

SEASONAL THERMOREGULATORY ADJUSTMENTS IN WHITE-CROWNED SPARROWS

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ABSTRACT.—Thermoregulatory responses to some aspects of winter climates were examined in the migratory finch, *Zonotrichia leucophrys gambelii*. After 3 months acclimation to either warm (28 C) or cold (4 C) conditions, the birds were tested for thermoregulatory capacities in June and January. Physiological responses of acclimated birds were compared to those of control birds housed in outdoor aviaries. Telemetered body temperature showed a daily cycle with a 1-C lower nocturnal temperature in summer and a 2-C difference in winter. The decreased nocturnal body temperature was found in winter regardless of thermal acclimation history. Thermal acclimation history had no significant effect on metabolism during subsequent exposure to cold test temperature. However, there were different apparent effects on metabolism at some exposure temperatures when results were expressed *per bird* as compared to *per gram* (normalized by factoring out mass variance). Fasting metabolic rate was higher in winter than summer when tested at low ambient temperature. White-crowned Sparrows maintained homeothermy in both winter and summer seasons even when exposed to cold temperatures down to -35 C for several hours. Received 17 November 1978, accepted 6 July 1979.

ACCLIMATION and acclimatization are forms of physiological and/or morphological adjustment that are distinguished from short-term regulatory response to environmental stresses. The term acclimation usually includes long-term adjustments observed in experimentally contrived constant conditions, whereas the term acclimatization usually refers to adjustments observed in free-living animals or in captives subjected to natural fluctuation of many environmental factors concurrently (Hart and Héroux 1953, Hart 1957, West 1962, Gordon et al. 1977).

In laboratory experiments on temperature acclimation, it can usually be shown persuasively that environmental temperature is the proximate factor inducing the compensatory responses. In studies of acclimatization, on the other hand, the complexity of environmental variation makes the identification of the proximate factor(s) very difficult or impossible. The fact that natural patterns of acclimatization cannot be induced by thermal stress alone is well known (Hart and Héroux 1953, Héroux et al. 1959, West 1962, Hart 1963, Chaffee and Roberts 1971). The ecological significance of seasonal acclimatization for animals living in variable environments is obvious, and information about the extent and timing of acclimatization is basic to a meaningful assessment of the stress to which an organism is exposed in different seasons. A number of studies provide data on modes of seasonal thermoregulatory adjustment in birds and are reviewed by Dawson and Hudson (1970), Chaffee and Roberts (1971), Calder and King (1974), and West (1976). However, the existing information about the capacities of various species of birds and mammals for thermal acclimation and seasonal acclimatization is conflicting. Some species show significant capacities for seasonal adjustment of thermal tolerance, heat production, and insulation, whereas other species show lesser or negligible capacities (cf. Hart 1962, West 1962, Rautenberg 1969, Barnett 1970, Biebach 1975, Dawson and Carey 1976, Weathers and Caccamise 1978). In part, these discrepancies may reflect differences

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TABLE 1. Environmental conditions of acclimation rooms.

Description (as used in text)	Air temperature (shaded mercury thermom- eter)	Photo- period (including dawn and dusk)	Illumi- nation (Weston illumina- tion meter 756)	Shortwave radiation (Star Pyra- nometer— 0.3 to 3 μ)	Air motion (hot-wire anemometer)	Relative humidity Hygro- dynamics electric hygrom- eter)
	°C		lux	cal cm ⁻² min ⁻¹	m/min	%
Warm	28 ± 1	Natural	0.1–360	0–0.05	12–15.5	35–55
Cold	4 ± 1	Natural	0.1–320	0–0.04	12–15.5	25–35
Control (in out- door aviary)	Natural (–24 min, +35 max)	Natural	0.1–6,500	0–0.85, winter; 0–0.99, summer	0–180; gusts to 600	20–99

in experimental procedures. But it is possible that in many cases they reflect real interspecific differences in the modes of adjustment and sensitivity of responses. Some species may supplement physiological acclimatization by nutritional or behavioral modes of adjustment.

The investigation reported here was designed to distinguish the environmental cues that determine acclimatization changes by dissecting the relative roles of temperature and photoperiod in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. This small (25–30 g) finch breeds in the high mountains of western Canada north to Alaska, and winters in river valleys of central Washington south to northern Mexico.

MATERIALS AND METHODS

White-crowned Sparrows were captured in southeastern Washington during migration and were kept in outdoor aviaries (2 × 3.5 × 2.5 m) until transferred indoors to acclimation rooms. The normal winter range of the laboratory population is unknown, although White-crowned Sparrows habitually overwinter in river valleys near the laboratory. Experimental groups (Table 1) of 25 birds each were either kept in the outdoor aviaries ("control") or transferred to 28 C ("warm") or 4 C ("cold") acclimation rooms in October and March and tested for thermoregulatory capacities in January and June, respectively. Three months of exposure to the acclimation temperatures was deemed adequate for the completion of thermal acclimation in these small birds (Gelineo 1955). The birds in the warm room were within their thermoneutral zone, while those in the cold room were 15–19 C below their lower critical temperature (King 1964, Maxwell and King 1976). They were housed individually in cages measuring 22 × 40 × 45 cm and had continuous access to water and chick-starter mash (20.7% protein, 74.7% carbohydrate, 3.1% fat, 1.5% ash), as did the outdoor controls. Additional details on experimental and control conditions are summarized in Table 1 and in Southwick (1971). Note in particular that all groups were exposed to the same annual photocycle, this being generated in the acclimation rooms by automatic time switches including gradual twilight transitions at dawn and dusk. The influence of twilight (as contrasted to the usual step changes between light and dark in photoperiodic experiments) cannot be ignored in the entrainment of biological rhythms (e.g. Aschoff and Wever 1965), although it is not known that this is significant in the present context.

The only controlled and known difference in environmental conditions for any given thermal regime, between seasonal studies, was the seasonally changing daylength. Thus, thermoregulatory differences found between summer and winter test groups (from the same acclimation temperature) must have been induced by changes in the length of day as the environmental cue (or by other uncontrolled and unknown geophysical events, as hypothesized by Brown 1969). Differences in thermoregulatory performance that occurred between two test groups (e.g. between cold and warm) in the same season must have resulted from the difference in conditioning temperature.

Dawson and Carey (1976) found that some small birds (American Goldfinches, *Carduelis tristis*) diminish in thermogenic capacity soon after capture (i.e. within a few days) as a result of reduction in some metabolic activity. This argues for using freshly caught birds in acclimation/acclimatization studies when possible. The exclusive use of freshly caught birds, however, forecloses experimentation on mechanisms and regulatory factors of central interest in this study. For the investigation of body temperature (T_b) and oxygen consumption ($\dot{V}O_2$) in relation to air temperature (T_a), a temperature cabinet was constructed of styrofoam-insulated plexiglass in which three metabolism chambers were mounted. Each chamber was large enough to permit free movement and contained a perch upon which the birds could stand in a normal posture. The chamber air temperature could be accurately controlled to within 0.5 C and monitored to 0.1 C. The air flowed through a copper-tube coil submerged in an ethylene glycol bath so as to obtain a temperature equivalent to the wall temperature of the chamber. The chamber temperature could be dropped at the rate of 1 C/min from +40 C to -40 C. One chamber was wrapped with a receiving antenna for telemetry of deep body temperature. The animals could be observed through a double-paned plexiglass window in the top of the cabinet. A small (0.86 g) temperature transmitter surgically implanted in the intraperitoneal cavity was used to monitor and record T_b and also provided a qualitative index of body movement. Details of construction and use were reported in Southwick (1973). Oxygen consumption was measured on a Beckman G-2 paramagnetic oxygen analyzer in an open circuit system described by King (1964). All metabolic measurements were taken on post-absorptive animals in the dark (less than 0.1 lux) at night between 2000 and 0430 to insure minimum metabolic rates (Aschoff and Pohl 1970, Pohl and West 1973). There was no food or water available to the test bird. It was hypothesized that this test period represented a stress that might occur in nature where the coldest temperatures usually occur at night. The birds were weighed to the nearest 0.1 g before and after the test run. The postabsorptive animals were placed in the darkened chamber at 28 C and were allowed 90 min to become accustomed to their surroundings before oxygen consumption measurements were begun. After completion of measurements at 28 C, the chamber temperature was reduced to 5 C at a rate of -1 C/min, where upon another hour was allowed for accommodation, followed by oxygen consumption measurements again. The chamber temperature was then reduced at the same rate to -20 C, followed by a reduction to -35 C with 1-h adjustment periods at each temperature. At any one test temperature, the smallest reduction in oxygen concentration that was maintained for at least 4 min was used for computation of the rate of oxygen consumed (Dawson 1954, King 1964). The animals frequently maintained minimal consumptions for 10 min or more. Each bird was utilized only once to avoid any conditioning effects in subsequent exposures. The experimental design utilized a three-way analysis of variance (AOV) with equal numbers of observations expected in each cell. The two variables were season (winter and summer) and acclimation temperature (+28, +4, and outdoor control). The analysis of data was carried out on the S.U.N.Y. computer utilizing the ANVA3 program. In addition, single-tailed t -tests were run on independent sets of data. All results in the text that are stated to be statistically different are significant at $P < 0.05$ (t - or F -test).

RESULTS

DAILY FLUCTUATION IN INTRAPERITONEAL TEMPERATURE

In winter, the birds generally maintained T_b 1.5 to 2.5 C higher during the daytime than at night (Fig. 1, top). In every case, T_b began to rise before dawn, before any detectable locomotor activity, and began to fall before cessation of activity at dusk. The warm-acclimated birds maintained the lowest T_b during the day, at least before 1400. There is an indication of two levels of regulation (night-day) in all groups and perhaps two daytime levels of regulation in the warm group. The diurnal amplitude of T_b in the winter was greatest in the control animals and less in the warm- and cold-acclimated animals. The difference between nocturnal and diurnal T_b 's was less for all groups in the summer than winter (Fig. 1). The summer day-night variation amounted to about 1.0-1.5 C (vs. 1.5-2.5 C in winter), higher in the day. In the summer the cold-acclimated group held significantly lower T_b 's than warm or control groups. The control group maintained the highest T_b , day and night. In both seasons, the animals acclimated to constant ambient temperatures showed less

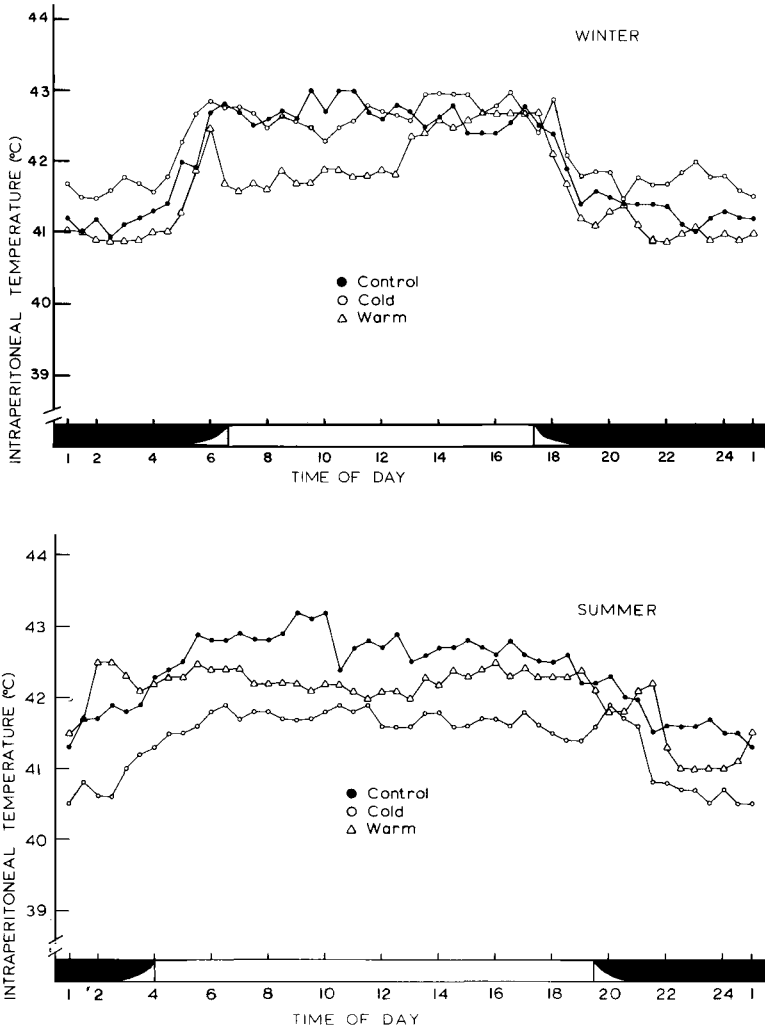


Fig. 1. Telemetered body temperatures of White-crowned Sparrows kept outdoors (control) or acclimated indoors (cold, warm) in winter (January, top), and in summer (June, bottom). The data points are means of 3–6 birds taken from continuous recordings at 0.5-h intervals. Sunrise, sunset, and twilight are indicated on the time scale.

fluctuation in telemetered T_b 's than the outdoor controls, which were encountering fluctuating air temperatures. During summer dawn, the cold and control groups showed a gradual rise in T_b that began 1–1.5 h before sunrise. The warm group showed steep gradients before dawn and after dusk.

RESPONSES TO CONTROLLED TEMPERATURE TESTS

Body temperature.—Body temperature maintained by the birds during exposure to cold differed according to the thermal acclimation histories of the birds. In no winter or summer tests did T_b fall much below 39 C. Only one case of progressive hypothermia was observed, while all other birds maintained T_b . In winter tests,

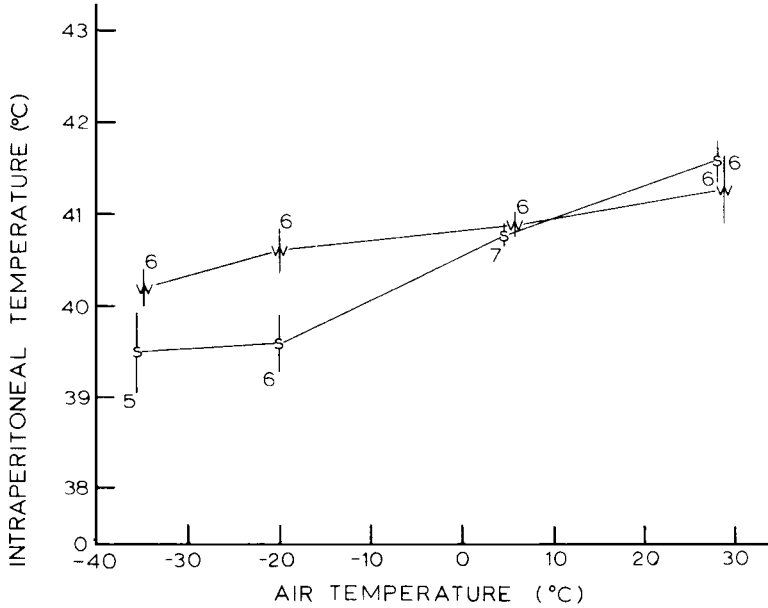


Fig. 2. Steady state telemetered body temperatures of White-crowned Sparrows during nocturnal cold exposure. The letters "w" and "s" represent mean values obtained in winter (January) or summer (June), control, cold, and warm groups combined. The numbers of values in each mean are indicated, and vertical lines indicate ± 1 SE each side of the mean.

birds held under constant temperatures showed larger drops in T_b (ca. 2.5 C) than a single control bird (ca. 0.3 C). Body temperature decreased with decreasing air temperature in birds tested in both summer and winter when the groups were combined without regard to thermal acclimation experience (Fig. 2). At 28 and 5 C, the grouped telemetered temperatures did not differ significantly. However, at -20 C ($P < 0.05$) and -35 C ($0.05 < P < 0.1$), the summer animals had significantly lower T_b than the winter birds.

Oxygen consumption.—Metabolic rates, as indicated by oxygen consumption, increased as air temperature was reduced. The data are plotted in Fig. 3 on a whole animal basis (*per bird*) and with per gram normalization (*per gram*). The mode of expression brings out apparent disparities in the results when they are grouped by season. Whereas the heavier birds tested in winter (mean weight of 28.3 g) showed significantly higher metabolism rates at all exposure temperatures when expressed *per bird*, results expressed *per gram* showed summer birds (mean weight of 26.3 g) with higher (but not significantly higher) rates of metabolism at 5 C and -20 C. Examination of the data by analysis of variance (Table 2) reveals no statistically significant effect of acclimation temperature on metabolic rate as a function of exposure temperature in either season, regardless of the mode of expression (*per bird* or *per gram*). At the extreme cold exposure of -35 C, the warm-acclimated birds had the highest (but not significantly higher) mean rate of metabolism, but lowest mean body temperature.

When the data were plotted *per bird*, the slope of the least squares fit at points below the thermal neutral zone (temperature coefficient) was greater in winter than

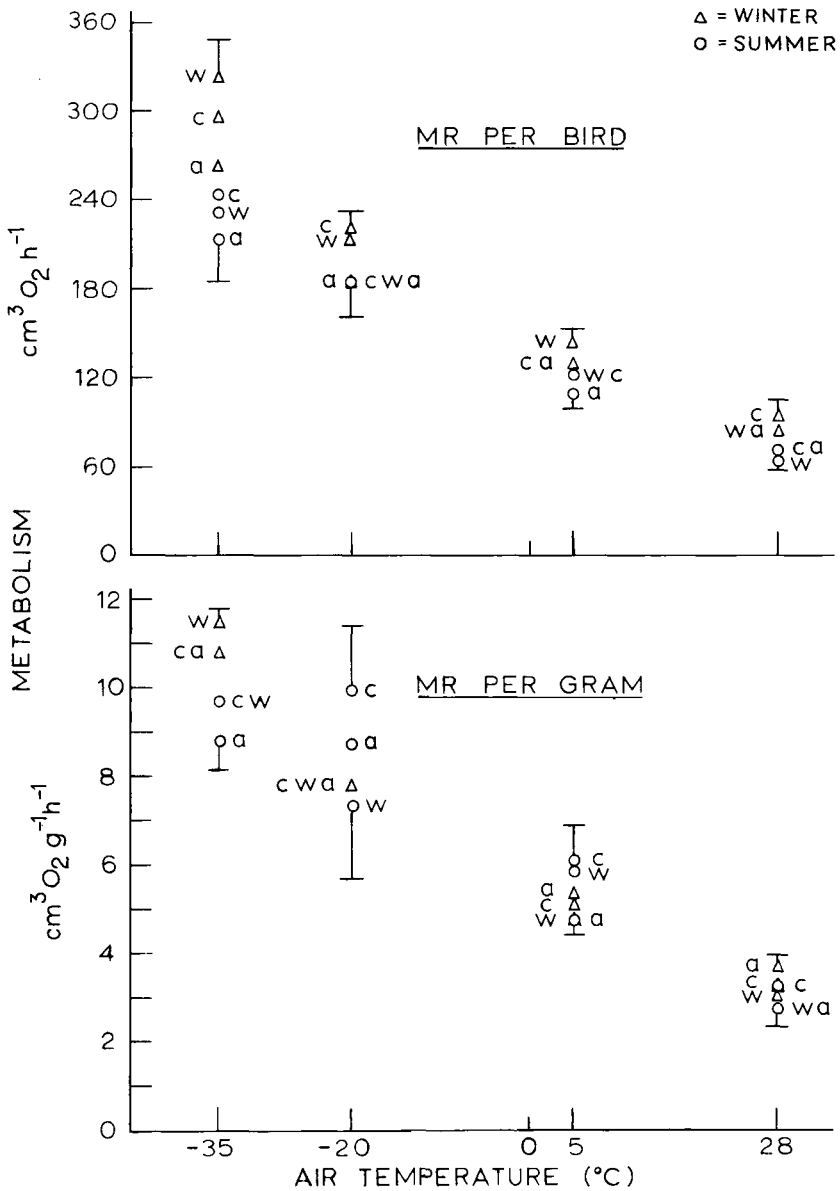


Fig. 3. Metabolic rates (oxygen consumption) of White-crowned Sparrows as a function of air temperature in winter and summer seasons. Data points indicated are means from 3-10 birds tested individually in metabolism chambers. Values obtained in winter (January) are indicated by letters to the left (Δ) and summer mean values to the right (O) of the vertical test temperature line. The letters indicate the acclimation history of the birds represented by that mean (i.e. "w" is warm acclimated, "c" is cold acclimated, and "a" is aviary control). Standard errors of the extreme means are shown as stopped vertical lines. (For conversion to SI units of $W\ kg^{-1}$ multiply $cm^3O_2g^{-1}h^{-1}$ by 5.58.)

TABLE 2. Analysis of variance of metabolic rates of White-crowned Sparrows.^a

Source	Sum of squares	df	Mean square	F ratio
Per bird ($n = 185^b$)				
Main effects				
a. Exposure T	214.873	3	71.624	148.088 ($P < 0.005$)
b. Acclimation T	2.521	2	1.260	2.607
c. Season	10.341	1	10.341	21.381 ($P < 0.005$)
Interactions				
a \times b	1.829	6	0.304	0.630
a \times c	4.312	3	1.437	2.971 ($P < 0.05$)
b \times c	0.602	2	0.301	0.623
a \times b \times c	1.191	6	0.198	0.410
Error within	77.869	161	0.483	
Per gram ($n = 168^b$)				
Main effects				
a. Exposure T	1097.917	3	365.972	127.148 ($P < 0.005$)
b. Acclimation T	6.497	2	3.248	1.128
c. Season	0.491	1	0.491	0.170
Interactions				
a \times b	10.649	6	1.774	0.616
a \times c	37.381	3	12.460	4.329 ($P < 0.01$)
b \times c	9.096	2	4.548	1.580
a \times b \times c	11.422	6	1.903	0.661
Error within	414.475	144	2.878	

^a AOV method incorporating 3-way classification (Winer 1962). Level of significance is shown in parentheses as determined from a table of values of F (Table A.6 in Steel and Torrie 1960). Those F values with no significance levels indicated are not statistically significant (i.e. $P > 0.05$).

^b Different n 's appear because some birds' weights were not known accurately.

summer, yet when plotted *per gram* this difference in slope disappeared. Data expressed *per bird* reveal higher metabolic rates in winter than summer as a main effect that is statistically very significant ($P < 0.005$, Table 2). Yet when the mass differences among birds are factored out, this main effect is no longer significant. The interaction of exposure temperature (28, 5, -20, -35 C) on metabolism as a function of season either *per bird* or *per gram* is significant, but the seasonal difference does not depend on acclimation temperature. In neither mode of expression was there a significant three-way interaction.

Body mass.—The warm- and cold-acclimated birds maintained their body mass during the 3-month acclimation period in early winter, while the controls lost a small but significant amount of mass. The warm-acclimated birds lost a mean of 0.52 g, or less than 2% of their initial body mass. The cold-acclimated birds gained 0.11 g, or less than 0.5% of their body mass. The controls lost 3.9 g, 15% of their initial mass. In the summer 3-month acclimation period, all groups showed some loss in body mass. The loss in the warm- and cold-acclimated animals amounted to 5 and 7%, respectively, while mean loss in the controls was only 1.5% of initial body mass.

DISCUSSION

In this study, increased oxygen consumption was found in the winter birds. Other investigators have also found that small winter birds have higher rates of heat production and are better able to maintain these rates (Gelineo 1934a, b, 1955, 1968; Hart 1962; West 1962; Veghte 1964; Biebach 1975; Weathers and Caccamise 1978).

Gelineo (1968) reported that cold acclimation of only 3 weeks duration resulted in higher metabolic rates in European Goldfinches (*Carduelis carduelis*). The increases found in the present study, however, cannot be assumed to be a result of cold-temperature acclimation, as birds acclimated to constant thermoneutral temperature showed similar increases of metabolism in winter.

Caution must be used in comparisons of literature data on metabolic rate, as the method of expression of results is critical (this study, King 1958, Hart 1962, Pohl 1971). Apparent differing effects were seen in this study at some exposure temperatures when metabolism was expressed on a *per gram* basis versus a *per bird* basis. Exposure to -35 C in winter resulted in significantly greater metabolism than in summer (i. e. *t*-test and interaction between exposure temperature and season showed a significant effect on the basis of *per bird* and *per gram*). The causal agent of this seasonal effect is not known. The enhanced thermogenic capacities at low temperatures in winter may be tied in with increased supplies of fat. As found in other birds, White-crowned Sparrows store fat in winter (West 1960, King et al. 1963, Chaplin 1974). An increased oxidative capacity of active tissues probably did not occur. It is suggested that greater active metabolic mass and ability to mobilize these substrates rapidly during cold stress occurred in winter, as was found in cardueline finches by Carey et al. (1978). This would be indicative of an increased ability in winter to maintain high rates of oxygen consumption, as shown in other small bird species by several investigators and summarized by Weathers and Caccamise (1978).

One summer-tested bird maintained a peak level of MR down to -35 C. However, it did not maintain T_b , which fell to 31.3 C before the bird was removed from the cold chamber. In comparison with the winter group, the summer birds were slightly hypothermic and therefore required somewhat lower rates of metabolism for maintenance of homeothermy (Fig. 2), or perhaps they could not maintain homeothermy at the preferred higher T_b . Body temperatures of all birds fell on exposure to cold, indicating a mode of energy conservation that becomes progressively more prominent as fasting continues. Similar results were shown by Ketterson and King (1977), and reduced cloacal temperatures were noted in wild bird species exposed to cold by Irving (1955), Misch (1960), Hart (1962), and Chaplin (1974). As in the Gray Jay (*Perisoreus canadensis*) (Veghte 1964), summer and winter daytime T_b 's were almost the same, but winter nocturnal T_b 's were much lower, indicating a thermoregulatory adaptation or lack of regulation.

In nature, a number of proximate factors probably affect thermoregulatory responses to cold exposure, including changes in ambient temperature and photoperiod and their interactions. This study revealed increased oxygen consumption and decreased nocturnal body temperature in all winter birds, *regardless* of their previous thermal experience, indicating that White-crowned Sparrows show thermoregulatory response to changing photoperiod. These modes of seasonal change resemble the pattern seen in several other migratory and non-migratory bird species (see Table 3 in Weathers and Caccamise 1978).

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