

## RELATION OF OXYGEN CONSUMPTION TO TEMPERATURE IN THE RED AND WHITE-WINGED CROSSBILLS

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IN a previous report (Dawson and Tordoff, 1959), we discussed problems confronting many small passerines in adjusting to cold, and considered various attributes of finches of the subfamily Carduelinae, which seem highly adaptive to severe winter conditions. We have continued our studies of carduelines, and in this paper describe results of an investigation of certain aspects of temperature regulation of the Red Crossbill (*Loxia curvirostra*) and the White-winged Crossbill (*Loxia leucoptera*).

### MATERIALS AND METHODS

The Red Crossbills used in this investigation are referable to the subspecies *Loxia curvirostra sitkensis*. Birds of this form are resident along the Pacific coast of North America, including islands, from central southern and southeastern Alaska south to northwestern California. However, they may wander widely and have been recorded as far south as Arizona and east to the Atlantic coast. The 28 individuals studied were obtained in the Huron Mountains, Marquette County, Michigan, during a large-scale invasion of the area by crossbills in summer, fall, and winter of 1960.

The White-winged Crossbills studied are referable to the subspecies *Loxia leucoptera leucoptera*. The breeding ranges of the two species overlap widely in North America, although the White-wing ranges considerably farther north than the Red. White-winged Crossbills breed, and are probably resident, from north-central Alaska eastward to central Labrador, and south to the northern tier of states. However, they may wander, chiefly in winter, south to such areas as central Oregon, Colorado, Kansas, West Virginia, and North Carolina. They may also move northward to northern Alaska and Baffin Island. The 12 birds used in this investigation were obtained with the Red Crossbills in the Huron Mountains of northern Michigan.

Metabolic measurements were made on Red Crossbills between late December, 1960, and late March, 1961, and on White-winged Crossbills in March, 1961. Except during experiments, the birds were housed outside in flight cages measuring either  $6 \times 6 \times 9$  feet or  $2 \times 4 \times 6$  feet. In these cages they were exposed to ambient temperatures that were generally below freezing and to natural winter photoperiods for the latitude of Ann Arbor, Michigan (approximately  $42^{\circ}$  N). The crossbills were provided with snow or water for drinking and with food consisting of sunflower seeds, piñon nuts, and hemp seeds. The birds maintained or in-

creased their weight during this investigation and generally appeared in excellent condition.

Each measurement of metabolism reported here was obtained at night on a resting bird that had been at a constant ambient temperature without food for at least five hours. The five-hour equilibration period exceeds that ordinarily used in metabolic studies of small passerines, but crossbills reach a postabsorptive state more slowly than most other birds of comparable weight (approximately 30 g). Metabolism was measured as oxygen consumption, using an open circuit system in which air was passed successively, via tygon tubing connections, from a low-pressure line through a drying train of "Drierite" (anhydrous  $\text{CaSO}_4$ ), a darkened metabolism chamber in which the animal rested, a second train containing Drierite and "Ascarite" (a  $\text{CO}_2$  absorbent), a flow meter, and, finally, a Beckman paramagnetic oxygen analyzer (model G-2). This analyzer was equipped with a multiple-sampling system that permitted the simultaneous use of as many as three metabolism circuits, although in most cases only two were used. Essentially continuous records of oxygen consumption in these three circuits were obtained by use of a Brown strip chart recorder which received the output from the analyzer.

The metabolism chambers in which the birds were housed during experiments were fashioned from new one-gallon or half-gallon paint cans by two simple modifications: a platform of half-inch wire mesh was placed inside each can for the bird to rest upon; the airtight lid of this can was equipped with fittings for the tygon tubing connections of the open circuit system, and with a housing for a thermometer.

The rate of air flow through the open circuit system approximated 525 cc/min (not corrected to standard conditions of temperature and pressure), and the pressure in the metabolism chamber was about 10 mm Hg above ambient pressure, thus approximating 750 mm Hg in most experiments. Air flow was generally adequate to maintain the  $\text{O}_2$  and  $\text{CO}_2$  levels in the chamber above 20 and below 1 per cent, respectively. As soon as a crossbill was in position, the metabolism chamber was placed in a 17 cubic foot constant temperature cabinet for experiments conducted above  $0^\circ\text{C}$ , or in a freezer for those carried out below this temperature. These arrangements served to maintain temperatures within  $0.2^\circ\text{C}$  of the desired level during experiments.

Rates of oxygen consumption by the birds were computed using the appropriate equation from Depocas and Hart (1957). In each case the value used in this equation as the percentage of oxygen in the air leaving the metabolism chamber represented the average of the points recorded at 3-minute intervals over a period of at least 20 minutes in which metabolism proceeded at a steady (maximum acceptable variation in the oxygen

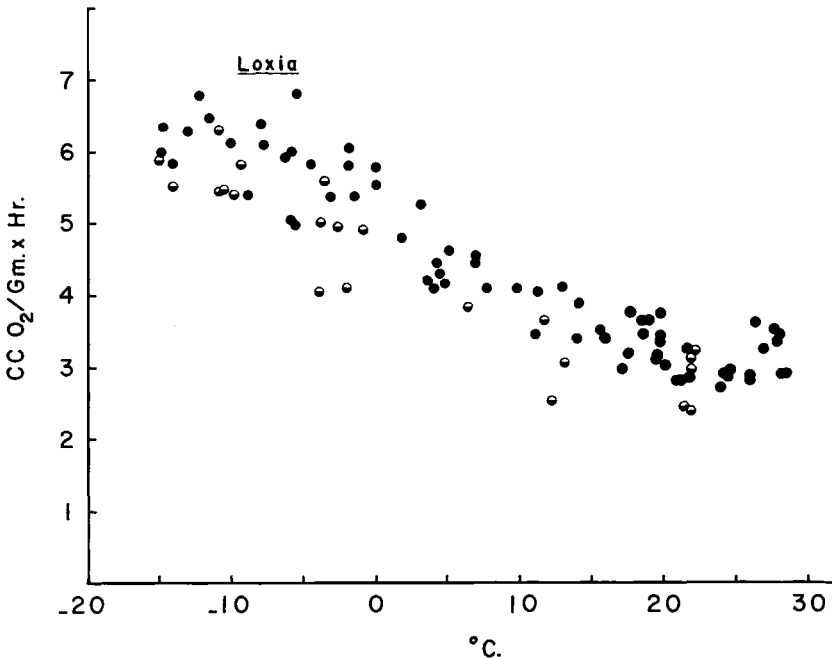


Figure 1. The relation of oxygen consumption to ambient temperature. Shaded circles: data obtained from 28 Red Crossbills. Half-shaded circles: data obtained from 12 White-winged Crossbills.

reading,  $\pm 0.02$  per cent), minimal rate. Sampling of other metabolism circuits was suspended during such periods so that a more detailed record could be obtained. These rates refer to volumes of dry gas under standard conditions of temperature and pressure ( $0^{\circ}\text{C}$  and 760 mm Hg).

Rectal temperatures of crossbills were measured at the conclusion of metabolic experiments, with either a mercury thermometer specially designed for small animal work, or a thermocouple fashioned from 30-gauge copper and constantan wires and enclosed in fine catheter tubing. Only values uncomplicated by activity are discussed.

#### RESULTS

The relation during winter of oxygen consumption of the Red Crossbill to temperature is illustrated in Figure 1. The basal metabolic rate (BMR) of this sample of this species—taken as the mean of the data for temperatures between  $20^{\circ}$  and  $28.5^{\circ}\text{C}$ , a range lying well within the zone of thermal neutrality for this species (see following)—is  $3.1 \text{ cc O}_2/\text{g} \times \text{hr}$  ( $\sigma = 0.33$ ) at this time of year. The birds for which the data on BMR were obtained had a mean weight of 29.4 g ( $\sigma = 4.0$ ).

We have defined the lower critical temperature of the Red Crossbill, that is, the lower limit of the zone of thermal neutrality, as the ambient temperature at which a line fitted to the metabolic values for  $-15^{\circ}$  to  $+10^{\circ}\text{C}$  intersects the level of basal metabolism. This intersection occurs at  $15^{\circ}\text{C}$ . The zone of thermal neutrality of the Red Crossbill must be at least  $15^{\circ}\text{C}$  wide, extending from  $15^{\circ}$  to above  $28.5^{\circ}\text{C}$ , the highest ambient temperature at which measurements were made.

The line fitted to the data for the Red Crossbill between  $-15^{\circ}$  and  $+10^{\circ}\text{C}$  has a slope of  $-0.12 \text{ cc O}_2/\text{g} \times \text{hr} \times ^{\circ}\text{C}$  and extrapolates to zero oxygen consumption at approximately  $40^{\circ}\text{C}$ , an ambient temperature lying within the range of body temperature observed for this bird in the course of the experiments. The essentially linear, inverse relation existing between oxygen consumption and ambient temperature below  $10^{\circ}\text{C}$  seems to give way to a curvilinear relation between  $10^{\circ}$  and  $20^{\circ}\text{C}$ . This suggests that the transition from regulation of body temperature primarily through control of heat loss to regulation primarily through adjustment of heat production occurs over a range of several degrees, rather than abruptly at a single ambient temperature. This also appears to be the case in the Cardinal (*Richmondia cardinalis*) studied by Dawson (1958), the Evening Grosbeak (*Hesperiphona vespertina*) studied by Dawson and Tordoff (1959), and several species discussed by Scholander *et al.* (1950). These findings tend to make designation of a single value for the lower critical temperature something of an abstraction. However, such an abstraction is a useful one from an analytical standpoint.

The relation of oxygen consumption of the White-winged Crossbill to temperature in late winter is also illustrated in Figure 1. Less information was obtained for this bird than for the Red Crossbill. The BMR of the White-winged Crossbill averages  $2.8 \text{ cc O}_2/\text{g} \times \text{hr}$  ( $\sigma = 0.39$ ), on the basis of 5 observations in the vicinity of  $22^{\circ}\text{C}$ . The birds on which these observations were made had a mean weight of  $29.8 \text{ g}$  ( $\sigma = 3.2$ ). Neither the BMR nor the weight of the White-winged Crossbills differs significantly from the corresponding value in the Red Crossbills.

The lower critical temperature of the White-winged Crossbill, defined in the manner described previously for the Red Crossbill, is approximately  $14^{\circ}\text{C}$ . The line fitted to the metabolic values obtained between  $-15^{\circ}$  and  $+10^{\circ}\text{C}$  has a slope of  $-0.11 \text{ cc O}_2/\text{g} \times \text{hr} \times ^{\circ}\text{C}$  and extrapolates to zero oxygen consumption at  $40^{\circ}\text{C}$ . Our data are inadequate to show whether or not the seemingly linear, inverse relation between oxygen consumption and temperature evident below  $10^{\circ}\text{C}$  gives way to a curvilinear one between  $10^{\circ}$  and  $20^{\circ}\text{C}$ , as was the case for the Red Crossbill.

At the conclusion of metabolic experiments conducted at constant ambient temperatures between approximately  $-15^{\circ}$  and  $+28^{\circ}\text{C}$ , the body

TABLE 1  
BASAL METABOLIC RATES OF SEVERAL SMALL PASSERINES

<i>Species</i>	<i>Weight</i> (g)	<i>Basal metabolic rate</i> (cc O <sub>2</sub> /g × hr)	<i>Reference</i>
<i>Chloris chloris</i>	31.1	3.1	Steen, 1958
<i>Fringilla montifringilla</i>	24.8	3.3	Steen, 1958
<i>Passer domesticus</i>	26.0	2.3	Kendeigh, 1944
<i>Passer domesticus</i>	27.3	2.7	Steen, 1958
<i>Emberiza citrinella</i>	26.4	3.1	Wallgren, 1954
<i>Zonotrichia leucophrys</i>	26.4	2.8	King and Farner, 1961
Hypothetical bird	30.0	2.7*	see Brody, 1945
Hypothetical bird	30.0	2.3**	see King and Farner, 1961

\* Predicted from the equation kcal/24 hr = 89 kg<sup>0.64</sup>. Production of 1 kcal is assumed to require the consumption of 0.21 liters of oxygen.

\*\* Predicted from the equation kcal/24 hr = 80.1 kg<sup>0.66</sup>. Production of 1 kcal is assumed to require the consumption of 0.21 liters of oxygen.

temperatures of both Red and White-winged crossbills all fell between 38.5° and 40°C, a range characteristic of small passerines at night in the absence of thermal stress (Dawson, 1954). No trend in these body temperatures was evident with respect to ambient temperature. The fact that crossbills maintained body temperature at a relatively high level in sub-freezing environments is of interest in view of the rather low (30°–38°C) temperatures noted by Steen (1958) in several small passerines studied overnight at low ambient temperatures, after having been freshly removed from winter conditions in the vicinity of Oslo, Norway.

#### DISCUSSION

*Basal metabolism.*—The BMR's of both crossbills considered in this report approximate those of other passerines of similar weight, which have been studied under comparable conditions (Table 1). The basal rates for these two carduelines are also within 20 per cent of the value predicted for a 30 g bird by the equation kcal/24 hr = 89 kg<sup>0.64</sup> (Table 1), the most widely-cited empirical expression of the relation of basal metabolism to body weight in birds (see Brody, 1945). On the other hand, the rates for these two birds exceed by more than 25 per cent the value predicted for a 30 g bird by the equation kcal/24 hr = 80.1 kg<sup>0.66</sup> (Table 1), a more recently developed expression for this relation (see King and Farner, 1961). However, as King and Farner (1961) point out, really precise definition of the relation of basal metabolism to body weight in birds of less than 0.1 kg must await more data for species in this size class.

*Insulation of crossbills.*—In both species of crossbill considered in this report, an apparently linear, inverse relation exists between the values of oxygen consumption and the ambient temperature between –15° and +10°C. The regression line for this relation extrapolates to zero metabo-

lism at a temperature within the normal range of body temperature. These observations indicate that between  $-15^{\circ}$  and  $+10^{\circ}\text{C}$  heat production is directly proportional to the temperature difference between body and environment, and the thermal conductance, and hence the insulation, is constant. This insulation would be difficult to measure directly. However, it can be estimated with reasonable confidence from the slope of the regression line referred to previously. This estimate is expressed in terms of the temperature difference between body and environment required to effect the loss of  $1 \text{ kcal/hr/m}^2$  of body surface. Consumption of  $1 \text{ l}$  of oxygen was taken as indicating the production of  $4.8 \text{ kcal}$ . The value for the surface area of each crossbill was estimated from the equation  $\text{m}^2 = 0.1 \text{ kg}^{0.67}$ . Misch (1960) found that values predicted for the surface area of Blue Jays (*Cyanocitta cristata*) from this equation showed excellent agreement with those obtained by direct measurement.

The estimated insulation of the Red Crossbill is  $0.56^{\circ}\text{C/kcal} \times \text{hr} \times \text{m}^2$ . The corresponding value for the White-winged Crossbill is  $0.62^{\circ}\text{C/kcal} \times \text{hr} \times \text{m}^2$ . The difference does not appear statistically significant.

The estimated insulation of each species of crossbill greatly exceeds the maximum value ( $0.39^{\circ}\text{C/kcal} \times \text{hr} \times \text{m}^2$ ) calculated by Misch (1960, Table 1) for several passerines weighing between  $12$  and  $37 \text{ g}$ . It also approximates or exceeds slightly those which she summarizes for some larger birds:  $0.52^{\circ}\text{C/kcal} \times \text{hr} \times \text{m}^2$  for the  $40 \text{ g}$  Cardinal,  $0.48^{\circ}\text{C/kcal} \times \text{hr} \times \text{m}^2$  for the  $40 \text{ g}$  Snow Bunting (*Plectrophenax nivalis*),  $0.55^{\circ}\text{C/kcal} \times \text{hr} \times \text{m}^2$  for the  $56 \text{ g}$  Evening Grosbeak, and  $0.57^{\circ}\text{C/kcal} \times \text{hr} \times \text{m}^2$  for the  $81 \text{ g}$  Blue Jay. Among the birds for which estimates are available, only the  $64 \text{ g}$  Gray Jay (*Perisoreus canadensis*) and a ptarmigan (*Lagopus* sp.) appear to have appreciably greater insulation, the value for each of these boreal forms being  $0.84^{\circ}\text{C/kcal} \times \text{hr} \times \text{m}^2$ . These comparisons indicate that for their size Red and White-winged crossbills have relatively effective insulation.

*Energy requirements in the cold.*—Even though the insulation of the two crossbills does compare favorably with that of other small birds, it still is inadequate to allow them to maintain a normal level of body temperature in the cold with only a basal rate of heat production, a capacity possessed by a number of larger homeotherms indigenous to cold climates (Scholander, 1955). Indeed, since both of these carduelines have lower critical temperatures in the vicinity of  $+15^{\circ}\text{C}$ , it appears that they must maintain elevated rates of heat production for months in winter. It is not possible with the data at hand to judge the effect of the extra cost of temperature regulation in the cold upon the total energy requirements of crossbills, since part of this cost is probably met merely by more effective conservation of that heat production occurring at all temperatures as a

result of specific dynamic action (calorigenic effect of food) and, perhaps, activity. However, the metabolic rates of these birds at night in the cold and under more moderate temperatures can be compared, since the nutritional state and level of activity of the animals during this period approach those in the metabolic experiments. At average nocturnal temperatures of 0°, -10°, and -35°C, crossbills would have rates 1.5, 2, and 3 times the basal level, respectively. Undoubtedly, the total nightly heat production of birds at the temperatures indicated would usually differ by more than the factors shown from that occurring on milder nights when a basal rate would suffice for maintenance of body temperature. This, of course, follows from the fact that cold conditions are most likely to prevail when nights are relatively long. Maintenance of an elevated metabolic rate over the long winter night in cold climates would seem to represent a major problem in the survival of crossbills, and probably other small passerines as well, since these birds probably cannot forage and replenish their energy reserves in the dark.

At present, it is uncertain how most birds effect any augmentation of heat production required of them in the cold. Cold-acclimated pigeons appear to depend upon increased muscular activity, including shivering (Steen and Enger, 1957). They apparently lack a capacity for non-shivering thermogenesis such as that which develops in rats as acclimation to cold proceeds (Sellers *et al.*, 1954; Hart *et al.*, 1956; Heroux *et al.*, 1956). Hart (1962) found that pigeons paralyzed by curare could not augment their heat production either in response to cold or the calorigenic hormone noradrenaline. Whether any birds are capable of non-shivering thermogenesis remains to be determined.

*Behavior and ecology.*—In view of the apparent demands made upon the energy resources of crossbills by cold weather, it is useful to review some aspects of their behavior and ecology which might reduce the effect of a cold environment and facilitate procurement of food during the short days of the northern winter. The social foraging habits which crossbills share with other carduelines facilitate discovery of food available from fruiting conifers and other trees, which may occur in widely scattered groups. These birds often remain in compact flocks while feeding, so that dispersal of individuals from good sources of food is minimized. Moreover, they will regularly call to passing flocks of the same species, and these individuals thereby gain an opportunity to share the food.

Crossbills and other carduelines are capable of storing relatively large amounts of food in a well-developed crop, a structure which is small or lacking in birds of related groups. This large storage capacity is probably responsible for the slowness with which the crossbills used in these stud-

ies reached a post-absorptive state. Such a capacity would be of great value in allowing these birds to maintain elevated metabolic rates overnight without serious depletion of their bodily reserves of energy.

Many small birds wintering in cold climates appear to evade extreme winter conditions by roosting in sheltered places. The use of holes in trees by chickadees (*Parus*) and nuthatches (*Sitta*) is an example of this. Such behavior probably allows the animals to pass the night at higher temperatures than would otherwise be possible and restricts radiational losses of heat, particularly to the night sky. Little is known about the roosting habits of carduelines. However, the behavior of captive birds suggests that Red Crossbills in nature may roost within the foliage of conifers, which should offer some protection from cold (Tordoff, 1954).

A number of features of the breeding biology of crossbills and other carduelines seem to be adaptive to cold climates. There is nearly continuous incubation of eggs and brooding of newly-hatched young by the female, which is fed at the nest by the male. This high level of attentiveness must facilitate the maintenance of relatively high nest temperatures in those species nesting in cold weather, as Irving and Krog (1956) have noted in a redpoll (*Acanthis* sp.), for example. The capacity of the young of some carduelines to thrive on vegetable matter provided them through regurgitation by the parents is also of significance here, for it makes breeding largely independent of a supply of insects, which may be difficult to obtain in cold weather. In at least some members of this subfamily, breeding seems largely keyed to the availability of seed crops, irrespective of season. Crossbills provide the best example of this. The timing of reproduction seems largely independent of photoperiod in these birds—breeding taking place when adequate concentrations of food, usually pine seeds, are found. Red Crossbills have been observed to nest in every month of the year, in such widely separated places as Maine and Colorado. In the latter, the peak of the breeding season is often in mid-winter. The success of this species in solving the energetic problems posed by cold weather is eloquently demonstrated by its ability to reproduce successfully during the shortest days of the year at temperatures ranging from +7° to -23°C, and with up to several feet of snow on the ground (Bailey *et al.*, 1953).

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#### SUMMARY

In winter the Red Crossbill (*Loxia curvirostra sitkensis*) has a basal metabolic rate of  $3.1 \text{ cc O}_2/\text{g} \times \text{hr}$ , and a lower critical temperature of  $15^\circ\text{C}$ . The transition from regulation of body temperature primarily by adjustment of insulation to regulation primarily by control of heat production occurs over a range of several degrees rather than abruptly at  $15^\circ\text{C}$ . An essentially linear, inverse relation exists between oxygen consumption by the Red Crossbill and ambient temperature between  $-15^\circ$  and  $+10^\circ\text{C}$ ; the slope of the regression line for this relation is  $-0.12 \text{ cc O}_2/\text{g} \times \text{hr} \times ^\circ\text{C}$ .

The White-winged Crossbill (*Loxia l. leucoptera*) has a basal metabolic rate of  $2.8 \text{ cc O}_2/\text{g} \times \text{hr}$  during winter, a value not differing significantly from that for the Red Crossbill. The basal metabolic rates of both of these 30 g birds are similar to those of other passerines of comparable size. The White-winged Crossbill has a lower critical temperature of  $14^\circ\text{C}$ . As in the Red Crossbill, an essentially linear, inverse relation exists between oxygen consumption and ambient temperature between  $-15^\circ$  and  $+10^\circ\text{C}$ ; the slope of the regression line for this relation is  $-0.11 \text{ cc O}_2/\text{g} \times \text{hr} \times ^\circ\text{C}$ .

Estimated values for the maximum insulation of the Red and White-winged crossbills are  $0.56^\circ\text{C}/\text{kcal} \times \text{hr} \times \text{m}^2$  and  $0.62^\circ\text{C}/\text{kcal} \times \text{hr} \times \text{m}^2$ , respectively. Comparisons with several other species indicate that these birds have relatively effective insulation for their size.

When metabolic experiments were concluded, in the middle of the night, body temperatures of the crossbills all were between  $38.5^\circ$  and  $40^\circ\text{C}$ , although the range of ambient temperatures was  $-15^\circ$  to  $+28^\circ\text{C}$ .

Since the lower critical temperatures of crossbills greatly exceed the ambient temperatures that they encounter regularly in winter in many areas, they must augment their heat production at this season. This probably requires an increased intake of food when the daylight period for feeding is shortest. Several aspects of the behavior and ecology of crossbills (and of other carduelines), seem to help them contend with this situation. Their social foraging habits and strong flight may facilitate location and exploitation of food. Their well-developed crops should enable them to store relatively large amounts of food at nightfall. Utilization of various types of shelter may help them to evade the full impact of the cold at night. The capacity of young crossbills to thrive on vegetable matter makes them largely independent of insect food, difficult to obtain in the cold weather in which breeding often occurs.

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