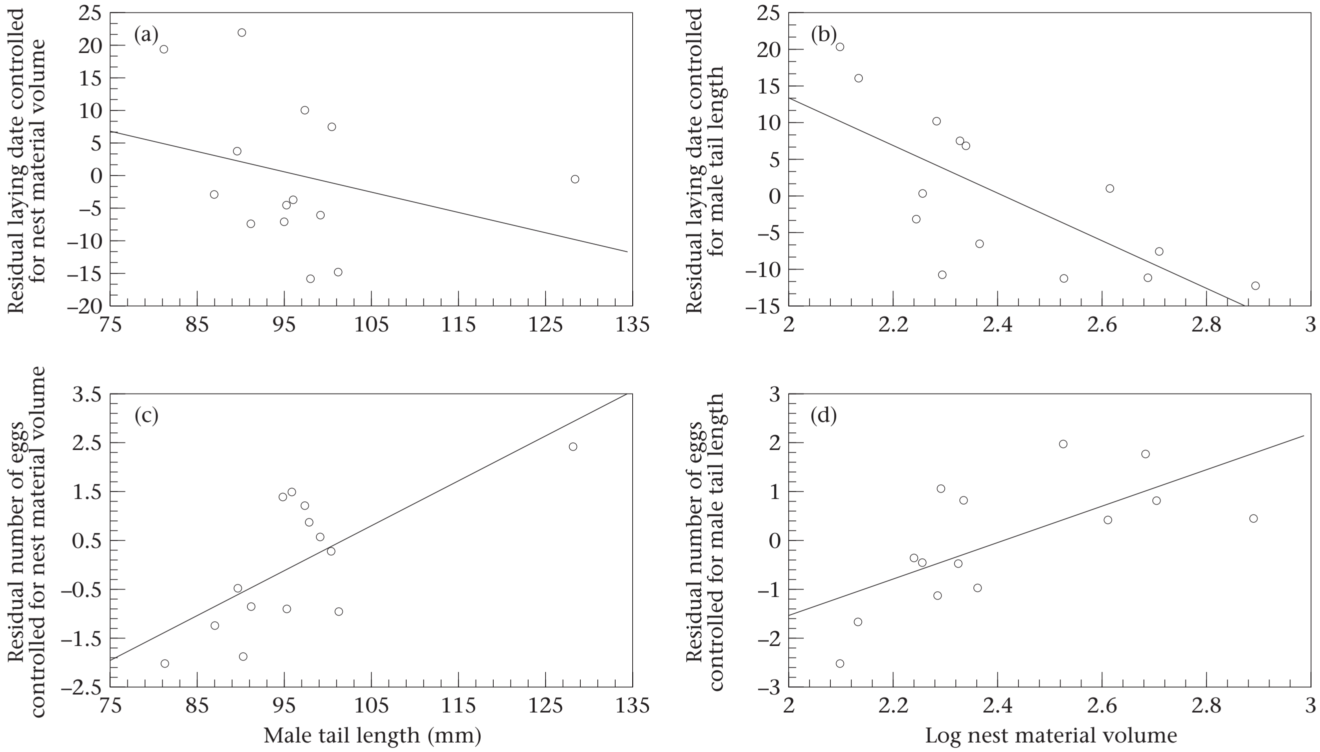

Figure 5. Relationship between (a) laying date controlled for nest material volume and male tail length, (b) laying date controlled for male tail length and nest material volume, (c) number of eggs laid during the breeding season controlled for nest material volume and male tail length, and (d) number of eggs laid during the breeding season controlled for male tail length and nest material volume. Linear regression lines are shown.

Reproductive Variables, Nest Size and Tail Length

Laying date

Pairs that carried more material to the nest and in which the male had a long tail bred significantly earlier than other pairs (multiple r=0.80, r^2 adjusted=0.57, $F_{2,11}$=9.47, P=0.004; correcting for arrival date: multiple r=0.82, r^2 adjusted=0.58, $F_{3,10}$=6.94, P=0.008) and both partial correlation coefficients explained a large amount of variance (Fig. 5; tail partial $r=-0.63$, t_{12}=2.67, P=0.021; volume of nest material partial $r=-0.71$, t_{12}=3.33, P=0.006; correcting for arrival date: tail partial $r=-0.54$, t_{11}=2.03, P=0.07; volume of nest material partial $r=-0.68$, t_{11}=2.92, P=0.014; arrival date partial r=0.34, t_{11}=1.15, P=0.28). However, the relationship between nest cup volume and male tail length in relation to laying date was not significant (multiple r=0.53, r^2 adjusted=0.14, $F_{2,11}$=2.09, P=0.17; correcting for arrival date: multiple r=0.64, r^2 adjusted=0.23, $F_{3,10}$=2.27, P=0.14), and the two partial correlation coefficients were also nonsignificant (tail partial $r=-0.37$, t_{12}=1.30, P=0.22; nest cup volume partial $r=-0.14$, t_{12}=0.45, P=0.66; correcting for arrival date: tail partial $r=-0.28$, t_{11}=0.92, P=0.38; nest cup volume partial $r=-0.11$, t_{11}=0.35, P=0.73; arrival date partial r=0.42, t_{11}=1.48, P=0.17). Therefore, nest material volume, but not nest cup volume, explains laying date after controlling for male tail length.

Total eggs laid in the breeding season

In pairs that carried more material to the nest and in which the male had a long tail, the female laid significantly more eggs during the breeding season (multiple r=0.82, r^2 adjusted=0.61, $F_{2,11}$=11.06, P=0.0023; correcting for arrival date: multiple r=0.82, r^2 adjusted=0.68, $F_{3,10}$=7.01, P=0.008) and both partial correlation coefficients were significant (tail partial r=0.72, t_{12}=3.45, P=0.0048; nest material partial r=0.68, t_{12}=3.06, P=0.01; Fig. 5; correcting for arrival date: tail partial r=0.67, t_{11}=2.85, P=0.016; nest material partial r=0.65, t_{11}=2.69, P=0.02, arrival date partial $r=-0.17$, t_{11}=0.56, P=0.59).

The relationship between nest cup volume and male tail length in relation to the number of eggs laid in the breeding season was not significant (multiple r= 0.63, r^2 adjusted=0.29, $F_{2,11}$=3.69, P=0.06; correcting for arrival date: multiple r=0.68, r^2 adjusted=0.29, $F_{3,10}$=2.80, P=0.095), neither was the partial correlation coefficient of male tail length (tail partial r=0.470, t_{12}=1.78, P=0.1; correcting for arrival date: tail partial r=0.41, t_{11}=1.43, P=0.18), nor the partial correlation coefficient of nest cup volume (partial r=0.16, t_{12}=0.54, P=0.60; correcting for arrival date: partial r=0.14, t_{11}=0.46, P=0.66). Therefore, nest material volume, but not nest cup volume, explains the total number of eggs laid during the breeding season after controlling for male tail length.

Male Tail Length and Nest Cup Volume

In agreement with our prediction, residuals of nest cup volume controlled for volume of nest material and clutch size (only first breeding attempts were included) were positively related to male tail length (r=0.58, t_{13}=2.48, P=0.03), and thus, nests of females paired with long-tailed males had larger cup volumes than expected for a given amount of nest material. Therefore, these females were maximizing nest cup volume.

DISCUSSION

The primary driving force in sexual selection is non-random variation in mating success. However, a number of different components affect sexual selection and these may best be described by a number of selection episodes which are sequentially related to each other. This view of sexual selection has several advantages: (1) the sexual selection process can be perceived as a natural chain of events where each leads to the next; (2) the process of sexual selection can be analysed in terms of the relative importance of different selection components; and (3) the different components of sexual selection and their relationships can be analysed by the use of path analysis or similar techniques (Møller 1994).

Møller (1992) showed that male barn swallows with long tails were more likely to acquire a mate than were short-tailed males, and short-tailed males were deserted by significantly more females than were long-tailed males. In relation to the timing of mate acquisition, the probability of recruitment for nestlings and the probability of producing a second clutch decrease rapidly as the breeding season progresses (Møller 1994). Therefore, early breeders will leave more descendants than others, resulting in sexual selection on male traits (Darwin 1871; O'Donald 1980a, b; Kirkpatrick et al. 1990). Møller (1988) showed experimentally that males with shortened tails took much longer to acquire a mate than control males, which took longer than males with elongated tails. The frequency of extrapair copulations that result in extrapair paternity is the most important selection component in barn swallows, and long-tailed males experience greater success in extrapair copulations than short-tailed males (Møller 1992). The female preference for long-tailed males results in such males acquiring mates in better body condition (Møller 1991), that breed earlier, and lay more eggs and clutches than females in poor condition (Møller 1992). However, long-tailed males, which are preferred by females, invest less in reproduction than their mates (Møller 1992), or than males with experimentally shortened tails (de Lope & Møller 1993). This differential allocation of female parental investment is related to the sexy son hypothesis, which states that some individuals may improve their fitness by incurring a short-term cost to obtain an attractive mate because this mate will provide long-term fitness in terms of higher genetic quality or a more extravagant degree of ornamentation of their offspring (Weatherhead & Robertson 1979; de Lope & Møller 1993).

There is considerable evidence that male tail length is a sexually selected trait in the barn swallow (Møller 1994; Møller et al. 1998). We found positive relationships between male tail length and variables related to laying date and female investment in reproduction, but these relationships were far from significant for female tail length.

Recently, Soler et al. (1998) proposed that nest-building behaviour in passerines could be a sexually selected trait, and that nest size would be a signal of the willingness of the pair that built the nest to invest in reproduction. If that were the case for the barn swallow, the male's contribution to nest building, which is negatively related to male tail length, can be interpreted as a postmating male sexual display showing the willingness of males to invest in reproduction. Therefore, in barn swallows two different sexual selection processes could occur: one premating, by which females select for male tail length, and another postmating, by which the female invests differentially in reproduction depending on the male's nest-building effort.

In accordance with this hypothesis, we found evidence that the owners of large nests bred earlier, and that the females of these pairs laid more eggs during the breeding season than those with small nests, after removing the effect of male tail length. Thus, nest size had an effect similar to that of male tail length, and both variables were negatively related to laying date and positively related to female investment in reproduction (total number of eggs laid during the breeding season).

Slagsvold (1989) showed experimentally that clutch size is positively related to nest capacity in passerines. In barn swallows, females paired with long-tailed males lay more eggs than those paired with short-tailed males (Møller 1982; this study) and, thus, they need nests with a larger capacity than those paired with short-tailed males. In accordance with this we found that male tail length was significantly related to nest cup volume, but not to nest material volume. This finding, together with the fact that female barn swallows invest proportionally more in nest building when paired with long-tailed males (Møller 1994), could indicate that such females are optimizing nest cup volume for a similar amount of nest material as other pairs use for building a nest with a small cup. In other words, females paired with long-tailed males can use the same amount of nest material as others that are paired with short-tailed males by reducing the thickness of the nest and, thereby, increasing the volume of the nest cup. In fact, that was the case, and our data revealed that residuals of nest cup volume controlled for volume of nest material and clutch size were significantly positively related to male tail length. Therefore, nests of females paired with long-tailed males had a larger nest cup volume, after controlling for nest material. Apparently, this reduction in nest thickness does not have costs since we did not detect any relationship between fledging failures (clutch size minus number of fledglings) and nest material volume (first clutches only, r=0.37, t_{13}=1.39, P=0.19), most of the nests persist the next year (Møller 1994), and in only two nests did an egg fail to hatch, and these were not due to nest characteristics (logistic regression, nest cup volume: χ^2_2=0.96, NS; nest-material volume: χ^2_2=1.82, NS). Thus, nest thickness could be seen as a postmating sexually selected trait indicating male willingness to invest in reproduction. However, female investment in nest building can also be a signal of her willingness to invest in reproduction (Soler et al. 1998), which may be why females paired with short-tailed males do not reduce their nest-building activity even when there are no apparent costs to doing so.

It is known that short-tailed males invest more in nest building than long-tailed males (Møller 1994), and that male tail length is negatively related to the amount of energy that males invest in reproduction (de Lope & Møller 1993; this study took place in the same barn swallow population as ours). Male activity in nest building is positively related to the amount of energy that the male invests in reproduction not only during nest building but also when feeding nestlings (Møller 1994). If a male with a short tail invests a lot in nest building, showing his willingness to invest in parental care (Soler et al. 1998), his mate could start breeding rather than wait for a male with a longer tail; hence she could lay earlier and lay more eggs than that expected from the male's tail length because she would gain an advantage in terms of male parental investment. In agreement with this idea, partial correlation coefficients of nest material volume (controlled for male tail length and arrival date) were significantly negatively related to laying date and positively related to total number of eggs produced during the breeding season. However, partial correlation coefficients of nest cup volume were not significant because nest cup volume is related to clutch size (Slagsvold 1982) and females paired with long-tailed males, which contribute very little to nest building (Møller 1994), lay large clutches but do not increase nest material volume (see above). An alternative explanation for the relationship between the male's contribution to nest building and clutch size optimization might be increased hatching success through better insulation in nests with a large volume of nest material. This is unlikely in our study, however, since only two eggs failed to hatch (see above) and nestling survival until fledging stage did not depend on nest volume (see above).

Males may be constrained in their ability to provide females with both direct (parental quality) and indirect (genetic quality) benefits because long-tailed males fly less efficiently than short-tailed males (Møller 1994; Møller et al. 1998), and feed the nestlings less often and with poor quality prey (de Lope & Møller 1993). Therefore, it would be difficult to find long-tailed males that show good parental quality by their contribution to nest building.

In conclusion, male barn swallows with short tails may improve their reproductive success by showing their willingness to invest in parental care (by their contribution to nest building), because females paired with males that contribute a lot to nest building lay earlier and lay more eggs than females paired with males that contribute very little to nest building (after removing the effect of male tail length). Therefore, two different traits may be sexually selected in the barn swallow: male tail length because of the good genes process and nest-building ability because of the good parent process (pre- and postmating, respectively).

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