

# MALE INCUBATION IN BARN SWALLOWS: THE INFLUENCE OF NEST TEMPERATURE AND SEXUAL SELECTION<sup>1</sup>

HENRIK G. SMITH<sup>2</sup> AND ROBERT MONTGOMERIE

*Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada*

**Abstract.** Male Barn Swallows (*Hirundo rustica*) help their mates to incubate in North America but not in Europe. In this study, conducted at four colonies in southeastern Canada, males contributed an average of 9% of the total amount of incubation during daylight hours. The total percent of time that eggs were incubated (nest attentiveness) by both sexes declined through the day, largely due to a response to increasing temperature. The nest attentiveness of both males and females was negatively correlated with nest temperature (i.e., air temperature near the nest) but not consistently with weather. In general a male seemed to incubate more when his help was needed—early in the day when the female had to recover energy lost during nighttime incubation and late in the incubation period when females should have been most stressed energetically. We found no evidence that male nest attentiveness was affected by their expected opportunity to obtain extra-pair copulations—neither differences in male attractiveness due to tail-length manipulation (shortening or elongation) nor changes in the operational sex ratio affected the male's relative share of incubation duties. Using DNA fingerprinting, we also found that the male contribution was not affected by his paternity in the brood. Since colony size and the mating system of this species appear to be similar in both North America and Europe, the intensity of sexual selection should not differ substantially between these populations. Instead we suggest that nest temperature or feeding conditions are the most likely factors influencing the differences in male incubation behavior between European and North American populations.

**Key words:** *Incubation; nest attentiveness; sexual selection; parental care; DNA fingerprinting; swallow; Hirundo rustica.*

## INTRODUCTION

The contribution of male passerine birds to incubation is highly variable both within and among species. Much of this variation is attributable to mating system and thus, indirectly, to the influence of sexual selection. In a survey of North American species, for example, Verner and Willson (1969, Table 4) found that males were more likely to incubate or at least occasionally cover the eggs in both monogamous and monomorphic species than in polygynous and dimorphic species. This suggests that in species where sexual selection is thought to be most intense (polygynous and dimorphic species), males devote less effort to parental care during the incubation period (but see Møller 1986 for a possible exception among European species).

Despite the apparently widespread occurrence of male incubation in passerine birds, the actual contribution to incubation by males has gener-

ally been poorly documented. Most studies examining the factors affecting incubation behavior have focused attention on females (Haftorn 1978, Morton and Pereyra 1985, Haftorn and Ytreberg 1988). In general, the amount and scheduling of incubation appears to be highly dependent both on the effects that weather and microclimate have on the embryos and the energetic requirements of parents (Kluyver 1950, White and Kinney 1974, Drent 1975, Cartar and Montgomerie 1985), but it is unknown whether males respond to these environmental factors in the same way as females when incubation duties are shared.

Unlike females, however, males are expected to pursue a mixed reproductive strategy caring for their own offspring when necessary but also seeking other matings whenever possible (Trivers 1972, Fitch and Shugart 1984). Hence, the contribution of males to incubation is expected to be influenced by the opportunities for extra-pair copulations (EPCs) (Westneat et al. 1989). In addition, male passerines usually lack an incubation patch (Drent 1975), and thus seem to be poorly adapted for directly incubating eggs. We might expect, therefore, that males would serve an ancillary role during incubation.

<sup>1</sup> Received 22 January 1992. Accepted 23 April 1992.

<sup>2</sup> Present address: Department of Ecology, Animal Ecology, Lund University, S-223 62 Lund, Sweden.

General models for the relative contribution of mates to parental care (Chase 1980, Houston and Davies 1985, Winkler 1987) can be readily applied to the specific case of male incubation as follows. (1) When both parents are able to incubate, the amount of work done by one parent should depend on the amount done by the other. Thus males should contribute as much to incubation as females, everything else being equal. (2) The evolutionary stable strategy (ESS) for both male and female will depend on differences between the parents in the costs and benefits of incubation. Thus, whenever males can increase their fitness by seeking EPCs, they are likely to incubate less than females (cf. Breitwisch et al. 1986). We should also expect the relative incubation effort of males and females to be related to their confidence of parenthood, in turn influenced by both EPCs (affecting confidence of paternity) and egg-dumping (affecting the confidence of maternity and possibly paternity; Rutberg and Rohwer 1980, Houston and Davies 1985). Since males usually have both a lower probability of parenthood and a higher gain from alternative reproductive tactics (e.g., seeking EPCs) than females, we expect them to participate in parental care only when the need is greatest (Howe 1979). As a result, the action of sexual selection might also be expected to have a profound effect on a male's contribution to incubation.

In this study, we looked at the incubation behavior of Barn Swallows (*Hirundo rustica*) to determine the effects of both microclimate and sexual selection on the male's contribution. Barn Swallows are particularly interesting in this regard because functional male incubation has been observed in North American (Ball 1983a, 1983b) but not in European populations of this species (Jones 1987, Turner and Rose 1989). Males also apparently provide no food to females during the incubation period in either population (Turner 1982). Moreover, recent work in both Europe (Møller 1988a) and North America (Smith and Montgomerie 1990) has shown that females appear to prefer males with longer tails, suggesting that sexual selection through female choice is reasonably intense. Thus a male's contribution to incubation might also vary with tail length because tail length should influence both his confidence of paternity and his opportunity for EPCs (see also Møller 1988a).

## METHODS

### SUBJECTS

This study was conducted during the summer of 1989 in the vicinity of the Queen's University Biological Station (QUBS), Chaffey's Lock, Ontario. Four isolated colonies were studied—one colony of seven pairs nesting inside and under the eaves of a small boat-house at QUBS (Colony QB) and three colonies with 3, 14 and ca. 50 nests on wooden beams inside large sand storage sheds within 40 km of QUBS (colonies PS, CS and ZS respectively).

Swallows were first sighted at the study colonies on 1 May and were studied until the last fledgling left the nest in mid-August. Before egg-laying began, most males and some females at colonies QB, CS and PS were caught by night using hand-held butterfly nets and mistnets, or by day using mistnets. Additional birds at those colonies were also caught during the nestling period. At colony ZS, birds were caught with mistnets during the incubation period before any observations started. Birds captured by day were released immediately; those captured at night were held until daybreak.

All captured birds were banded with color bands and one aluminum band. The wings and/or chest of each bird were also marked with acrylic paint or aniline dye to facilitate later identification. Captured birds were sexed by tail length and plumage criteria (Pyle et al. 1987) and sometimes by the presence of a cloacal protuberance (indicating male, cf. Brown and Brown 1989) or incubation patch (indicating female, Ball 1983a).

We determined the body mass of each bird caught to the nearest 0.1 g using a Pesola balance, and their flattened wing length to the nearest 1.0 mm using a ruler with a stop. To control for variation in body mass over the breeding season, we used only those masses obtained before egg-laying. On males we measured the length (to the nearest 0.5 mm) of the outermost tail feather on each side (from base to tip) using dividers and a ruler. In all analyses we used the average of these two tail feather lengths for each male.

### BREEDING DATA

The location of each nest was marked on a scale map of the colony and nests were identified by numbers painted on the walls beside them. Nests were inspected with a mirror mounted on a pole and a strong flashlight every 1–3 days during the

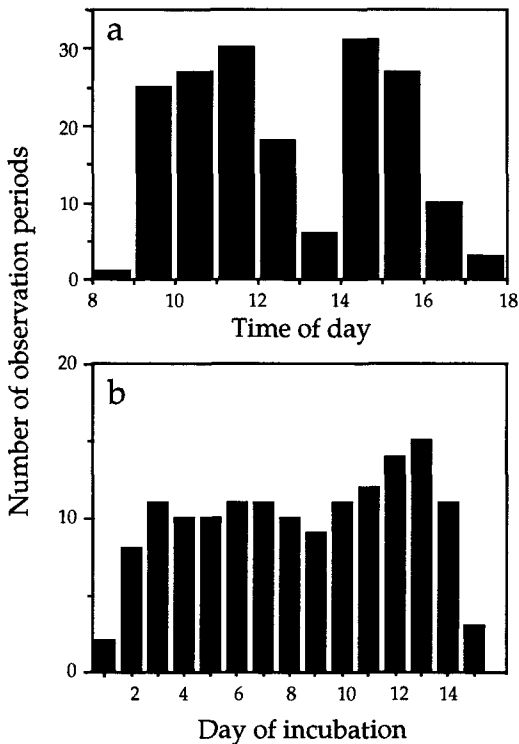


FIGURE 1. Distribution of 178 observation periods at 31 nests (a) over the day and (b) over the incubation period.

egg-laying period and daily around hatching. When the date that the first egg in a clutch was laid was not determined directly, it was calculated assuming that the female laid one egg per day. The date of hatching was determined as the first day that any egg hatched in a nest. Egg-laying dates were not determined at colony ZS.

#### INCUBATION SCHEDULING

Nest ownership was determined by observing the adults incubating and feeding nestlings. At one nest neither of the parents was banded, but sexual dimorphism of the parents was large enough to allow reliable identification of the sexes by observation alone.

To obtain information on incubation scheduling, nests were either observed directly or videotaped using a camcorder set on a tripod. Nests were usually watched from a dark corner of the building, but we used hides when the parent birds reacted to our presence or when we had to sit nearby to allow accurate identification. Nests were watched simultaneously only when they were close together and the birds were easy to identify. Preliminary tests showed that usually only two

and never more than three nests could be carefully observed at the same time. Video cameras were set up ca. 4 m from the nests and did not seem to disturb the birds (parents started incubating within seconds after we left the building).

Our choice of nests to study was based on their accessibility and visibility and on the availability of observers. We also attempted to study about equal numbers of first ( $n = 16$ ) and second ( $n = 15$ ) nesting attempts. In total we observed seven first and two second nests at colony QB, nine first and three second nests at CS, 2 second nests at PS, and 8 second nests at ZS. Only 2 pairs were observed for both their first and second nesting attempts.

On average each nest was observed 5.7 times (range 2–12) between 08:00 and 18:00 Eastern Daylight Savings Time. The average length of observation periods was 68 min—all but seven of the 139 periods observed directly were at least 1 hr long and the 39 videotaped periods were usually 90 min long. Observation periods were distributed fairly uniformly over the daylight hours (Fig. 1a) and over the incubation period (Fig. 1b). Each nest was observed only once per day except at colony ZS where nests were observed twice per day.

From each observation period and for each sex, we recorded the number of incubation bouts initiated, the duration of complete incubation bouts (i.e., bouts started and finished within the observation period), the duration of complete recess bouts (i.e., bouts away from the nest) and the total time that eggs were incubated.

#### MICRO- AND MACROCLIMATE

Before or after each observation period, we recorded the air temperature (to the nearest 0.1°C) at a point about 5 cm over the nest (hereafter called nest temperature). To determine this nest temperature we used a thermistor (YSI General Purpose Probe 401) mounted on a long pole connected to a digital thermometer (Cole-Parmer Model 8522-10; accurate to  $\pm 0.35^\circ\text{C}$ ). We also recorded hourly averages of temperature ( $^\circ\text{C}$ ), relative humidity (%) and wind speed (m/sec) from data collected every minute at a weather station at QUBS. We used the average weather data for the hour that overlapped most with each observation period.

#### SEXUAL SELECTION

In Europe, it has been observed that females paired to males with shortened tail streamers had

more extra-pair copulations than females paired to males whose tails were experimentally elongated (Møller 1988a). Hence, we manipulated tail length in an attempt to influence the male's confidence of paternity in his brood—the two longest (outermost) tail feathers of every male caught were either shortened or lengthened by 20 mm. Methodological details of the tail length manipulations are presented elsewhere (Smith and Montgomerie 1990, Smith et al. 1991). Because we did not catch every male in each colony, some males did not have their tail length manipulated and are thus not valid controls for the manipulations. As a result, all comparisons are made between males with shortened and elongated tails.

To test the effect of males seeking EPCs on their contribution to incubation, we calculated the operational sex ratio (OSR) in each colony for every day during the incubation period as follows. We first assumed that a female's fertile period began five days before the start of egg-laying and continued until the end of the day that the penultimate egg was laid (cf. Møller 1987a). We also assumed that males were able to distinguish between females that were fertile and those that were not (cf. Jones 1986). This seems to be a realistic assumption for Barn Swallows since mate-guarding is more intense when the female is fertilizable than when she is not and the intensity of mate-guarding varies with the OSR (Møller 1985, 1987a, 1987b, 1987c). We then defined the OSR as the number of fertilizable females divided by the number of males present each day (see also Emlen and Oring 1977).

We estimated paternity by DNA fingerprinting as many adults and nestlings as possible (see also Smith et al. 1991). For this paternity analysis we included only those first clutches in which the attending male had his tail length manipulated. From each bird we collected 100–150  $\mu$ l of blood by jugular venipuncture so that DNA could be extracted for later fingerprinting analysis. This method had no noticeable effect on the birds. Blood was transferred immediately to vacutainers coated with EDTA (pH 8.0) and frozen.

Technical details about the DNA fingerprinting are provided in Smith et al. (1991). In short, extracted blood was digested with *Alu* I, mixed with a lambda DNA marker (*Bst*E II + *Hind* III/*Eco*R I cocktail) and electrophoretically size-fractionated through an agarose gel. Southern blots were then probed with Jeffreys 33.15 (Jeffreys et al. 1985), *Per* (the M2.5 repetitive se-

quence from the *Per* gene in mice; Georges et al. 1988) and bacteriophage lambda DNA (Galbraith et al. 1991). Autoradiograms were scored independently by both authors (see Smith et al. 1991 for details). From the fingerprinting data we calculated the proportion of nestlings in a brood that the male attending the nest had fathered.

#### STATISTICAL ANALYSES

Statistical analyses were performed with SYSTAT (Wilkinson 1987). Before analyses, the proportion of time that nests were attended (nest attentiveness) and the proportional male share of incubation were arcsine transformed, and length of incubation periods and periods off the eggs (recesses) were log transformed to normalize data. When analyzing nest means, we used the means of these transformed variables. In all analyses of variance (ANOVA) and covariance (ANCOVA), we first tested for interactions and excluded any interactions that were not significant.

Sample sizes often differed slightly between analyses because not all information (e.g., weather data) was available for every nest and observation period. Because several data were taken from the same nest, there is some risk of pseudoreplication (cf. Hurlbert 1984). On the other hand, we feel that the analysis of nest means alone might be misleading when looking at effects of variables that changed between observation periods. Thus we used nest means only when analyzing effects of characters that did not change between observation periods (e.g., colony site, clutch size, morphology). In addition, when analyzing the effect of morphology, we used data only for first nests. When we analyzed the effect of variables that changed between observation periods (e.g., temperature, OSR), we initially treated observation periods as independent, but checked the robustness of our conclusions by repeating analyses using nest means or by performing ANCOVAs with nests as a factor.

## RESULTS

### NEST ATTENTIVENESS

During the 178 observation periods, clutches were incubated for 3.5–97.3% of the time. On average, parents began 6.6 incubation bouts per hour (range 0.83–21,  $n = 178$  observation periods) and incubated for 6.9 min per bout (range 0.7–57.6,  $n = 178$ ). Total nest attentiveness at first clutches (63.9%,  $n = 16$  nest means) was significantly

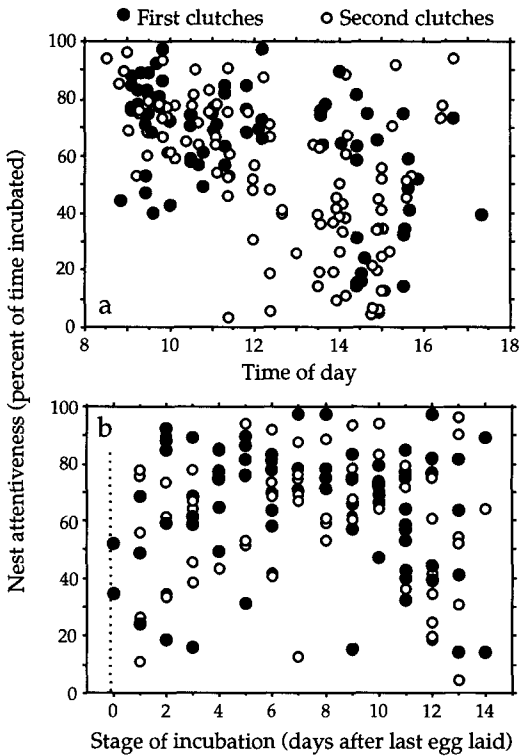


FIGURE 2. Variation in overall nest attentiveness with (a) time of day ( $n = 178$  observation periods at 31 nests) and (b) stage of incubation ( $n = 148$  observation periods at 26 nests).

higher than at second clutches (48.1%,  $n = 15$ ,  $t = 2.21$ ,  $P = 0.035$ ). This was due mainly to a significant difference in incubation bout length (9.06 vs. 5.02 min,  $t = 2.30$ ,  $P = 0.029$ ,  $n = 16$ , 15) rather than in the length of recesses (4.45 vs. 4.85 min,  $t = 0.16$ ,  $P = 0.88$ ,  $n = 16$ , 15).

Total nest attentiveness (by both parents) declined significantly during the course of the day ( $r = -0.51$ ,  $P < 0.0001$ ,  $n = 178$ ; Fig. 2a) such that clutches were incubated only about 25% of the time by late afternoon. There was also a significant time-of-day effect within nests (ANCOVA with nest as a factor:  $F_{1,146} = 54.65$ ,  $P < 0.0001$ ). Total nest attentiveness did not vary systematically during the incubation period ( $r = 0.05$ ,  $P = 0.56$ ,  $n = 148$ ; Fig. 2b).

We also looked for relations between total nest attentiveness during observation periods and both weather and nest microclimate using partial correlation analyses. In this way, the influence of each variable on nest attentiveness could be examined with the other variables held constant

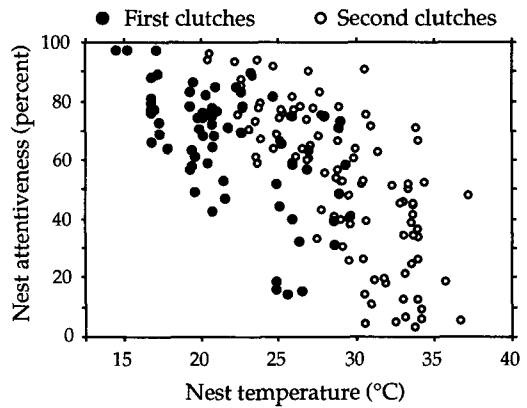


FIGURE 3. Overall nest attentiveness as a function of nest temperature ( $n = 169$  observation periods at 31 nests).

(see also Cartar and Montgomerie 1985). Humidity and windspeed were both log-transformed to normalize. Only nest temperature was significantly correlated with nest attentiveness when the other variables were controlled statistically (partial  $r = -0.41$ ,  $P < 0.01$ ,  $n = 164$  observation periods). Nest temperature accounted for 42% of the variation in total nest attentiveness ( $r = -0.65$ ,  $P < 0.0001$ ,  $n = 169$ ; Fig. 3) and had a significant effect on nest attentiveness within nests (ANCOVA with nest as a factor:  $F_{1,137} = 65.31$ ,  $P < 0.0001$ ). The addition of a second-order term to the regression model did not significantly improve the fit ( $P > 0.10$ ), suggesting that the relation between nest temperature and nest attentiveness is linear at least down to 14°C.

Nest temperature also accounted for some of the time-of-day effect described above but, when nest temperature was statistically controlled, nest attentiveness still declined significantly during the day (partial  $r = -0.25$ ,  $P < 0.01$ ,  $n = 169$ ). Over the incubation period, however, nest attentiveness did not vary significantly when nest temperature was statistically controlled (partial  $r = 0.03$ ,  $P > 0.1$ ,  $n = 139$ ).

The decrease in nest attentiveness with temperature was due to a decrease in the length of incubation bouts ( $r = -0.57$ ,  $P < 0.0001$ ,  $n = 167$ ) and an increase in the length of recesses ( $r = 0.26$ ,  $P = 0.0003$ ,  $n = 168$ ) as nest temperature increased. Both relationships were also significant within nests (ANCOVAs with nest as a factor:  $F_{1,135} = 68.16$ ,  $P < 0.0001$  and  $F_{1,136} = 4.25$ ,  $P = 0.041$ , respectively).

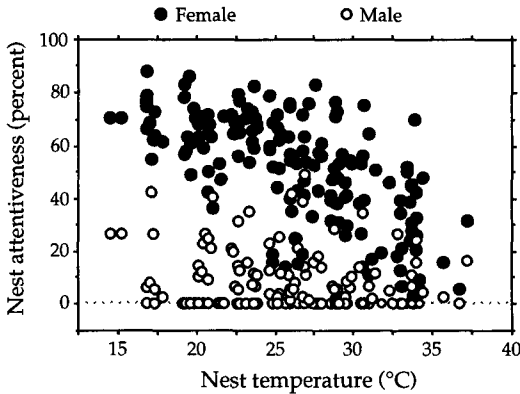


FIGURE 4. Male and female nest attentiveness as a function of nest temperature ( $n = 169$  observation periods at 31 nests).

#### MALE CONTRIBUTION

On average, males incubated for only 9.0% (average of 31 nest means) of the total time that clutches were incubated during daylight hours. Because females almost certainly incubated all night, the overall proportion of incubation by males would have been much lower. Male nest attentiveness was also more variable than that of females (CV = 152% for males, 45% for females; data from Fig. 4).

The proportion of observation time that both males and females incubated decreased significantly with nest temperature ( $r = -0.66$ ,  $P < 0.0001$ ,  $n = 169$ ; Fig. 4). These relationships were also significant within nests (ANCOVAs with nest as a factor:  $F_{1,137} = 43.53$ ,  $P < 0.0001$  and  $F_{1,137} = 4.32$ ,  $P = 0.039$ , respectively.). Thus the general relationship between nest temperature and nest attentiveness described earlier was due to changes in both male and female nest attentiveness.

The relative contribution of males to daytime incubation was smaller for first (7.0%) than for second clutches (11.1%), though the difference is not significant ( $t = 1.63$ ,  $P = 0.11$ ,  $n = 31$ ). This difference in relative contribution was due to a significantly lower proportion (9/16) of first than second clutches (14/15) having male assistance (Fisher exact test,  $P = 0.037$ ). Considering only those nests where males incubated, their relative contributions at first (12.5%,  $n = 9$ ) and second clutches (11.8%,  $n = 14$ ) were very similar ( $t = 0.02$ ,  $P = 0.98$ ). When males did incubate, they had significantly shorter incubation bouts than females (3.64 vs. 7.85 min,  $t = 4.70$ ,  $P = 0.0001$ ,

$n = 24$ ) and they began fewer incubation bouts per hour (1.36 vs. 5.55, Wilcoxon test,  $z = 4.20$ ,  $n = 23$ ,  $P < 0.0001$ ).

The male's relative contribution decreased over the day ( $r = -0.16$ ,  $P = 0.034$ ,  $n = 178$ ) and increased as the incubation period progressed ( $r = 0.18$ ,  $P = 0.026$ ,  $n = 148$ ). Both of these relations were also significant within individuals (ANCOVAs with nest as a factor:  $F_{1,146} = 4.02$ ,  $P = 0.047$  and  $F_{1,111} = 3.91$ ,  $P = 0.05$ , respectively).

Few other variables were significantly correlated with the proportion of incubation by males. For example, the male's relative contribution was not affected by first egg date (first clutches,  $r = 0.13$ ,  $P = 0.64$ ,  $n = 16$ ; second clutches,  $r = 0.19$ ,  $P = 0.60$ ,  $n = 10$ ) or clutch size ( $r = -0.16$ ,  $P = 0.39$ ,  $n = 31$ ), nor by male body mass ( $r = -0.16$ ,  $P = 0.59$ ,  $n = 14$ ), wing length (first clutches,  $r = -0.21$ ,  $P = 0.44$ ,  $n = 16$ ), or original tail length (first clutches,  $r = 0.12$ ,  $P = 0.66$ ,  $n = 16$ ).

Because tail manipulation influenced female choice, apparently making longer-tailed males more attractive (Møller 1987a, Smith and Montgomerie 1990), we reasoned that males with longer tails might spend more time seeking EPCs and less time incubating. There was, however, no difference between males with elongated and shortened tails in their relative contribution to the incubation of first clutches ( $t = 0.52$ ,  $P = 0.61$ ,  $n = 13$ ). Similarly, the proportion of incubation done by males was not significantly correlated with the mean operational sex ratio experienced by each male during first clutches ( $r = -0.10$ ,  $P = 0.70$ ,  $n = 16$  males) nor was there any pattern within individuals (ANCOVA with nest as a factor:  $F_{1,59} = 1.38$ ,  $P = 0.25$ ).

Using DNA fingerprinting, we found that males fathered from 0–100% of the nestlings in their own nest (Smith et al. 1991). There was, however, no significant correlation between a male's relative contribution to incubation and the proportion of young that he fathered in that nest (both variables arcsine transformed— $r = -0.19$ ,  $P = 0.63$ ,  $n = 9$ ; Fig. 5).

## DISCUSSION

### NEST ATTENTIVENESS

Barn Swallows are much like other passerine birds in that nest attentiveness declines to zero when the nest temperature reaches that at which eggs

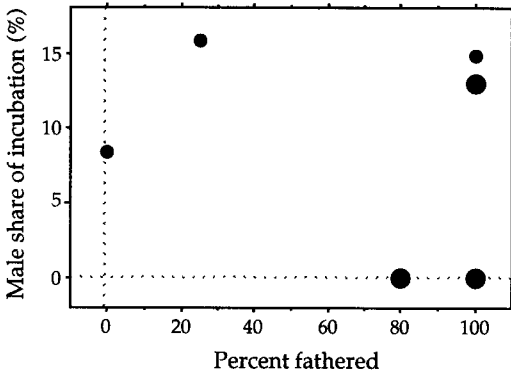


FIGURE 5. Relation between a male's share of incubation and the proportion of the brood that he fathered ( $n = 9$  nests). Larger dots represent two coincident data points.

are normally incubated (see White and Kinney 1974). Barn Swallow eggs are normally incubated at about 36°C (Turner 1982, Ball 1983a), close to the temperatures at which nest attentiveness was near zero in our study (see Fig. 3). The reason for this pattern is clear—at such temperatures the presence of an adult bird is not necessary to keep the eggs warm enough for proper embryo development (see White and Kinney 1974, Webb 1987 for reviews). An increase in nest attentiveness with decreasing temperature helps to maintain egg temperature close to the optimum for incubation, though some cooling does occur during inattentive periods.

Comprehensive information on the relation between nest attentiveness and temperature for passerine birds has so far been available only for female incubators (Drent 1975). In those species, nest attentiveness tends to increase at a decreasing rate as temperature declines, reaching an asymptote at about 80% attentiveness for ambient temperatures below 20°C (White and Kinney 1974). This asymptote in the relation between nest attentiveness and temperature is thought to reflect a trade-off between the parent's need for food and the disadvantages (e.g., longer incubation period, lower hatchability) of letting the eggs cool during incubation (White and Kinney 1974). In Barn Swallows, however, the relationship between nest attentiveness and temperature was linear across the temperature interval that we studied (14–37°C) and nest attentiveness often exceeded 80% even when nest temperature was above 20°C (Fig. 3). These unusual patterns were at least partly due to the male contribution. Thus, biparental incubators, like Barn Swallows,

may be able to buffer any adverse effects of cool temperatures on developing embryos by continuing to increase nest attentiveness as nest temperature declines, even below 20°C.

Nest attentiveness declined during the day even when nest temperature was controlled statistically, suggesting that some other factor also influenced incubation scheduling. The most likely candidate is food availability. Turner (1982), for example, found that the foraging efficiency of swallows is positively correlated with air temperature, thus being best in the afternoon. Parents might be expected to devote proportionally less time to incubation when foraging efficiency is highest, everything else being equal.

#### MALE RESPONSE TO TEMPERATURE

During both first and second clutches, male nest attentiveness was considerably lower than that of females (Fig. 4). Nonetheless, males, like females, increased nest attentiveness as ambient temperature decreased though their response to temperature was much more variable.

Part of the reason for this greater variability might be that males did not respond only to changing nest temperature and foraging conditions. For example, the male contribution relative to that of females decreased during the day and increased over the incubation period. Thus, the male's share of incubation duties was highest early in the day when females might have been recovering from the stress of nighttime incubation and late in the incubation period when females are also expected to be energetically stressed (Yom-Tov and Hilborn 1981). These results parallel those from studies of incubation feeding—both observational (Nilsson and Smith 1988, Liffield et al. 1987) and experimental (Smith et al. 1989)—showing that male effort increased in response to increasing energetic demands on his mate.

#### MALE RESPONSE TO OPPORTUNITIES FOR EPCS

We found no evidence that males adjusted the amount of time that they spent incubating in response to their apparent opportunities for seeking EPCs. We expected, for example, that males might incubate less when their natural or manipulated tail lengths were longer (and thus males were more attractive; Møller 1988a, Smith and Montgomerie 1990), or when the OSR was more female-biased. The trade-off in time between

searching for EPCs and incubating, however, may be small, since a male can leave his nest at any time a receptive female is nearby without substantially reducing his contribution to incubation. The situation might be radically different for polygynous species if males have to spend time attracting additional mates (Westneat et al. 1989, Webster 1991). Alternatively, males may not be able to spend time seeking EPCs in the morning, when most copulations occur (Møller 1987a), because their help is most critically needed for incubation duties at that time of day (this study).

#### MALE RESPONSE TO PATERNITY

The absence of a relationship between paternity and male incubation is surprising, especially since Møller (1988b) found that a male's contribution to feeding nestlings in this species was positively correlated with his perception of paternity (based on copulation and EPC rates by his mate). While the relation between male nest attentiveness and paternity was in the opposite direction to that expected, it was not significant and should be further investigated with larger samples. It is possible, however, that males may not be able to predict their paternity very accurately. Burke et al. (1989) found that male dunnocks (*Prunella modularis*) adjusted their effort to cues that might indicate paternity, whereas paternity itself was a poor predictor of male investment. A recent theoretical model also suggests that a male's contribution to parental care should be all or none, rather than a gradual change in effort with paternity (Whittingham et al. 1992). Thus a positive linear relation between male contribution and paternity might not be expected.

#### NORTH AMERICA VS. EUROPE

Because male nest attentiveness in our study was influenced by nest temperature and time of day, these factors may also explain why male Barn Swallows share incubation duties in North America but not in Europe. Such a pattern with respect to nest temperature would be found, for example, if European nest sites were warmer during the incubation period than those in North America. There is some evidence to suggest that this might be so. For example, a high proportion of nest sites studied by Møller (1983) were inside buildings whereas those in North America are usually on the outside of buildings or other man-made structures (e.g., Jackson and Burchfield

1975, Snapp 1976, Peck and James 1987). This may, in part, reflect their longer period of cohabitation with humans in Europe than in North America. In North America, Barn Swallows apparently nested mainly in caves and on cliffs before European settlement (Speich et al. 1986) and have occupied buildings for less than 300 years, expanding their range in parallel with human settlement. Moreover, in North America, even today, the majority of Barn Swallow nests in buildings are in open structures like abandoned barns whereas in Europe swallows often nest inside active cowsheds (Møller 1983, pers. observ.).

Reduced male contribution later in the day, irrespective of temperature, might be due to increased foraging opportunities, as we argued above. Foraging conditions might also help to explain differences in male incubation between Europe and North America. For example, if aerial food supplies near European Barn Swallow colonies are more dense and readily available, females might be able to incubate without male assistance. Such a difference in the availability of food could allow males in Europe to abandon incubation duties, without a substantial loss in fitness in their own nest, so that they could spend more time seeking EPCs.

It is also possible that sexual selection contributes to this difference between populations, although we found no evidence for this in our study. In both Europe and North America, females appear to use male tail length as a criterion in mate choice (Møller 1988a, Smith and Montgomerie 1990) but in Europe males have longer tails than in North America, suggesting that sexual selection is more intense in European populations. Our failure to find any relations between male nest attendance and either their attractiveness or the OSR may further reflect the weak influence of sexual selection on North American males.

There are, however, no obvious differences in either colony size or mating system between European and North American populations that might create differences in the OSR or the opportunity for EPCs and as a result affect the intensity of sexual selection. Moreover, because most copulations (both within and between pairs) occur early in the day (Møller 1987a) and because males provide an obvious advantage to females when they assist with incubation (this study), we might expect males to help with in-



cubation during the afternoon in Europe when the opportunity for successful extra-pair fertilizations should be low. Therefore, it seems unlikely that sexual selection alone could account for the absence of male incubation in European populations.

Because the incubation behavior of male Barn Swallows differs so strikingly between Europe and North America, this species is an excellent model system for exploring the factors affecting male parental investment in birds. If our conclusion that nest temperature is the main contributing factor is correct, then the mating systems and opportunities for sexual selection in birds may be a consequence rather than a cause of their breeding tactics. Murray (1984) has made a similar argument with reference to the effect of life history parameters on mating systems and this suggestion deserves to be explored more fully.

#### ACKNOWLEDGMENTS

We are particularly grateful to the Ontario Ministry of Transportation and Communications for allowing us to work in their sandsheds and to the Queen's University Biological Station for logistic support throughout this study. Susie Everding, Karen Holder and Tarmo Poldmaa provided field assistance throughout the study; Tammy Fessenden, Marty Leonard, Mike Ohh, and Pat Weatherhead also helped out during particularly busy periods. During the study HGS held a post-doctoral fellowship from the Swedish NFR and RM held a University Research Fellowship from the Natural Sciences and Engineering Research Council of Canada (NSERCC). The research was funded by an operating grant from NSERCC and an equipment grant from the Advisory Research Committee of Queen's University (both to RM).

#### LITERATURE CITED

- BALL, G. F. 1983a. Evolutionary and ecological aspects of the sexual division of parental care in Barn Swallows. Ph.D.diss., Rutgers University, Newark, NJ.
- BALL, G. F. 1983b. Functional incubation in male Barn Swallows. *Auk* 100:998-1000.
- BREITWISCH, R., P. MERRITT, AND G. H. WHITESIDES. 1986. Parental investment by the Northern Mockingbird: male and female roles in feeding nestlings. *Auk* 103:152-159.
- BROWN, C. R., AND M. B. BROWN. 1989. Behavioural dynamics of intraspecific brood parasitism in colonial Cliff Swallows. *Anim. Behav.* 37:777-796.
- BURKE, T., N. B. DAVIES, M. W. BRUFORD, AND B. J. HATCHWELL. 1989. Parental care and mating behavior of polyandrous Dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* 338:249-251.
- CARTAR, R. V., AND R. D. MONTGOMERIE. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. *Behaviour* 95:261-289.
- CHASE, I. D. 1980. Cooperative and noncooperative behavior in animals. *Am. Nat.* 115:827-857.
- DRENT, R. 1975. Incubation, p. 333-420. In D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian Biology*, Vol. 5. Academic Press, New York.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197:215-223.
- FITCH, M. A., AND G. W. SHUGART. 1984. Requirements for a mixed reproductive strategy in avian species. *Am. Nat.* 124:116-126.
- GALBRAITH, D. A., P. T. BOAG, H. L. GIBBS, AND B. N. WHITE. 1991. Sizing bands on autoradiograms: a study of precision for scoring DNA fingerprints. *Electrophoresis* 12:210-220.
- GEORGES, M., A.-S. LEQUARRI, M. CASTELLI, R. HANSERE, AND G. VASSART. 1988. DNA fingerprinting in domestic animals using four different minisatellite probes. *Cytogenet. Cell Genet.* 47:127-131.
- HAFTORN, S. 1978. Egg-laying and regulation of egg temperature during incubation in the Goldcrest *Regulus regulus*. *Ornis Scand.* 9:2-21.
- HAFTORN, S., AND N.-J. YTREBERG. 1988. Incubation rhythm in the Pied Flycatcher *Ficedula hypoleuca*. *Fauna norv. Ser. C, Cinclus* 11:71-88.
- HOUSTON, A. I., AND N. B. DAVIES. 1985. The evolution of cooperation and life history in the Dunnock, *Prunella modularis*, p. 471-487. In R. Sibly, and R. Smith [eds.], *Behavioural ecology: ecological consequences of adaptive behavior*. Blackwell, Oxford, England.
- HOWE, H. F. 1979. Evolutionary aspects of parental care in the Common Grackle, *Quiscalus quiscula* L. *Evolution* 33:41-51.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187-211.
- JACKSON, J. A., AND P. G. BURCHFIELD. 1975. Nest-site selection of Barn Swallows in East-central Mississippi. *Am. Midl. Nat.* 94:503-509.
- JEFFREYS, A. J., V. WILSON, AND S. L. THEIN. 1985. Hypervariable 'minisatellite' regions in human DNA. *Nature* 314:67-73.
- JONES, G. 1986. Sexual chases in Sand Martins (*Riparia riparia*): cues for males to increase their reproductive success. *Behav. Ecol. Sociobiol.* 19:179-185.
- JONES, G. 1987. Time and energy constraints during incubation in free-living swallows (*Hirundo rustica*): an experiment study using precision electronic balances. *J. Anim. Ecol.* 56:229-245.
- KLUYVER, H. N. 1950. Daily routines of the Great Tit, *Parus m. major* L. *Ardea* 38:99-135.
- LIFJELD, J. T., T. SLAGSVOLD, AND G. STENMARK. 1987. Allocation of incubation feeding in a polygynous mating system: a study on Pied Flycatchers *Ficedula hypoleuca*. *Anim. Behav.* 35:1663-1669.
- MØLLER, A. P. 1983. Breeding habitat selection in the swallow *Hirundo rustica*. *Bird Study* 30:134-142.
- MØLLER, A. P. 1985. Mixed reproductive strategy

- and mate guarding in a semi-colonial passerine, the swallow, *Hirundo rustica*. *Behav. Ecol. Sociobiol.* 17:401-408.
- MØLLER, A. P. 1986. Mating systems among European passerines: a review. *Ibis* 128:234-250.
- MØLLER, A. P. 1987a. Behavioural aspects of sperm competition in swallows (*Hirundo rustica*). *Behaviour* 100:92-104.
- MØLLER, A. P. 1987b. Extent and duration of mate guarding in swallows *Hirundo rustica*. *Ornis Scand.* 18:95-100.
- MØLLER, A. P. 1987c. Mate guarding in the swallow *Hirundo rustica*: an experimental study. *Behav. Ecol. Sociobiol.* 21:640-642.
- MØLLER, A. P. 1988a. Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature* 332:640-642.
- MØLLER, A. P. 1988b. Paternity and paternal care in the swallow, *Hirundo rustica*. *Anim. Behav.* 36:996-1005.
- MORTON, M. L., AND M. E. PEREYRA. 1985. The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*). *Auk* 102:25-37.
- MURRAY, B. G. 1984. A demographic theory on the evolution of mating systems as exemplified by birds, p. 71-141. *In* M. K. Hecht, B. Wallace, and G. T. Prance [eds.], *Evolutionary biology*, Vol. 18. Plenum Press, New York.
- NILSSON, J. A., AND H. G. SMITH. 1988. Incubation feeding as a male tactic for early hatching. *Anim. Behav.* 36:648-652.
- PECK, G. K., AND R. D. JAMES. 1987. Breeding birds of Ontario: nidology and distribution, Vol. 2. Passerines. Misc. Publ. Royal Ont. Mus., Toronto.
- PYLE, P., S.N.G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American Passerines. Slate Creek Press, Bolinas, CA.
- RUTBERG, A. T., AND S. ROHWER. 1980. Breeding strategies of male Yellow-headed Blackbirds: results of a removal experiment. *Auk* 97:619-622.
- SMITH, H. G., H. KALLANDER, J. HULTMAN, AND B. SANZIN. 1989. Female nutritional state affects the rate of male incubation feeding in the Pied Flycatcher *Ficedula hypoleuca*. *Behav. Ecol. Sociobiol.* 24:417-420.
- SMITH, H. G., AND R. MONTGOMERIE. 1990. Sexual selection and the tail ornaments of North American Barn Swallows. *Behav. Ecol. Sociobiol.* 28:195-201.
- SMITH, H. G., R. MONTGOMERIE, T. POLDMAA, B. N. WHITE, AND P. T. BOAG. 1991. DNA fingerprinting reveals relation between tail ornament and cuckoldry in Barn Swallows, *Hirundo rustica*. *Behav. Ecol.* 2:90-98.
- SNAPP, B. D. 1976. Colonial breeding in the Barn Swallow (*Hirundo rustica*) and its adaptive significance. *Condor* 78:471-480.
- SPEICH, S. M., H. L. JONES, AND E. M. BENEDICT. 1986. Review of the natural nesting of the Barn Swallow in North America. *Am. Midl. Nat.* 115:248-254.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 136-179. *In* B. Campbell [ed.], *Sexual selection and the descent of man 1871-1971*. Aldine, Chicago.
- TURNER, A. K. 1982. Timing of laying by swallows (*Hirundo rustica*) and Sand Martins (*Riparia riparia*). *J. Anim. Ecol.* 51:29-46.
- TURNER, A. K., AND C. ROSE. 1989. A handbook to the swallows and martins of the world. Christopher Helm, London.
- VERNER, J., AND M. F. WILLSON. 1969. Mating systems, sexual dimorphism, and the role of male North American passerine birds in the nesting cycle. *Ornithol. Monogr.* 9.
- WEBB, D. R. 1987. Thermal tolerance of avian embryos: a review. *Condor* 89:874-898.
- WEBSTER, M. S. 1991. Male parental care and polygyny in birds. *Am. Nat.* 137:274-280.
- WESTNEAT, D. F., P. W. SHERMAN, AND M. L. MORTON. 1989. The ecology and evolution of extra-pair copulations in birds, p. 331-369. *In* D. M. Power [ed.], *Current ornithology*, Vol 7. Plenum Press, New York.
- WHITE, F. N., AND J. L. KINNEY. 1974. Avian incubation. *Science* 186:107-115.
- WHITTINGHAM, L. A., P. D. TAYLOR, AND R. J. ROBERTSON. 1992. Confidence of paternity and male parental care. *Am. Nat.* 139:1115-1125.
- WILKINSON, L. 1987. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, IL.
- WINKLER, D. W. 1987. A general model for parental care. *Am. Nat.* 130:526-543.
- YOM-TOV, Y., AND R. HILBORN. 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. *Oecologia* 48:234-243.