

SHORT COMMUNICATIONS

Song Sparrow "Rules" for Feeding Nestlings

JONATHAN R. REED

Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA

Smith (1978) concluded that parent Song Sparrows (*Melospiza melodia*) partition the brood, each parent feeding only certain fledglings, and suggested that division of the brood occurs late in the nestling period. Hailman (1978), however, stated that Smith's conclusion does not necessarily follow from his data and suggested that more meaningful results might be obtained by the intensive study of a single brood in which all parents and young could be individually identified. I undertook such a study and here report the most salient results that test Smith's hypothesis and other hypotheses concerning "rules" by which Song Sparrows feed their nestlings.

I studied a nest located on the ground in a 20-cm high patch of thistle (*Carduus* sp.) and clover (*Trifolium* sp.) at a site on the Leopold Memorial Reserve in northern Sauk County, Wisconsin. Observations were made from a blind 3.5 m east of the nest. On 29 June 1978, which was 5 days after hatching ("day 6"), I banded the male parent (no brood patch) and the five nestlings, additionally marking each of the latter's distal maxilla with a color of Testor's model paint: green (G), orange (O), red (R), white (W) and yellow (Y). The unbanded adult was assumed to be the female. I observed the nest from 1000 to 1620 CDT daily from 30 June to 3 July. A "feeding bout" is defined as the event in which a parent fed at least one nestling between arrival and departure, and such a bout could contain multiple actual feedings. A "feeding interval" is the number of feedings of other nestlings that occur before a given nestling is fed again, regardless of the number of bouts involved.

Parents approached the nest via one or the other of two specific routes, and the nestlings gaped apparently in response to the sight of the parent rather than vibratory stimuli. The first nestling to gape appeared to stimulate the others to do so. Of 152 feeding bouts, 71% were of 1 feeding, 24% of 2, and 5% of 3, with the female engaging in almost twice as many multiple feedings as the male. Both parents were at the nest concurrently in only five bouts. The mean interval between bouts was 258 s, each nestling receiving an average of three food items per hour. A parent remained about 10 s after feeding to remove the fecal sac of the first (or only) nestling fed (70% of bouts: 81% of male's and 61% of female's bouts). There was little variability in nestling weight on day 6 (14, 14, 13, 12, and 11 g) and little variability in number of feedings on days 7 to 9 (43, 41, 40, 39, 39, respectively).

There is no evidence for Smith's (1978) suggestion that parents partition the brood (Fig. 1), and Chi-square tests for individual days are in no case significant ($P > 0.1$). Day-to-day, chance variation occurred (e.g. Y's being fed almost exclusively by the female on day 8), but such patterns did not persist.

The results are also inconsistent with two other suggested "rules" of feeding passerine nestlings. Gabrielson (1913) and others (Lack 1956, Maxwell and Putnam 1972) have noted that the largest and most aggressive nestling was preferentially fed in certain species. Alternatively, Fautin (1941) and others (Conder 1948, Hussell 1972) report that the nestling most frequently fed early outcompetes its sibs later for parental attention. In my Song Sparrow nest, however, the nestlings were of about equal weight and were fed about equally.

A fourth hypothesis is that feeding is rotational (Campbell in Bent 1942, Redfield in Bent 1953), progressing systematically from one nestling to the next. This model predicts that the modal feeding interval will be four, which is to say that the other four nestlings will be fed before the first is fed again. In fact, the modal feeding interval is one, with high variability between zero and the rare occurrence of 14 feedings before a given nestling is fed again (Fig. 2). Inspection of individual records reveals no systematic sequence of feeding nestlings in turn and no regularity in the feeding intervals of any nestling.

A related hypothesis is that the hungriest nestling is fed preferentially (Skutch 1976: 272). This hypothesis makes the same prediction as the last one, although differently based: the hungriest bird will be the one fed longest ago, so the result should again be a rotational sequence with a feeding interval of four. No such pattern occurs in the data.

A sixth hypothesis is closely related to and essentially a variant of the hungry-nestling hypothesis: the parent feeds any nestling, but, if it does not swallow the food quickly, the parent removes the food and places it in a different gape (Herrick 1901, Pickwell 1931, Campbell in Bent 1942, Hjermsman in Bent 1942, McClanahan in Howell 1942, Pullen 1945, Skutch 1976: 272). At my nest only nine of the 204 food-transfers were unsuccessful, these involving large items (caterpillars and a dragonfly) or in one case

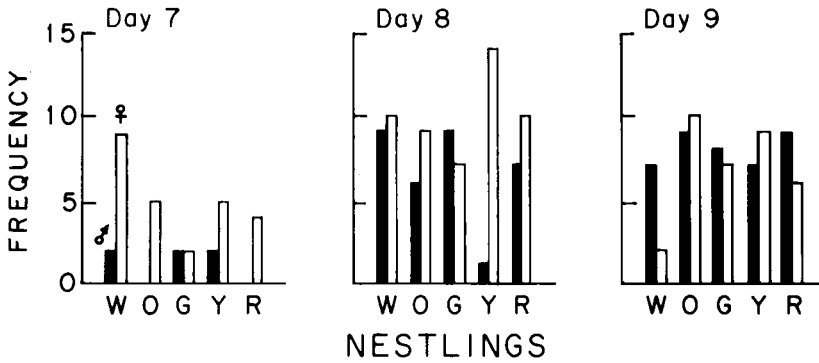


Fig. 1. Comparison of male (solid bar, $n = 78$) and female (open bar, $n = 93$) feedings of five Song Sparrow nestlings.

a spider. The items that fell from the nestling's gape or were removed by the parent were offered to other nestlings. The fact that eight of nine unsuccessful food transfers occurred within a 2-h period suggests that withdrawing of food occurs only when the young are being fed unusually large food items.

The lack of predicted structure in feeding data suggests a seventh and disarmingly simple hypothesis: namely that nestlings are fed "randomly." This hypothesis may be more precisely stated as "the probability of a given nestling being fed remains constant, regardless of how recently it has been fed." The hypothesis predicts that the cumulative frequency of feeding bouts will show geometric decay when regressed on the interval between bouts. The simple test is to regress the logarithm of the cumulative frequency against the interval, which should deliver a straight line of negative slope [see mathematical development in Hailman (1974) for details]. Figure 3 shows that the Song Sparrow data conform to the expected function, the covariance (r^2) accounting for 99.5% of the variability in bout intervals. Such "random" feeding insures that all nestlings are fed equally over the long run and shifts the entire question from general "rules" of feeding to specific behavioral actions that bring about the randomness.

Analyses of polar plots of the data show a correlation between the approach direction of the parent

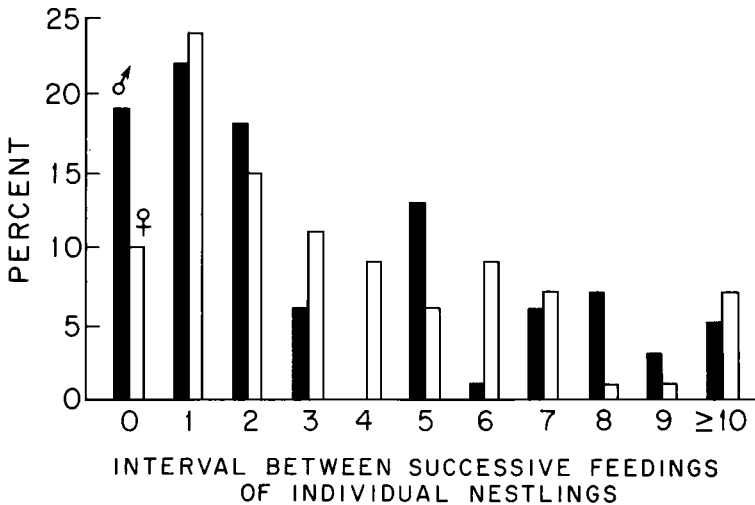


Fig. 2. Interval analysis (see text for definition) of the feeding patterns of the male (solid bar, $n = 72$) and female (open bar, $n = 105$) parents.

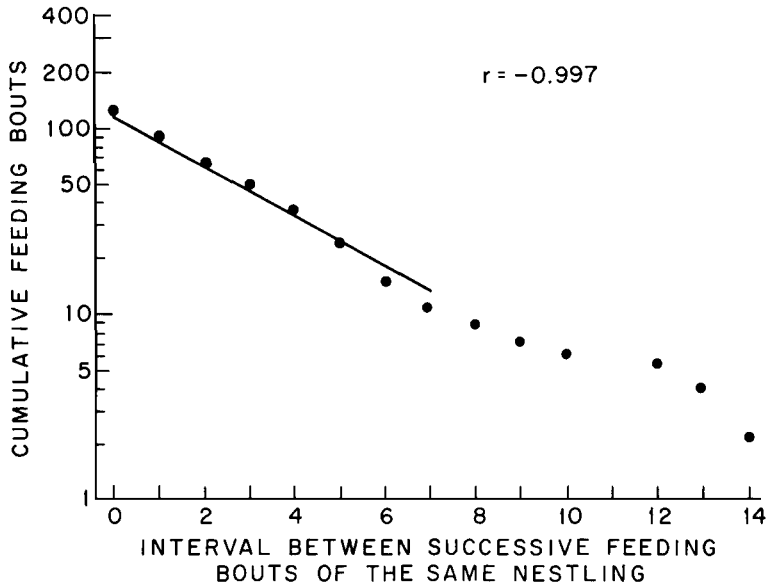


Fig. 3. Least-squares regression line for the logarithm of the cumulative number of feeding bouts and the interval between successive bouts. Each point represents the number of bouts that have an interval at least as large as that indicated on the abscissa.

and the position of the nestling that is fed. Parents fed from the three western 45° sectors (SW, W, NW) in 92% of bouts, and the nestling first fed was within this 135° section 54% of the time. The first-fed nestling was in the same 45° sector as the parent during a quarter of the observations and in this or an adjacent sector during two-thirds of the observations. Furthermore, the first-fed nestling was the closest to the parent in 44% of the bouts. Similar data have been reported for other passerines (Pickwell 1931, Skutch 1976: 272). Because the parents' approach direction is relatively constant, the closest nestling has the highest probability of being fed, and the young are fed randomly; it must be that the nestlings shift position in the nest more or less randomly. Shifting has been reported for Field Sparrows (*Spizella pusilla*) and other passerine nestlings (e.g. Best 1977, McCabe and Mullins pers. comm.).

Shifting of nestling positions was recorded during 335 intervals between bouts. Three-quarters of the intervals resulted in a nestling shifting from one 45° sector to another. The first-fed nestling had shifted sectors prior to being fed in 88% of the observations. The mean time interval between nest visits for this set of observations was 7.4 min, and nestlings shifted position 32 times/h, so that shifts occurred on the average every 1.9 min. In other words, there were about four shifts between each feeding.

Finally, the question devolves to factors that cause the continual shifting of position among the nestlings. Perhaps surprisingly, the mean number of shifts is fairly constant regardless of the length of the interval between feeding bouts: 3.7 shifts/interval when intervals are 0–5 min, 3.6 when 6–10 min, and 4.1 when 11–15 min. This means that nestlings are not shifting regularly with the passage time, but rather that shifting is an event tied to the feeding bout cycle. Skutch (1976: 272–273) found that a nestling's turning to present its fecal sac resulted in loss of its position in the nest, but no phenomenon such as this is evident in the Song Sparrow data. The mean number of nestlings shifting position after a removal of a fecal sac was 3.7 (SD = 1.04, $n = 35$), which is less than the mean of 4.3 nestlings (SD = 0.90, $n = 11$) when no fecal sac was removed, and the difference is not significant ($t_s = 1.52$, $df = 44$, $0.1 < P < 0.2$, two-tailed).

Most of the shifting of nestlings occurs during and just after feeding. Once the brood has settled down in the nest, lateral movement is nearly impossible; on five occasions, however, a nestling from the eastern section climbed over and eventually sat upon its more westerly siblings. When a parent arrives at the nest and the young extend vertically to gape, lateral shifting often occurs and then continues for about 20 s after feeding, until the young are resettled. It appears that each nestling tried to gain a position in the western part of the nest, but I cannot distinguish on the basis of the data between the two following

possibilities: a general attempt to be westerly or an attempt to gain the position nearest the parent or the place it just occupied.

In sum, six hypotheses proposed in the literature for "rules" about how parents determine which nestling is fed on a given visit are not supported by detailed data from a Song Sparrow nest. Such proposed "rules" could easily be generated by a small sample of data, but the present large sample reveals that nestlings are fed randomly overall. The mechanism promoting this randomness, however, and its consequent parity of feeding among nestlings, is based on shifting of the young in the nest. The parents approach from a given direction and tend to feed the nearest nestling; all nestlings appear to compete about equally effectively for the position most likely to receive food through shifts that occur primarily at and just after feeding. Thus, the nestling fed on a given visit is randomly determined by these shifts. This mechanism would allow larger and more aggressive nestlings to dominate the feedings (although no such individuals occurred in the study brood) and hence could include more specific hypotheses proposed in the literature. There is no evidence, however, for Smith's (1978) suggestion that male and female parents partition the brood or that they can distinguish among their nestlings in any way.

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