METABOLIC AND BEHAVIORAL RESPONSES TO FASTING IN THE
WHITE-CROWNED SPARROW (ZONOTRICHIA
LEUCOPHRYS GAMBELII) 1

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During winter, ground-feeding bird species may occasionally be forced to fast when weather conditions (e.g., snowstorms, icing) make food temporarily inaccessible. To describe the response of White-crowned Sparrows to fasting, we (1) investigated variations of body weight and temperature in fasting and fed birds confined in a cold room for up to 64 h, and (2) periodically measured oxygen consumption and locomotor activity of fasting and fed birds through a 39-h night/day/night cycle while simulating natural conditions of temperature and daylength. Our data indicate that the unusual White-crowned Sparrow might survive 3 nights and 2 days without food at air temperatures near freezing, but typical individuals could not be expected to survive longer than 1 day and 2 nights. Males lose weight at a greater rate than females, but are able to endure fasting longer because they are initially heavier. This suggests that males may be more resistant to winter storms and food deprivation, and that this attribute may have contributed to the evolution of geographic variation in the sex ratio in this species. Physiological and metabolic responses to fasting included a nighttime decline in body temperature (ca. 3° C) that was greater than that observed in fed birds, and a 21% decline in oxygen consumption on the second night of the fasting cycle when compared to the first night. The drop in body temperature would be sufficient, in terms of the van't Hoff effect, to account for the decline of metabolic rate, but visual inspection of the fasting birds at night suggested that adjustments in ptiloerection and posture may also play a role in effecting the decline. During the day, locomotor activity was 1.5–10 times greater in fasted than fed birds. Oxygen consumption, however, did not differ, indicating (as one possibility) that fasting birds may be able to utilize heat generated by exercise to meet some of the cost of thermoregulation. The short-term adjustment to starvation under natural conditions may thus include a moderately reduced energy requirement and a partial diversion of energy expenditure from thermoregulation to foraging.

Several recent investigations (e.g., Fretwell 1972, Ivacic and Labisky 1973) have emphasized the synergistic effects of climatic and trophic stresses on the survival of homeotherms in extreme environmental conditions. Individuals of avian species that overwinter even in temperate latitudes are periodically confronted by low environmental temperatures and by snow cover that prevents foraging or reduces its yield. Small-bodied ground-feeding passerines are likely to be especially vulnerable to mortality under such conditions. We selected such a bird, the White-crowned Sparrow (Zonotrichia leucophrys gambelii), as the subject of an investigation focusing on metabolic and behavioral responses to simulated conditions of winter severity, in particular low air temperatures and food deprivation. We

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chose this species not only because of its size and foraging characteristics, but also because comparatively much is known of its physiology and energy metabolism (King 1964; Merkel 1966; De Jong 1976; Robinson, Campbell, and King 1976), and because it is a species that displays geographic variation in its sex ratio during winter. Northerly populations are predominantly male, the proportion gradually decreasing southward (King, Farner, and Mewaldt 1965). We thought that this differential distribution of the sexes in winter might be interpretable on the basis of sexual differences in response to cold stress and starvation.

Investigations of weight loss during food deprivation (hereafter called fasting) and the survival time of fasting individuals in the laboratory are not new (Kendeigh 1934, 1945; Latham 1947; Koskimies 1950; Jordan 1953; Kabat et al. 1956; Hine and Plaka's 1957; Tester and Olson 1959; Hanson and Kossak 1963; Brenner 1965; Brenner and Malin 1965; Ivacic and Labisky 1973). From these investigations we know that heavier individuals (and species) tend to endure fasting longer than lighter ones (Kendeigh 1945; Ivacic and Labisky 1973) and that some species exhibit sexual differences in survival time when fasting (Kendeigh 1945, Latham 1947; Jordan 1953; Ivacic and Labisky 1973). Energy metabolism during prolonged fasting (greater than 1 night) has been studied frequently in domesticated birds (e.g., Philips, Ashworth, and Brody 1932; Henry, Magee, and Reid 1934; Benedict and Lee 1937; Dukes 1937; Barott et al. 1938; Smith and Riddle 1944; Infantellina and Rubino 1951), but much less frequently in wild species (Koskimies 1950; Ivacic and Labisky 1973).

In the field, the endurance of fasting by overwintering small passerines (weighing less than 30 g) has been estimated from the ratio of the caloric values of fat stores and metabolic rate estimated from laboratory data (summarized by King 1972; see also Chaplin 1974; Ketterson and Nolan 1976).

**METHODS**

Our observations consist of measurements of (1) body temperature and rates of weight loss in fasting birds (experiments) and birds feeding voluntarily (controls) when both were kept indoors at constant temperature, and (2) oxygen consumption and locomotor activity of fasting birds and their controls when both were subjected to varying thermal conditions simulating their natural winter environment on overcast, windless days and nights at the northern limit of their winter range (Mahoney 1976). All birds were winter acclimatized in outdoor aviaries and had been in captivity for 1–3 yr.

**CONSTANT AIR TEMPERATURES (COLD ROOM)**

**Treatment.**—To determine how long fasting could be endured and the accompanying changes of body weight and body temperature, 32 White-crowned Sparrows were denied food (but given water) until considered near death, while weight and body temperature were periodically recorded. Control was provided by 12 birds supplied with chick starter mash and millet seed as well as water, but otherwise similarly treated. We assigned subjects randomly to these categories. All birds were subjected in a cold room to the following microclimatic conditions: air temperature range, 6.5–8 C; windspeed, 0.09–0.18 m/s; wall temperature, 4.3–4.8 C; relative humidity, 60%–63%; photoperiod, 10L:14D, lights on at 07:00. Observations were made between January 1 and March 1, 1975.

Around noon on day 1 of an observation sequence (N = 11), four White-
crowned Sparrows were taken from an outdoor aviary, weighed (nearest 0.1 g), measured (wing length, chord), and placed in cages in the cold room. Four hours later (ca. 16:30) they were removed one at a time and transported to an adjoining room where we determined body temperature by inserting a Schult- heis quick-responding thermometer into the cloaca for 15 s (98% response time in a water bath). Body temperature measurements were made as rapidly as possible in an effort to minimize the influence of disturbance (Southwick 1973). The usual interval between the first and fourth readings was 3 min. The birds were then weighed again and returned to the cold room. We considered that gut contents would have been voided during the first 4 h of fasting, so the weight obtained at about 16:30 was used as the initial weight in the computations that follow. The sequence of temperature and weight measurements was repeated at 4-h intervals (except 04:30 and often 00:30) until: (1) 68 h had elapsed since the birds were removed from the aviary, (2) death occurred, or (3) birds showed signs of stress believed to be associated with approaching death. Birds facing imminent death (within the next 4 h) had the feathers of head, breast, and back erected, were very lethargic, held their eyes only partially open, and were sometimes too weak to feed themselves when food was presented. Their appearance resembled photographs of birds believed to be suffering the effects of the harsh British winter of 1962/63 (Dobinson and Richards 1964) and the verbal description of starving pheasants by Tester and Olson (1959). These criteria are admittedly subjective, and no doubt some of the birds terminated at a given time might have survived another 4-h period without food. However, it was not our objective to starve any birds to death, but only to learn their reactions to pro-

longed fasting in thermally realistic conditions. Nevertheless, in spite of our intentions to spare their lives, two birds were dead at the end of the sequence; four died within 48 h later despite special treatment consisting of glucose feedings, confinement at room temperature, and exposure to prolonged photoperiod to allow voluntary feeding at odd hours; 10 lived but were given the same special treatment just described, and in our opinion five of the 10 would have died without it; and 16 were able to feed themselves at the end of the sequence when subjected to the experimental temperature and photoperiod. Of these last 16, three were certainly terminated too soon and were omitted from the calculations of weight loss that follow. At the end of each experiment, the sex of the birds was ascertained by laparotomy.

Analysis.—Parametric statistics were employed throughout this report. Their suitability was verified initially by tests for equality of variance (F-test) and for normality (criterion: zero be included within two standard deviations of the $g_1$ and $g_2$ scores). Mean wing length and initial weight were calculated for experimentals and controls to determine whether birds in both groups represented the same population (table 1: difference in wing length $= 0.27$ min, $t = 0.29$, df = 34, NS; difference in initial weight $= 1.35$ g, $t = 1.36$, df = 39, NS). The populations were considered comparable.

An attempt to correlate average individual weight loss among experimental with the sequence of weighings (i.e., time since fasting began) was nonsignificant ($r = -0.308, N = 12, 2$-tailed $P = .33$), and we therefore concluded that the rate of weight loss was constant.

VARIABLE AIR TEMPERATURE (METABOLIC CHAMBER)

Treatment.—Between January 28 and February 26, 1975, we measured metabolic rate, weight loss, and locomotor
activity of White-crowned Sparrows confined in metabolism chambers and subjected to natural temperatures and day-length through a night/day/night cycle. To initiate an experiment, we removed three birds from an outdoor aviary at the end of their feeding day (16:30–17:30), weighed and measured them, and placed them individually in 29 × 21 × 19 cm (11.6 liter) metabolism chambers constructed from transparent plexiglass except for an aluminum floor (covered by a sheet of paper) that served as a heat exchanger. The chambers contained perch-activated microswitches to record locomotor activity, and dishes of snow as sources of drinking water. Fat, rather than lean, birds were deliberately selected to improve the likelihood that they would survive the fasting period. The results therefore represent optimal initial conditions. Three chambers were used per trial, two of them housing fasting experimentals, and one housing a control given a superabundance of food. Nine trials involving 27 birds were completed. Between 17:00 and 18:00 the chambers were placed in an environmental cabinet set at 2 C. The lights were left on for several minutes to allow the birds to locate a perch and then snapped off. Air temperature in the cabinet (controlled by an automatic programmer) began to fall at about 17:30 at a rate of about 2 C/h until 00:00 when it was –10 C. Temperature was then held steady at –10 C until the following morning at 08:00 (lights were snapped on at 07:00). Between 08:00 and 14:00 air temperature rose at about 2.5 C/h to reach 5 C at 14:00, where it remained steady until 16:00. A second cycle duplicating the first was initiated at 16:00. The sequence was terminated at 08:00 on the second morning and final weights were determined. Several days later sex was ascertained by laparotomy. The cycle of air temperature and duration of fasting were selected on the basis of data obtained in the microhabitat of wintering flocks of White-crowned Sparrows in southeastern Washington. The combination of –10 C nights and 5 C days and snow cover preventing feeding for one day is extreme, occurring no more than once a winter during one or two winters per decade (Mahoney 1976).

Oxygen consumption.—Oxygen consumption was measured in an open circuit conforming with configuration C of Hill (1972). The smallest reduction in oxygen concentration maintained for at least 4 min was selected for computing the rate of consumption. All volumes were corrected to standard temperature and pressure. Every 4 h beginning at 20:00 of night 1 (excepting 04:00 on nights 1 and 2), the analyzer was recalibrated and the oxygen consumption of all three birds was sampled in succession. One of the three chambers during each trial could be monitored continuously, and records from these birds were later read at 2-h intervals and at 07:00 on mornings 1 and 2 (just before the lights were snapped on). This sample included nine experimentals and two controls. Because initial and final body weights were known and the decrease of body weight in fasting birds was linear with time, as already mentioned, it was possible to compute weight-specific metabolic rate at the times of measurement by linear extrapolation of weight change. We decided, however, that cm³ O₂/bird-h was a more appropriate measure in this investigation because, even though weight losses were substantial, there was no reason to believe that the metabolizing mass of the animal had altered.

Perch activations were recorded graphically and on digital counters that kept a running total. These were re-
corded at 2-h intervals during the day and at 4–8-h intervals at night when locomotor activity was slight.

**Analysis.**—Duplicating the methods used in the cold-room studies, we compared mean wing length and initial weight (this time including gut contents) for experimental and controls (table 3: wing length difference = 1.7 mm, $t = 1.47$, df = 22, NS; initial weight difference = 1.4 g, $t = 1.67$, df = 25, NS). The populations were statistically alike. The duration of fasting was not relevant here, since the number of hours was fixed, but not all birds survived the entire period and endurance was compared by sex.

**Results**

**Constant air temperature (cold room)**

**Weight loss.**—Summary data (table 1) suggest that a typical White-crowned Sparrow during winter can survive 37 h at 7°C without food while losing 20% in body weight. The extreme case lost 10.7 g or 33% of body weight over 68 h. Only five of 32 individuals survived 68 h; the shortest survival period was 20 h. Individual differences in survival time as large or larger than this in response to starvation or other stresses are commonly observed in small homeotherms (e.g., Kendeigh 1945; Kleiber 1961; Brenner and Malin 1965). Weight loss in the controls (table 1) remains unexplained but may be partially due to the fact that experiments tended to end in the morning when weights are lower than at noon, when the experiments began.

A comparison of the sexes reveals the greatest rate of weight loss in the experimental males; but because males were initially heavier than females and were able to lose a greater amount and percentage of weight, they endured fastering longer than females. The final weights of males and females were es-

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**TABLE 1**

<table>
<thead>
<tr>
<th>CATEGORY</th>
<th>Both sexes</th>
<th>Fasted Males</th>
<th>Fasted Females</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length (mm)</td>
<td>25.40 ± 2.57 (29)</td>
<td>25.67 ± 3.01 (12)</td>
<td>25.06 ± 2.33 (12)</td>
<td>NS</td>
</tr>
<tr>
<td>Final weight (g)</td>
<td>26.07 ± 1.67 (12)</td>
<td>26.21 ± 1.72 (12)</td>
<td>26.03 ± 1.58 (12)</td>
<td>NS</td>
</tr>
<tr>
<td>% weight loss</td>
<td>5.49 ± 4.27 (29)</td>
<td>8.45 ± 6.39 (12)</td>
<td>0.80 ± 6.24 (15)</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>Rate (g/h)</td>
<td>0.152 ± 0.024 (29)</td>
<td>0.163 ± 0.020 (15)</td>
<td>0.143 ± 0.005 (15)</td>
<td>&lt;.05</td>
</tr>
<tr>
<td>Hours endured</td>
<td>36.86 ± 16.28 (29)</td>
<td>42.57 ± 10.42 (12)</td>
<td>39.37 ± 2.62 (15)</td>
<td>&lt;.05</td>
</tr>
</tbody>
</table>

**Notes:**
- * Mean ± SD (no. of birds).
- b Sum of sample sizes does not equal sample size of both sexes because sex was not always accurately ascertained.
- c $t$-value for male-female comparisons.
- d Chord.
- e After observations began (i.e., gut contents voided).
- *4 h after observations began (i.e., gut contents voided).
sentially the same (table 1), contrary to expectation (King and Farner 1966). We therefore asked whether females had inadvertently been favored, i.e., when trials terminated, were females still carrying nutritional reserves and males not? Seven of 23 cases were female, so 30.4% of all termination categories (dead at end of trial, dead within 48 h, alive but requiring special treatment, alive with no special treatment) should have been occupied by females if experimental treatment of the sexes was equal. This expectation was met ($\chi^2 = 1.07$, df = 3, NS).

The importance of initial weight in predicting fasting ability was confirmed by regression analysis. Greater initial weight predicts greater percentage body weight loss ($% \text{ wt loss} = 1.82 \text{ initial wt} - 29.15$, $F = 70.61$, $s_b = 0.216$, $N = 29$) and a greater number of hours of fasting endured ($h \text{ endured} = 5.09 \text{ initial wt} - 100.99$, $F = 190.7$, $s_b = 0.37$, $N = 29$). Initial weight is not a significant predictor of the rate of weight loss ($g/h = -0.0004 \text{ initial wt} + 0.16$, $F = 0.06$, $s_b = 0.001$, $N = 29$). Wing length, a commonly used size indicator, does not accurately predict any of the other variables reported in table 1.

**Body temperature.**—Extreme body temperatures recorded for experimentals were 35.4 C and 43.8 C, while for controls the extremes were 39.0 C and 43.2 C. Mean body temperatures according to time of day are compared for experimentals and controls in figure 1. Fasting

![FIG. 1.—Mean body temperature of fasted (○) and fed (●) White-crowned Sparrows kept in a cold room at 7 C. Vertical bars denote ±1SD. Sample size is shown below the bars. See text for additional details.](image)
birds registered temperatures like those of controls during the daylight hours (except 12:30 on day 3, \( t = 3.3, P < .01 \)) but were significantly lower at night (20:30 on night 2, \( t = 4.25, P < .001; 20:30 \) on night 3, \( t = 2.82, P < .005 \)). The measures at 00:30 on both nights were also lower in starved than in fed birds, but small sample sizes prohibit meaningful statistical comparisons. Differences in body temperatures for given individuals from night to night (table 2), when averaged for experimental and controls, indicate that nighttime body temperatures continue to fall as fasting proceeds, although the trend is not statistically significant. An average drop of 3.4 C from initial levels was seen among birds fasted for 56 h. Controls showed little change over the same time period.

**VARIABLE AIR TEMPERATURE (METABOLISM CHAMBERS)**

*Weight loss.*—Twelve of 18 White-crowned Sparrows survived stressful conditions of food deprivation and low air temperature for about 40 h, i.e., a day, a night, and a day. Four individuals died during the second night and two others were removed at 00:30 on the same night because death was believed imminent. At least one of this latter group would probably have survived until morning (final weights of removed birds were 21.5 and 23.3 g). Since fat birds were selected for the metabolism chamber trials, it is not surprising that the mean initial weight is greater than that of birds used in the cold-room trials (cf. tables 1 and 3). Mean initial weight was also greater than among the cold-room birds, suggesting that starvation might have been endured even longer. Finally, chamber birds exceeded cold-room birds in rate of weight loss. This is attributable in part to lower air temperature and accompanying higher metabolic rates, and in part to the fact that weight loss in chamber birds initially included fecal matter, thereby falsely inflating the rate.

Further differences in results between chamber and cold-room birds are apparent in sexual comparisons. Chamber experimental did not show significant sexual differences in initial weight, weight loss, percentage of weight loss, or rate of weight loss, nor were there apparent differences in survival ability (table 3). With the exception of rate of weight loss, these findings obviously follow from lack of sexual differences of initial weight among chamber experimental. This lack is further confirmed by a comparison of chamber experimental and controls: initial weight was the same in the two groups (see Methods) but sex ratios were almost reversed (experimental: 13 males, three females, two unknown; controls: six females, two males, one unknown). Thus, it appears that males selected at random (i.e.,

### TABLE 2

**MEAN DECREASE OF BODY TEMPERATURE IN FASTED AND FED BIRDS IN A 7 C COLD ROOM**

<table>
<thead>
<tr>
<th>Nights of Comparison</th>
<th>Fasted</th>
<th>Fed</th>
<th>( t )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 vs. 2</td>
<td>( 1.87 \pm 1.15 ) ((14))</td>
<td>( -0.06 \pm 0.56 ) ((8))</td>
<td>4.43*</td>
</tr>
<tr>
<td>2 vs. 3</td>
<td>( 1.31 \pm 1.99 ) ((7))</td>
<td>( 0.40 \pm 0.52 ) ((4))</td>
<td>0.88</td>
</tr>
<tr>
<td>1 vs. 3</td>
<td>( 3.40 \pm 0.50 ) ((3))</td>
<td>( 0.55 \pm 0.85 ) ((4))</td>
<td>5.09*</td>
</tr>
</tbody>
</table>

* Mean \( \pm SD \) (no. of birds), °C.
* Slight increase between nights 1 and 2.
* \( P < .001 \).
* Large SD produced by increase of \( T_b \) in a single individual.
### TABLE 3

**CHARACTERISTICS OF FASTED AND FED WHITE-CROWNED SPARROWS IN A METABOLIC CHAMBER WITH SIMULATED CONDITIONS OF NATURAL TEMPERATURE AND DAYLENGTH**

<table>
<thead>
<tr>
<th>Category</th>
<th>Both Sexes</th>
<th>Fasted %</th>
<th>Fed</th>
<th>Fasted Males</th>
<th>Fasted Females</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length (mm)</td>
<td></td>
<td>75.60 ± 2.69 (15)</td>
<td>73.89 ± 2.88 (9)</td>
<td>76.18 ± 2.56 (11)</td>
<td>72.66 ± 0.58 (3)</td>
<td>2.30</td>
<td>&lt;.05</td>
</tr>
<tr>
<td>Initial weight (g)</td>
<td></td>
<td>29.98 ± 1.03 (18)</td>
<td>28.62 ± 1.83 (9)</td>
<td>30.05 ± 2.18 (13)</td>
<td>29.90 ± 1.25 (3)</td>
<td>0.10</td>
<td>NS</td>
</tr>
<tr>
<td>Final weight (g)</td>
<td></td>
<td>23.11 ± 3.31 (18)</td>
<td>25.27 ± 1.67 (9)</td>
<td>22.94 ± 2.39 (13)</td>
<td>23.37 ± 1.67 (3)</td>
<td>0.29</td>
<td>NS</td>
</tr>
<tr>
<td>Weight loss (g)</td>
<td></td>
<td>7.03 ± 0.96 (18)</td>
<td>3.36 ± 1.08 (9)</td>
<td>7.11 ± 0.91 (13)</td>
<td>6.53 ± 0.55 (3)</td>
<td>1.04</td>
<td>NS</td>
</tr>
<tr>
<td>% weight loss (%)</td>
<td></td>
<td>23.55 ± 3.64 (18)</td>
<td>11.67 ± 3.42 (9)</td>
<td>23.78 ± 3.46 (13)</td>
<td>21.81 ± 0.27 (3)</td>
<td>0.96</td>
<td>NS</td>
</tr>
<tr>
<td>Rate (g/h)</td>
<td></td>
<td>0.191 ± 0.032 (18)</td>
<td>0.085 ± 0.028 (9)</td>
<td>0.094 ± 0.033 (13)</td>
<td>0.178 ± 0.013 (3)</td>
<td>0.76</td>
<td>NS</td>
</tr>
<tr>
<td>Survival</td>
<td></td>
<td>12 of 18 (4 died, 2 removed)</td>
<td>9 of 9</td>
<td>9 of 13 (3 died, 1 removed)</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
</tbody>
</table>

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*a* Mean ± SD (no. of birds).

*b* Sum of sample sizes does not equal sum of both sexes because sex was not always accurately ascertained.

*c* t-values for male-female comparisons.

*d* Chord.

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Activity.—When total activity is considered, the groups in 2- to 8-h blocks, the experiments are seen to be much more active in the day in spite of the two groups in the night 2 compared with night 1 in sequence 2 (fig. 2). The identical rates of the two groups in the night 2 compared with night 1 in sequence 2 (fig. 2) during the night/day/night/day blocks, the experiments are seen to be much more active in the day in spite of the two groups in the night 2 compared with night 1 in sequence 2 (fig. 2). The identical rates of the two groups in the night 2 compared with night 1 in sequence 2 (fig. 2) during the night/day/night/day blocks, the experiments are seen to be much more active in the day in spite of the two groups in the night 2 compared with night 1 in sequence 2 (fig. 2) during the night/day/night/day blocks.

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lights were off. It should be noted, however, that several of the experimentals that died during night 2 showed sporadic bouts of activity, indicating that hungry birds may be somewhat more restless at night. Merkel (1966) noted a similar phenomenon in this species.

DISCUSSION

SURVIVAL ABILITY

To the extent that members of natural populations of White-crowned Sparrows resemble our captive birds, our data (tables 1 and 3) suggest that the unusual White-crowned Sparrow might

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TABLE 4

COMPARISON OF OXYGEN CONSUMPTION OF FASTED AND FED WHITE-CROWNED SPARROWS DURING DAYTIME AND NIGHTTIME PERIODS

<table>
<thead>
<tr>
<th>PERIODa</th>
<th>Mean O₂ Consumption, cm³/bird-hb</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fasted</td>
</tr>
<tr>
<td>08:00–16:00 (day)</td>
<td>120.5 ± 30.04 (67)</td>
</tr>
<tr>
<td>20:00–04:00:</td>
<td></td>
</tr>
<tr>
<td>Night 1</td>
<td>85.2 ± 21.32 (56)c</td>
</tr>
<tr>
<td>Night 2</td>
<td>67.2 ± 13.42 (55)c,d</td>
</tr>
</tbody>
</table>

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* Excluding measurements near light-dark transitions (06:00 and 18:00).
  b Mean ± SD, no. of measurements in parentheses.
  c,d Significance of differences in both c-c and d-d comparisons: *P < .001.*
survive 3 nights and 2 days without food at temperatures near freezing, but typical individuals could not be expected to survive longer than 1 day and 2 nights, and some members of the population less than that. These findings may be compared with estimates from King and Farner (1966) who found that White-crowned Sparrows wintering in southeastern Washington have a mean lipid content of 3.0 g during January. This amount was considered sufficient to permit survival through a single night at extremely low temperatures by about 85% of the population, but sufficient, even at temperatures near freezing, for a night/day/night fast by less than 11%. Their conclusion is similar to those reported for a variety of fringillids (literature summarized by King 1972), i.e., that most of a population has energy stores sufficient for only a single night’s fast and that daily feeding is obligatory. Survival time under any particular set of circumstances is obviously determined by a variety of organismal and environmental variables, not all of which were included in our experiments; but our data suggest that small birds may be more resistant to periods of food shortage caused by snow cover than is generally believed. Larger birds such as Ring-necked Pheasants (Phasianus colchicus) can endure fasting much longer than the White-crowned Sparrow (2–4 wk in captivity: Tester and Olson 1959) and might be considered immune to the effects of prolonged snow. Lehtonen (1975) and Roseberry (1962), however, have suggested that stressful winters that force larger birds to consume nearly all their fat reserves may impair reproductive output the following spring and thus indirectly influence fitness.

Because the sex ratio of White-crowned Sparrows varies geographically during winter, sexual differences in fasting ability are of particular interest. Ketterson and Nolan (1976) have suggested that farther north, where the likelihood of enforced fasting due to snow cover is greater, males may be more likely to survive because their larger size permits greater fasting endurance. Calder (1974) notes that the relationship between body size and fasting ability is determined by the ratio of energy stored to the rate of its use, the numerator being proportional to body weight raised to the 1.0 power, and the denominator body weight raised to the 0.42 power (allometric expression

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**TABLE 5**

<table>
<thead>
<tr>
<th>Time</th>
<th>Fasted Median</th>
<th>Fasted N</th>
<th>Fed Median</th>
<th>Fed N</th>
<th>U*</th>
<th>Pb</th>
</tr>
</thead>
<tbody>
<tr>
<td>20:00–00:00</td>
<td>1</td>
<td>17</td>
<td>0</td>
<td>9</td>
<td>94</td>
<td>NS</td>
</tr>
<tr>
<td>00:00–08:00</td>
<td>335</td>
<td>17</td>
<td>192</td>
<td>9</td>
<td>98</td>
<td>NS</td>
</tr>
<tr>
<td>08:00–10:00</td>
<td>1,638</td>
<td>17</td>
<td>321</td>
<td>9</td>
<td>120</td>
<td>&lt;.002</td>
</tr>
<tr>
<td>10:00–12:00</td>
<td>1,814</td>
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<td>74</td>
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* Mann-Whitney statistic, Wilcoxin two-sample test (Sokal and Rohlf 1969).  
  b Two-tailed test.
of metabolic rate at 0°C, according to Kendeigh [1969]). This means that large birds will survive longer than small ones having proportionately the same energy stores. Our data are qualitatively consistent with this relationship. Males endured fasting significantly longer in the cold-room trials than females. When initial weight was similar, as in the metabolism chamber trials, there was no apparent sexual difference in survival ability. King and Farner (1966) reported that wintering males weigh more than females in natural populations of White-crowned Sparrows, but that the percentage fat content of the carcass was the same in the sexes; i.e., the absolute amount of fat is greater in males. We provisionally conclude that a greater proportion of male White-crowned Sparrows might be expected to survive a prolonged snow storm at the northern edge of the winter range, and suggest that this may have played a role in the evolution of geographic variation in winter sex ratio. Females have responded to this selection pressure by overwintering farther south than males, on the average, rather than evolving a larger body size.

**Body Temperature**

A decrease of body temperature is a typical physiological response to fasting (Lusk 1919; Grande 1964). Among avian species, slight decreases of daytime $T_b$ have been reported for fasting domestic geese (Benedict and Lee 1937), Chukars (*Alectoris graeca chukar*: Hine and Flakas 1957), Hungarian Partridges (*Perdix perdix*: Hine and Flakas 1957), Mourning Doves (*Zenaida macroura*: Ivacic and Labisky 1973), and White-crowned Sparrows (Merkel 1966). We did not detect a similar daytime decrease of $T_b$ in this investigation. Nighttime decreases in fasting birds have been reported for pigeons (*Columba livia*: Chossat 1843), Swifts (*Apus apus*: Koskimies 1950), and Mourning Doves (Ivacic and Labisky 1973). Thus, the moderate decrease (3–4°C) noted here in fasting White-crowned Sparrows is not without precedent, even among species usually considered to maintain a very narrow range of $T_b$. Lehtonen (1975) has suggested that Ring-necked Pheasants overwintering in Finland may conserve energy during the shortest days by undergoing hypothermia at night and to some extent even by day. We will presently return to a consideration of the adaptive role of $T_b$ reduction during fasting in the White-crowned Sparrow.

**Energy Metabolism**

According to Grande (1964), “reduction of basal metabolism is one of the more constant findings in [studies of] undernutrition.” Spiders (Anderson 1974), intertidal invertebrates (summarized by Newell 1973), fish (Saunders 1963; Muir and Niimi 1972), snakes (Benedict 1932), rats (Kleiber 1961), dogs (cited by Grande 1964), bovids (Zarinya and Latvietis 1972), and humans (Grande 1964; Apfelbaum, Bostsarron, and Lacatis 1971) have all been reported to reduce oxygen consumption during food deprivation. Among birds, Benedict and Lee (1937) observed progressive decreases of BMR (per animal) in domestic geese, attaining 33%–50% after 30 days of fasting. In domestic pigeons, BMR diminished by an average of 29% (per unit weight) between the first and tenth days of fasting (Smith and Riddle 1944).

Even though the decrease of BMR in response to fasting is widespread among animal groups, its functional basis is controversial, some investigators arguing that weight loss alone accounts for the decrease, while others argue that it results from a reduction of metabolic
intensity per unit weight (for review, see Grande 1964). The resolution of this controversy has been complicated by differences in the methods of expressing and comparing metabolic rates (Keys et al. 1950). In this report we have expressed metabolic rate on a per individual rather than per gram basis because our major objective is ecological rather than physiological interpretation. Regardless of the functional basis of the diminished metabolic rate attending fasting, “to the extent that it permits the prolongation of life of the individual, such a response must be considered an adaptation” (Grande 1964).

We found that the oxygen consumption of resting White-crowned Sparrows decreased by about 21% between the first and second nights of fasting, while that of controls was unchanged. We assume that this was accompanied by a 3°C drop in body temperature in fasted birds and no change in controls, as shown by the cold-room experiments. The obvious variables that might explain this decrease of nocturnal metabolic rate during fasting include the decrease (if any) of metabolically active tissue attending weight loss, the van’t Hoff effect of the concurrent decrease of body temperature, the attendant decrease of thermal gradient through the body, and facultative adjustments of body resistance to heat loss.

Assuming that the $Q_{10}$ of the energy metabolism of White-crowned Sparrows is the same as the average (2.3) for a variety of thermochemical processes in organisms, a 3°C decrease of body temperature would cause a 22% decrease of oxygen consumption from a level of 150 cm$^3$/bird-h, and thus account fully for the decrease of nocturnal metabolic rate in fasting birds. This explanation, however, may be too simple. Observations of White-crowned Sparrows during nocturnal cold exposure revealed marked differences of posture, ptiloerection, and behavior between experimentals and controls that suggest differences in the adjustment of insulation. Controls sat erect and fluffed their body feathers over the anterior margins of the primaries; experimentals buried their heads in their scapulars and fluffed all the body feathers. They also responded somewhat more slowly to disturbance at night, suggesting a deeper level of sleep, which might also affect oxygen consumption.

In short, several physiological adjustments may contribute to the reduction of oxygen consumption observed on night 2 in fasting birds, but we cannot discriminate their relative importance on the basis of the data now available.

**Locomotor Activity**

The impact of starvation on voluntary activity seems to vary with animal group. Man and shrimp become less active (Grande 1964; Hagerman 1970). Spiders do not vary activity with duration of food deprivation (Anderson 1974); laboratory rats and other rodents (Richter 1927; Jakubezak 1967; Morris, Dill, and Soholt 1975) and birds become hyperactive (Wagner 1937; Eyster 1954; Merkel 1966; present study). During the day, fasting White-crowned Sparrows literally flung themselves from side to side of the metabolism chamber for many minutes without a pause. Certainly, a spontaneous increase of activity when food is lacking but needed can be considered as adaptive. Our data suggest that White-crowned Sparrows prevented from feeding by snow cover or some other form of food shortage would change foraging sites more often and be generally more active. Presumably in this way they are more likely to find previously undiscovered food sources.
METABOLIC RATE, FEEDING ACTIVITY, AND LOCOMOTOR ACTIVITY

One of the unique and most intriguing aspects of our data is the identical level of total daytime oxygen consumption in fasted and fed birds. The energy costs of daytime existence in these two groups would be expected a priori to differ by the algebraic sum of the heat increment of feeding (absent in fasting birds), the heat increment of locomotor activity (greater in the fasting birds), and the greater convective heat loss attending greater motion in the fasting birds. Both the heat increment of feeding and the heat of locomotion might substitute for thermoregulatory costs in cold surroundings, although these are controversial subjects (for review, see Pohl and West 1973; Calder and King 1974) in which various studies have shown that thermoregulatory substitution may be either complete, partial, or undetectable. Our data cannot untangle this intricate problem, but we offer some observations that may assist in clarifying it.

First, the almost ninefold greater perch-hopping activity in the fasting birds does not necessarily imply a ninefold difference in heat production from this source. Pohl (1970) has shown in Chaffinches (Fringilla coelebs) that energy expenditure at $T_a = 18-20°C$ is a rather weak function of perch-hopping activity (kcal/day = 10.84 + 0.00027 $h$, where $h =$ number of perch activations per day). At this moderate air temperature the heat of locomotion probably does not substitute for the thermoregulatory requirement. If White-crowned Sparrows resemble Chaffinches in similar recording systems, then the difference in perch-hopping activity between fasting and fed birds (about 6,000 hops) during the daytime would elevate the metabolic rate of fasting birds by about 15% above that of controls, assuming no thermoregulatory substitution. If the heat increment of feeding is 10%-15% above the resting level of metabolism (which is a reasonable estimate; King and Farner 1961; Kendeigh 1973) and likewise does not substitute for thermoregulatory costs, then the daytime oxygen consumption of controls (augmented above the resting level by the heat increment of feeding) and experimentals (augmented by locomotor activity) will be nearly identical. This is merely speculation, but it helps to delimit one extreme of the problem. At the other extreme, the heat of locomotor activity and of feeding may substitute fully for an equal amount of heat otherwise required by thermoregulation. Between these extremes we can envisage cases of partial substitution, further complicated by the greater effect of convective heat loss in the hyperactive fasting birds. The latter is not even roughly quantifiable at present, and we have ignored it.

Regardless of the unresolved physiological complications, the ecological or adaptive implications of our experiments are clear. White-crowned Sparrows deprived of food in cold surroundings respond by reducing body temperature at night, with a consequent 21% saving in overnight energy expenditure. Furthermore, they are able to hunt intensely for food during the day, owing to compensatory adjustments in their energy budgets, without increasing their daytime energy expenditure above that of full-fed birds.

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