

TABLE 2. Lateral bias in bill-tucking: sample from entire Black Skimmer flock.

A. Before disturbance			B. After disturbance from right		
Half of flock	Bill on		Half of flock	Bill on	
	Left	Right		Left	Right
Left	8	3	Left	11	9
Right	5	15	Right	2	12
P (Left half = Right half) = 0.014, One-tailed Fisher Exact Test (FET ₁)			P (Left half = Right half) = 0.018, FET ₁		
P (No shift with disturbance from right): Left half = 0.282, FET ₁ ; Right half = 0.378, FET ₁					

fend its most exposed side. The bill and sensory organs on the head will be directed toward the side of tucking when the bird first raises its head (and in some species, are most exposed to that side even when the bill is tucked). The suggestive, though not statistically significant, tendency for birds to tuck their bills toward the side of recent disturbance also supports this hypothesis. Jack P. Hailman has suggested

another possible explanation for the bill-tucking behavior of undisturbed birds: turning the bill and head away from the majority of conspecifics may be an appeasement signal, as Tinbergen (1960) has described in pairs of interacting gulls.

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Functional Incubation in Male Barn Swallows

GREGORY F. BALL¹

Institute of Animal Behavior, Rutgers University, 101 Warren Street, Newark, New Jersey 07102 USA

In many bird species a brood patch develops to facilitate heat transfer during incubation (Tucker 1943, Bailey 1952, Jones 1971). In general among species that develop brood patches, there is a correlation between the sex that incubates and the possession of this structure (Eisner 1960, Lehrman 1961, Drent 1975). An exception to this rule occurs among males in the suborder Passeres (oscines), many of whom incubate but do not possess a brood patch (Bailey 1952; Skutch 1957, 1962, 1976). Although from behavioral observations alone, it often seems that these males are incubating (Verner and Willson 1969), there is still some question as to whether or not they functionally incubate (Drent 1975), i.e. apply "the heat necessary for embryonic development" (Beer 1964: 396). In this paper I report data on egg temperature in Barn Swallows (*Hirundo rustica*), an oscine species in which males share in incubation but lack a brood patch (Samuel 1971a, 1971b). I conclude that during

the day under mild breeding-season temperatures (20-25°C) male Barn Swallows can incubate as effectively as females.

I observed three nests in 1980 and four in 1981, each for one watch. I conducted six of the watches in June and one watch in late May. The watches were all conducted from a canvas blind about 3 m from the nest. They varied in length from 1 to 3 h (\bar{x} = 108 min, SD = 37.6 min) and were performed between 1100 and 1730 EDT. All observations were made at a colony of 90 pairs nesting under the decking of the Rutgers Marine Field Station on Little Egg Harbor, about 40 km north of Atlantic City, New Jersey. Adults were caught, sexed, banded, and individually color marked during May. Test eggs were taken from fallen or abandoned nests. A small hole was made in the egg with a 30-gauge needle and the temperature probe was inserted in the egg and attached with a dab of cyanoacrylic cement and a small piece of white adhesive tape. The test egg was initially placed in the center of the natural clutch but it was usually shifted to the edge by the incubating bird. The temperature probe was connected by extension wire to

¹ Present address: Field Research Center, Rockefeller University, Tyrrel Road, Millbrook, New York 12545 USA.

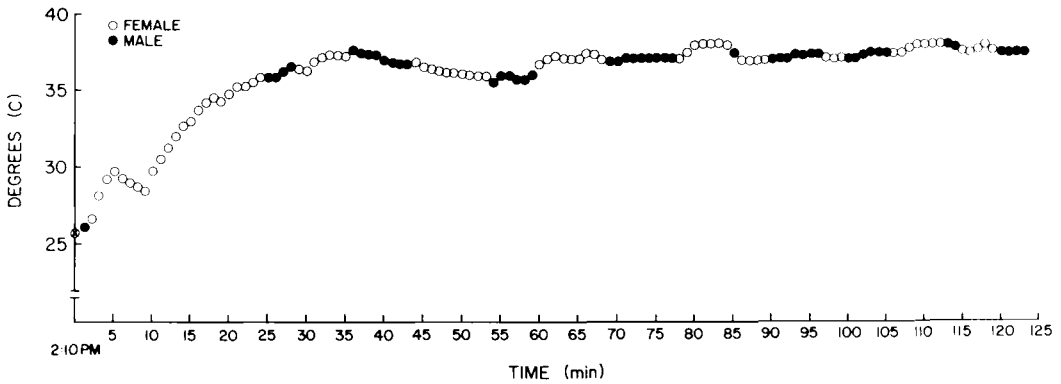


Fig. 1. Egg temperature during male and female sitting bouts at nest D42.

a Bat-8 digital thermometer (Bailey Instrument, Saddle Brook, New Jersey) in the blind. This thermometer is accurate to within 0.1°C. The thermometer was connected to the AC power source in the field station above by an extension cord. At the beginning of each observation period, the ambient temperature under the deck was recorded, and then at 1-min intervals the sex of the sitting bird and the egg temperature were recorded. In six of the seven nests both parents were color marked; in the seventh nest only the female was marked.

Changes in egg temperature were striking when either sex sat firmly on the nest after the eggs had been uncovered. Rises in temperature of 8° or 9°C within a few minutes were not uncommon. Both males and females were equally able to increase egg temperature when they covered eggs that had cooled. The female in all pairs incubated for a greater percentage of time than the male. The total amount of male sitting recorded during egg-temperature measurements varied from a high of 48 min during an observation period of 123 min to a low of 9 min during an observation period of 139 min. When one compares male and female incubation temperature, it is improper to combine all individuals of each sex, because pairs were recorded at different ambient temperatures, which affects the absolute temperature attained (Huggins 1941). I therefore calculated a mean male and female temperature for each pair by averaging the female temperatures and male temperatures for any 30-min interval in which the male sat. For example, the score for the male with 9 min is his average over the 9 min bout, and his mate's score is her average for the 16 min of the 30-min interval during which she sat. I recorded temperatures at that nest for 139 min, but I ignored the female temperatures during 30-min intervals in which the male did not sit so that fluctuations in the ambient temperature did not bias the female's score.

Data from this analysis indicate that there is very little difference between the average temperature of

the eggs with males or females sitting (Table 1). The greatest difference is found for the pair at nest D42, where the male's average is 2.1°C higher than the female's. Surprisingly, in five out of the seven cases, the male's average is actually higher than the female's, although these differences are generally very slight. I tested these differences statistically using a *t*-test for matched pairs and failed to reject the null hypothesis ($t = 0.1$, $df = 6$, $P > 0.05$). In four of the nests, the average temperature is low by comparison with the average temperature of 34.2°C during the attentive period reported by Huggins (1941) for other passerines. White and Kinney (1974) report an average temperature of 35.3°C. This discrepancy results from the parents in the four nests moving the test egg to the extreme edge of the nest cup. Huggins (1941) found that eggs on the edge of Chipping Sparrow (*Spizella passerina*) nests could be as much as 4.6°C cooler than an egg in the center of the nest.

Egg temperatures during male and female attentive periods are shown for a single nest in Fig. 1. The male was especially diligent in covering the eggs in the absence of the female. This is unusual for Barn Swallows. During eight bouts of 2-9 min duration, 48 min of male attentiveness occurred. The male's reliable compensation for the periods of the female's inattentiveness insures that the egg temperature, once established, does not fall below 35°C. This pair suggests that a biparental incubation rhythm, with continuous effective incubation of the eggs, is possible in this species.

The data presented here (Table 1) indicate that, when male Barn Swallows sit tightly on the nest, they can incubate as effectively as the female despite their lack of a brood patch. This finding is consistent with Peterson's (1955) conclusion of effective male incubation existing in another oscine species without male brood patches, the Bank Swallow (*Riparia riparia*). He recorded incubation temperature at a single nest by inserting a thermometer bulb and observing temperature changes. The female did not incubate,

TABLE 1. Overall average egg temperature (°C) during male or female incubation and the difference between means for each nest.

Nest number	\bar{x} egg temperature		Difference
	Male on	Female on	
D26	30.2	29.7	0.5
H44	29.3	30.6	-1.3
D10	31.7	31.6	0.1
D42	36.5	34.4	2.1
H34	30.3	30.1	0.2
L12	34.8	36.4	-1.6
B31	35.5	35.1	0.4

but the male sat for several bouts and was able to raise the temperature to 35°C. In addition (as shown in Fig. 1), because male Barn Swallows can incubate the eggs effectively, the mates are capable of keeping the eggs constantly covered with continuous effective incubation. This pattern, characteristic of many species with biparental incubation, is not usually observed among oscines (Skutch 1962).

Effective incubation in the absence of the brood patch raises questions concerning the function of the patch. If the brood patch is not essential for effective incubation, why have so many species acquired it? As noted by Bailey (1952), the patch may confer an advantage that is only apparent during times of thermal stress, e.g. at night. I have no data on egg temperature during times of thermal stress, but I have always found the female on the nest at dusk in Barn Swallows (35 observations), as do all reports in the literature (e.g. Bent 1942). To the degree that it has been studied, this pattern seems to be widespread among oscines (Kendeigh 1952, Bailey 1952, Skutch 1976). Further studies that compare egg temperature between male and female oscines during times of thermal stress would be useful for understanding the need for and function of the brood patch.

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