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THE DAILY ACTIVITY PERIOD OF NESTING WHITE-CROWNED SPARROWS IN CONTINUOUS DAYLIGHT AT 65°N COMPARED WITH ACTIVITY PERIOD AT LOWER LATITUDES¹

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Time-and-activity budgets attempt to express how animals allocate time to vital activities such as foraging, courtship, and territorial defense. The baseline of an activity budget is the duration of an animal's voluntary activity period per 24-hr cycle. An accurate estimate of this period is therefore an indispensable element of the budget, as Hussell (1985) recently emphasized in an analysis of the correlation between clutch size and daylength or activity period. Daan and Aschoff (1975) found that the daily activity span of captive finches is a shallow sigmoidal function of civil daylength, so that the activity span is nearly the same as daylength at middle values (ca. 8 to 16 hr) but is longer than daylength when days are very short and shorter when days are very long. For instance, captives are active for 17 to 18 hr per day in continuous daylight. In the handful of cases in which comparisons are possible, free-living birds reflect fairly closely the daily activity span in relation to daylength found in captives (cf. Armstrong 1954, Aschoff 1969, Daan and Aschoff 1975). Analysis of my own field records and of published reports yielded a reasonably detailed picture of the daily activity cycle in a subarctic breeding population of White-crowned Sparrows (*Zonotrichia leucophrys*) and estimates of their daily activity span in localities at lower latitudes where midsummer cycles of daylight and darkness are clear-cut. These data help in designing realistic experiments with captives and in analyzing the time budgets of free-living birds.

MATERIALS AND METHODS

The majority of the original data reported herein were obtained from *Zonotrichia leucophrys gambelii* near Fairbanks, Alaska (64°51'N, 147°52'W), during the breeding

seasons of 1962 through 1965, 1967 to 1968, and 1972. Daylight (civil daylength plus civil twilights) is continuous from 16 May to 28 July at this latitude. Male White-crowned Sparrows usually arrive in the second week of May, females about one week later. Nesting is very well synchronized in the population. Except for unusual re-nestings following loss of a nest, young have left the nest by 1 July, when postnuptial molt begins in all but failed nesters. Southward migration begins soon after mid-August (King et al. 1965, 1966; Wingfield and Farner 1979).

A few comparative data were available also from *Z. l. oriantha* at Tioga Pass, California, Niwot Ridge, Colorado, and Hart Mountain, Oregon. See King and Hubbard (1981) for details about these localities. All lie between 38°N and 42°N, and hence have similar daylengths.

Measures of activity used herein include (1) incidence of singing, (2) records of periods in which White-crowned Sparrows could not be heard or found in the study area, and (3) observation of the schedules of parents feeding nestlings. Except for the latter (1972 only), the results are presented as a composite of data from the six earlier years, all from the same sample site. My assistants and I routinely counted the number of White-crowned Sparrow songs heard in a 10-min sample of every hour that we were afield. During the twilight hours we recorded the times in which we could neither see nor hear White-crowned Sparrows in the study area, and in 1972 we systematically searched for males during the quiescent period (when females were incubating or brooding and therefore known to be inactive).

RESULTS AND DISCUSSION

ACTIVITY PERIOD AT FAIRBANKS

White-crowned Sparrows can be heard singing at nearly any time of the day during the nesting season at Fairbanks, although there is a consistent lull lasting about 3.5 to 4 hr before midnight and a shorter lull centered at about 1530 (Fig. 1). This pattern is repeated from year to year and is not an artifact of merged data. The daily cycle of song intensity reflects the number of singers rather than the

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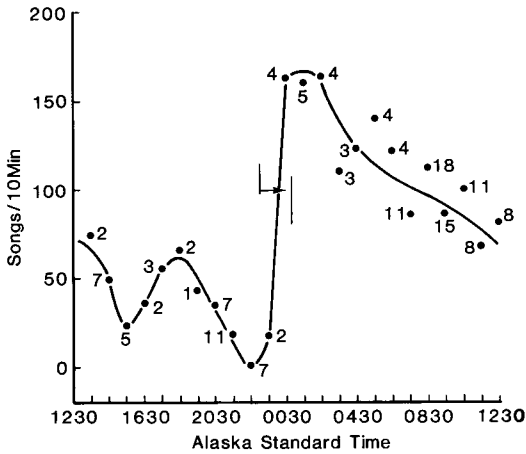


FIGURE 1. The daily cycle of singing intensity by White-crowned Sparrows at Fairbanks, Alaska, expressed as songs per 10-min sample period within the 1-hr periods along the abscissa. Numerals at data points are sample sizes. The arrow pointing right in the center of the figure shows how much the onset of the evening song chorus drifts to a later hour between late May and late June (see text). Clock times are Alaska standard time. Corrections to local solar time range from +11 min on 1 June to +5 min on 1 July.

frequency of singing by individuals. By analyzing singers in the background of voice-tape field notes, I found that song frequency averaged 5.6 songs/min (SE = 0.27, $n = 36$ singers) and was independent of the hour of the day (slope of regression of frequency on hr = -0.014 , $P \gg 0.5$ by ANOVA).

A very sharp resurgence of song following an evening lull (Fig. 1) occurs also in Golden-crowned Sparrows (*Zonotrichia atricapilla*) at 62°N (Holmes and Dirks 1978) and in many other species of birds in continuous daylight (Armstrong 1954). The recruitment of singers is usually very quick at the onset of the "chorus," and it is easy to time its beginning with an accuracy of plus or minus a few minutes. Figure 1 is a composite of records ranging from 29 May to 28 June at Fairbanks, when the onset of the evening chorus was advancing from about 2253 on 29 May to 0046 on 28 June, without evidence of reversal upon passing the summer solstice. ANOVA shows that this trend is significant ($r^2 = 0.71$, $F = 33.7$, $df = 1, 24$, $P < 0.001$) at +3.8 min/day. A third-order polynomial regression is likewise essentially linear and does not significantly improve the correlation ($r^2 = 0.72$). Hence, there is no evidence that the onset of evening song at Fairbanks tracks light intensity or solar cues as a U-shaped relationship across the solstice, as it does in Golden-crowned Sparrows at 62°N (Holmes and Dirks 1978). Most of the White-crowned Sparrows at Fairbanks stop singing on about 1 July and do not provide a significant postsolstitial sample. Golden-crowned Sparrows continued to sing until 17 July in the population studied by Holmes and Dirks.

The evening lull in singing suggests that males tend to become inactive following their afternoon peak of territorial song (ca. 1830, Fig. 1). Direct observations verify this. My records extend from 17 May through 29 June, thus spanning the nesting season. Scans for White-crowned Sparrows were made at about 20-min intervals all night during recesses from other observations. Records of activity onset and end thus have a maximum error of about +20 min (onset) or -20 min (end) and a probable error of about 10 min. On the average (in decimal hr \pm SD, three years of data merged) through the season, White-crowned Sparrows were last seen foraging or flying in the

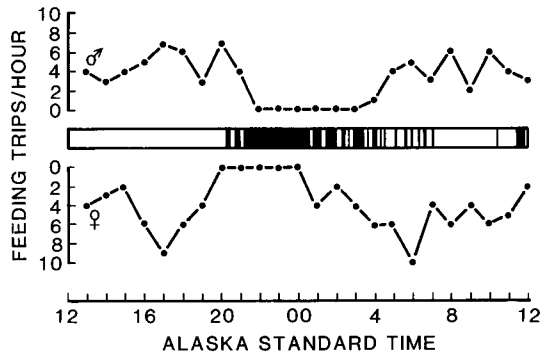


FIGURE 2. A composite daily schedule (17 to 21 June) of a pair of White-crowned Sparrows attending five nestlings three to seven days old at Fairbanks. Blackened spans of horizontal bar show when the female was on the nest brooding the young. Points connected by lines show number of times per hr that the nestlings were fed by the male (upper) or female (lower).

evening at 20.8 ± 0.81 ($n = 47$ days) and were first seen foraging in the morning at 03.0 ± 0.49 ($n = 53$) as the midnight song chorus began to wane (Fig. 1). The greater precision of the onset than the end of activity (compare SDs) is in accord with the analysis by Daan and Aschoff (1975) of the activity of several species of captive fringilids during the arctic summer. The average period of inactivity (which includes singing by males) is 6.2 hr during the nesting season. Males are quiescent (or at least out of sight) for about half of this span and sing almost continuously through the other half. Females are incubating or brooding through most or all of this span. Males roost in dense vegetation from the time that they disappear from view until they resume singing and are not easy to flush from their refuges. It requires persistent effort to find them during their quiescent period.

TABLE 1. Daylength (civil daylength plus civil twilights) and estimates of activity period in White-crowned Sparrows at three montane localities (time in decimal hr).

Place and date	Daylength	Activity period		
		All active ^a	Female active ^b	Song period ^c
Tioga Pass, 37°55'N				
10 Jun	15.68	—	15.69	—
21 Jun	15.73	—	15.47	—
30 Jun	15.70	—	15.29	—
10 Jul	15.58	—	15.09	—
20 Jul	14.99	—	14.67	—
10 Aug	14.67	—	14.47	—
Niwot Ridge, 40°03'N				
5 Jun	15.96	16.33	—	—
20–21 Jun	16.12	16.73	15.75	16.50
3–5 Jul	16.02	16.63	15.48	16.63
16–20 Jul	15.73	16.23	15.20	16.03
Hart Mountain, 42°42'N				
31 May	16.15	—	—	16.47
10 Jun	16.30	—	—	16.58
20 Jun	16.38	—	—	17.00
30 Jun	16.35	—	—	16.58
10 Jul	16.19	—	—	16.48

^a Based on direct observation of earliest and latest activity (Hubbard 1978).

^b Based on span of continuous nighttime incubation (Zerba and Morton 1983; fig. 4; Hubbard 1978).

^c Based on span from onset of dawn song chorus to end of dusk chorus (data from this investigation).

Observation of the daily routine of brooding and feeding by parents at the nest helps to verify or extend the picture of daily activity patterns derived from the indirect methods already mentioned. By merging observations made in various spans of the day on 17 through 21 June, I recorded a 24-hr diary from one White-crowned Sparrow nest containing five nestlings three to seven days old. Every hour of the 24-hr cycle was sampled once. Activities at the nest were clearly visible from a blind 3 m away even at midnight. Color bands on the parent birds were visible on about 85% of the visits, and the sex of the visitor could be assessed otherwise with reasonable reliability by behavior and the timing of visitation.

The female began intermittent brooding at 2022 and continuous brooding at 2108. She continued to brood without interruption until 0052 and then brooded intermittently until 0704 (Fig. 2). She was on the nest for 3.7 hr continuously, and intermittently for 3.3 hr more through the next 6.20 hr. The male alone fed the nestlings for 112 min before the onset of continuous night brooding by the female. The female did not bring food after 1914, even though she returned once to brood briefly. It seems likely that she was foraging during this span to feed herself in preparation for her nocturnal fast. The female immediately brought food to the nestlings at the end of her period of continuous brooding (0052). The male did not resume feeding them until 0418 (Fig. 2), about 40 min after his singing intensity began to wane. During this interval he was presumably foraging to feed himself at the end of his overnight fast. The nestlings were without food for 3.7 hr and were fed more or less continuously (Fig. 2) for 20.3 hr per day. The male brought food 77 times and the female brought food 93 times (55%). The male was active for 17.8 hr/day if the song period is excluded (ca. 21 hr/day if it is included), and the female was active (off the nest) for 17.0 hr/day. By phasing separately their feeding of the nestlings, however, the adults extended the feeding day to more than 20 hr.

In contrast, a pair of White-crowned Sparrows (*Z. l. oriantha*) at Tioga Pass (37°55'N) fed their brood of four seven-day-old nestlings 187 times (57% by the female) between 0520 and 1952 (Morton et al. 1972). The active feeding day (date not stated) lasted 14.5 hr, or only 72% as long as the active day at Fairbanks. Additional quantitative comparisons would be incautious because of small sample sizes and the differing number of nestlings and their differing ages at the two localities. It seems clear, however, that a pair of White-crowned Sparrows at Fairbanks fed five nestlings at about half the rate per nestling-hr that a pair of White-crowned Sparrows at Tioga Pass required to sustain four nestlings ($[170/20.87]/5 = 1.63$ vs. $[187/14.53]/4 = 3.22$ feedings/nestling-hr). Total feedings per day (170 vs. 187) did not differ greatly, however, nor did the growth rates of the nestlings (King and Hubbard 1981).

DAILY ACTIVITY PERIODS AT OTHER LOCALITIES

Midsummer nights at latitudes less than about 61° include a period of darkness from the end of civil twilight to the onset of civil twilight next morning. This inhibits activity and makes it easier than at higher latitudes to estimate the duration of a bird's daily activity period. Montane White-crowned Sparrows engage in rather sharply delimited bouts of singing before sunrise and after sunset. The beginning of the dawn chorus and the end of the dusk chorus can be estimated with a maximum uncertainty of about ± 10 min on a typical day. The minimum span of wakefulness by males can thus be estimated from their song cycle. The observed activity span matches closely the activity span estimated from song at Niwot Ridge (Table 1), and presumably in other localities at similar latitudes. The data are from diverse sources and are not fully con-

cordant for the three sites, but they suffice to show that the activity span approximately equals daylength and tracks its variation across the solstice. On the average (Table 1) females are active for 98% of the daylight hours at Tioga Pass (range: 97 to 100%) and 97% (96 to 98%) at Niwot Ridge. Males are active slightly longer per day than females: 103% of daylight hours at Niwot Ridge, and 102% at Hart Mountain. On the average, male activity is about 26 min longer, and female activity is about 21 min shorter, than the daylight period. This is the inverse of the relationship reported by Daan and Aschoff (1975) for several species of small birds in captivity, at least at higher latitudes.

In sum, the daily activity spans of White-crowned Sparrows during the nesting season on clear days in middle latitudes can be accurately estimated as equal to the span between the beginning of civil twilight in the morning and the end of civil twilight at dusk, plus or minus 20 to 25 min depending on sex. The daily activity span in continuous daylight at higher latitudes is not so easy to define. At 65°N in June, White-crowned Sparrows move around and forage for ca. 17.8 hr/day. Males are nearly immobile but sing frequently for ca. 3 hr more.

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