RELATION OF OXYGEN CONSUMPTION TO TEMPERATURE IN THE EVENING GROSBEAK

By WILLIAM R. DAWSON and HARRISON B. TORDOFF

Information now at hand indicates that most larger birds and mammals living in cold climates have adapted to them through extensive capacities for heat conservation. These capacities permit the animals to maintain body temperatures at normal levels with a minimal rate of heat production even under extreme conditions (Scholander, 1955). This economical mode of climatic adaptation does not appear to have been utilized by small birds (Scholander *et al.*, 1950*b*; Dawson, 1958), but information is limited on physiological responses of species which actually encounter severe and prolonged cold weather in nature. Therefore, we welcomed an opportunity to study the eastern race of the Evening Grosbeak (*Hesperiphona vespertina vespertina*), which winters in cold climates. Our studies of this species permit definition of its basal metabolic rate and lower limit of thermal neutrality, comment upon its temperature regulation in cold environments, and consideration of the bioenergetic problems which confront it and other small birds in winter.

ACKNOWLEDGMENTS

We are grateful to Nicholas L. Cuthbert for supplying us with 20 Evening Grosbeaks freshly trapped at his banding station near Mount Pleasant, Isabella County, Michigan, during February, 1958. Our study on these birds was supported in part by grants from the National Science Foundation (G–2096) and from the Horace H. Rackham School of Graduate Studies, The University of Michigan.

MATERIALS AND METHODS

Birds of the eastern race of the Evening Grosbeak breed from northern Alberta and New Brunswick south to central Alberta, Canada, and the northern parts of Minnesota, Michigan, New York, and New England. They winter throughout the breeding range and, sporadically, south to Kansas, Arkansas, Tennessee, and the Carolinas. Although nesting in northern regions in which coniferous forests predominate, the Evening Grosbeak is much less closely associated with conifers than are some other members of its group, the subfamily Carduelinae. A variety of trees, including hardwoods, are used for nesting sites. Important food plants include, in addition to conifers, various wild cherries (*Prunus*), box elder (*Acer negundo*), and many other kinds of deciduous trees and herbaceous seed-bearing plants.

Metabolic measurements were made on 16 birds—7 males and 9 females—between February 24 and April 5, 1958. During this period the birds, when they were not being used in experiments, were housed outside in a large flight cage measuring 6×6×9 feet or in a smaller one measuring 2×4×6 feet. The grosbeaks were provided with snow or water for drinking and with food consisting of sunflower seeds and chicken scratch. The birds maintained their weight or became slightly heavier while in captivity. All except those purposely sacrificed were in excellent condition when released six months after capture.

The measurements of oxygen consumption reported here were made at night on resting birds that had been without food for at least three hours. An open circuit system was used in which air from a low pressure line passed successively, via tygon tubing connections, through a drying train of "Drierite" (anhydrous $CaSO_4$), a darkened metabolism chamber in which the animal rested, a second train containing a carbon dioxide absorbent

("Ascarite") as well as Drierite, a flow meter, and, finally, a Beckman paramagnetic oxygen analyzer (Model F–2). This analyzer was equipped with a multiple sampling system which allowed use of up to 3 metabolism circuits simultaneously. The metabolism chambers were fashioned from new, one gallon paint cans by two simple modifications: horizontal platforms of ½-inch wire mesh on which the birds could perch during the experiments were placed inside the cans, 3 cm. from the bottom; the airtight lids of these cans were equipped with fittings for tygon tubing connections and with a housing for a thermometer.

The rate of air flow through this open circuit system was approximately 550 cc./min. (not corrected to standard conditions of temperature and pressure), and the pressure in the chamber was about 12 mm. Hg above atmospheric pressure, thus approximating 750 mm. Hg absolute pressure during most of the experiments. The rate of air flow was generally adequate to maintain the oxygen and carbon dioxide levels above 20 and below one per cent, respectively. It also kept the relative humidity below 40 per cent at experimental temperatures above 20°C. Temperature within the chambers was maintained within 0.2°C. of the desired level by keeping them in a 17 cu. ft. constant-temperature cabinet for experiments conducted above 0°C. or in a freezer for those below that temperature.

True rates of oxygen consumption by the birds were computed with the method described by Depocas and Hart (1957) for the above type of metabolism system. All gas volumes specified for metabolism have been corrected to standard conditions of temperature and pressure (0°C. and 760 mm. Hg).

The oxygen analyzer was used in conjunction with a recording potentiometer, so that a continuous record of the fractional concentration of oxygen in the air leaving the metabolism chamber could be obtained. This record was useful in the detection of restlessness and in the determination of the time at which metabolic rate had declined to a minimal level for the particular experiment.

A few measurements of respiratory quotient (RQ) were made at the close of metabolism experiments with a method outlined by Peters and Van Slyke (1946). Data on body temperature reported in this paper were obtained with copper-constantan thermocouples fashioned from 30 gauge duplex wire. Those thermocouples employed for determination of deep body temperature were inserted through the cloaca into the large intestine. They were held in place by fastening the lead wires to the tail feathers with stiff paper and staples. The thermocouples used to obtain subcutaneous temperatures were initially fitted with lead wires only a few inches long. One of these wires was threaded through a needle and then sewn through the skin on the breast in such a manner that the thermocouple junction was brought beneath one of the ventral feather tracts. The lead wires were then bent so that the junction was immobilized at the desired position. These wires were then connected to the appropriate sides of a longer duplex lead. This duplex lead was anchored to the dorsal feather tract with thread. The bird with its two thermocouples in position was then placed in a small screen cage in which it could stand but neither move forward or backward, nor turn around. This cage could then be placed in a darkened freezing compartment and the skin and body temperatures of the bird followed during the several hours of the experiment.

RESULTS

Oxygen consumption.—The relation of oxygen consumption of the Evening Grosbeak during winter and early spring to environmental temperature is illustrated in figure 1. The basal metabolic rate (BMR) of this bird—taken as the mean of the data for temperatures between 20°C. and 31°C., a range lying well within the zone of thermal neutrality (see following)—is 2.5 cc. 0_2/gm./hr. ($\sigma = 0.23$) at this time of year. The lower limit of thermal neutrality ("lower critical temperature"), which we have defined as the temperature at which the line fitted to the points between −16° and +10°C. reaches the level of 2.5 cc. 0_2/gm./hr. (the BMR), is 16°C. Therefore the zone of thermal neutrality for this species is at least 18°C. wide, extending from 16°C. to at least 34°C., the highest temperature at which measurements were made.

As shown in the figure, the line fitted to the points between −16°C. and +10°C. extrapolates to zero oxygen consumption at 41°C., a temperature lying within the normal range of body temperature for this species. We shall subsequently discuss the implications of this fact. The essentially linear, inverse relation which exists between oxygen consumption and environmental temperature at temperatures between −16°C. and approximately +12°C., seems to give way to a curvilinear relation in the vicinity of 16°C. which we have defined as the lower critical temperature. This suggests that the transition from regulation of body temperature primarily through control of heat loss to regulation through adjustment of heat production occurs over a range of several degrees of environmental temperature, rather than abruptly at a single temperature. This also appears to be true in the Cardinal, *Richmondena cardinalis* (Dawson, 1958), and in some other species discussed by Scholander *et al.* (1950*b*:253). It makes the designation of a single value for the lower critical temperature somewhat an abstraction, but it is a useful one from a theoretical standpoint. It was because of this apparent departure from linearity in the vicinity of the lower critical temperature that data for temperatures above 10°C. were not used in fitting the regression line referred to above.

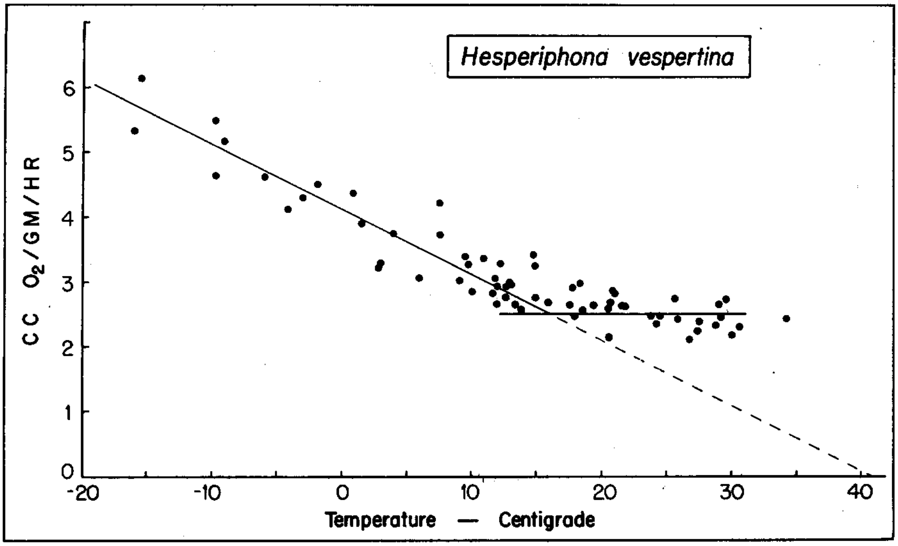

Fig. 1. The relation of oxygen consumption to environmental temperature in the Evening Grosbeak between late February and early April.

Respiratory quotient of fasting birds.—The respiratory quotient (RQ) was determined for six Evening Grosbeaks that had fasted at temperatures between 25°C. and 27°C. for 3 to 12 hours, to facilitate selection of a proper caloric equivalent for oxygen for use in certain calculations presented in the subsequent section of this report. It was assumed that the RQ of fasting animals would be independent of temperature except in warm environments. This assumption appears justified on the basis of Irving *et al.*'s (1955) measurements on the Northwestern Crow (*Corvus caurinus*). The mean RQ for the grosbeaks uncorrected for protein metabolism is 0.735 (σ=0.039). The value obtained for one bird, 0.66, was much lower than those for the others, which were all above 0.70. This low value does not appear to be an artifact as it was checked twice. According to King (1957), RQ's between 0.65 and 0.71 are normal and fairly common in birds fasting under experimental conditions. As a result of the mean value obtained for the RQ, a caloric equivalent of 4.7 cal./cc. 0_2 will be used in the subsequent calculations.

Body temperatures.—Measurements of skin temperature were made on four birds at the conclusion of experiments on oxygen consumption, by placing a fine thermocouple on one of the ventral feather tracts just as the animal was removed from the metabolism chamber. These indicated skin temperature to be relatively uniform, ranging between 35.5°C. and 38°C. at environmental temperatures from 15.8°C. down to −13.6°C. The results of two experiments in which implanted thermocouples were employed on birds confined within a wire cage in a freezing compartment also indicated skin temperature to be maintained at a high level in the cold. During an exposure of 4 hours to −8°C., one of these individuals maintained body temperature at 40.6°C. and skin temperature between 39.3°C. and 38.4°C. During an exposure of 2 hours to −12.9°C., a second bird maintained body temperature between 40.8°C. and 41.5°C. and skin temperature between 38.0°C. and 39.6°C. The somewhat higher values noted here probably reflect the fact that in these two instances the thermocouples were beneath the skin, whereas in those four cases mentioned above they were in contact with its outer surface. The maintenance of skin temperature at a high level over a wide range of environmental conditions suggests that the plumage is the major instrument of insulation for the main portion of the body in Evening Grosbeaks.

DISCUSSION

Basal metabolism.—The value obtained for the BMR of the Evening Grosbeak during winter and early spring, 2.5 cc. 0_2/gm./hr., is in close agreement with the few other values available for passerine birds in the same size range (50–65 gm.) and with that predicted by Brody's equation relating BMR to body weight in birds generally (Brody, 1945; Scholander *et al.*, 1950*a*; Dawson, unpublished observations). This suggests that the adjustment of this boreal species to winter conditions does not entail elevation of the BMR, although measurements at other seasons are necessary to resolve this conclusively. The scanty evidence available (see Dawson, 1958) indicates that BMR of birds existing under natural conditions is not influenced by seasons, although it can undergo considerable modification in response to experimental conditions involving prolonged exposure to constant low or high temperatures (Gelineo, 1955). These observations illustrate the dichotomy, discussed by Hart (1957) and Fry (1958), between the natural process of seasonal acclimatization and laboratory-induced acclimation.

Lower critical temperature and energy requirements in the cold.—The fact that the Evening Grosbeak actually encounters severe winter conditions in nature renders its physiological responses to temperature of considerable comparative interest. The lower critical temperature of this bird, 16°C., is at least 6°C. lower than those reported for most other passerines weighing less than 75 gm. (see Dawson, 1958, table 1), excepting the Cardinal (*Richmondena cardinalis*), the Snow Bunting (*Plectrophenax nivalis*), and the Gray Jay (*Perisoreus canadensis*), for which the lower critical temperatures are 18°C., 10°C., and between 0°C. to −10°C., respectively. The relatively high critical temperatures of the grosbeak and other small birds which encounter low temperatures in nature provide support for the view that small and medium-sized passerines existing in cold climates must sustain elevated rates of heat production for long periods of time. Even the Gray Jay with its relatively low critical temperature must augment its heat production during winter if body temperature is to be maintained at normal levels, for it frequently encounters temperatures below −10°C. at this season in the northern regions which it inhabits.

The fact that the Evening Grosbeak must resort to increased heat production for maintenance of body temperature in cold environments prompts estimation of the metabolic rate required under various thermal conditions. This can easily be accomplished graphically or with knowledge of the critical thermal gradient (the difference between body temperature and the lower critical temperature), which is 25°C. for this species. Doubling of the basal rate of heat production would, if overall insulation remained at the level existing at the lower critical temperature, permit maintenance of body temperature at 41°C. in an environment at −9°C.; the 50° difference between these temperatures representing twice the critical thermal gradient. Trebling the basal rate of heat production would allow the animal to remain at 41°C. in an environment at −34°C.; the 75° difference between these temperatures representing three times the critical thermal gradient. Obviously, under natural conditions, rate of air movement, factors affecting radiational losses, and others, would make modification of the above estimates necessary. However, they are useful for indicating in a general way the extent of the energetic problems posed to the Evening Grosbeaks by cold.

The apparent necessity of this species for augmenting its heat production during winter raises an important question for future investigation. This concerns the nature of the mechanisms responsible for maintaining thermogenesis at elevated levels for prolonged periods. Recent work by Sellers, Scott, and Thomas (1954); Hart, Heroux, and Depocas (1956); and Heroux, Hart, and Depocas (1956), for example, has shown that there is a reduction of shivering accompanied by increased heat production in rats during chronic exposure to cold. This indicates that mechanisms for chemical regulation of metabolism, rather than increased muscular activity, are primarily responsible for maintenance of elevated heat production in these animals when cold-acclimated. Relatively little is known of this subject in birds. Steen and Enger (1957) found that short-term adjustment of heat production to cold in pigeons depended upon shivering. Unpublished observations by Hart mentioned in his review paper (1958) suggest that shivering is the primary mechanism for heat production in winter acclimatized birds. When paralyzed by curare, such animals cannot augment their heat production in response to either the calorigenic hormone noradrenaline or cold.

Estimation of thermal conductivity.—A number of authors, notably Scholander *et al.* (1950*b*), have discussed the principles governing heat exchange of homeothermic animals in relation to environmental temperature. In the generalizations which have been developed, the homeotherm is regarded as a heat machine with a certain minimal heat production which pertains in the range of environmental temperature known as the zone of thermal neutrality. Within this zone heat loss can be maintained at the same level as the minimal heat production by adjustment of overall insulation, that is, through vasomotor activity and through adjustment of the plumage or pelage. This overall insulation is considered to reach a maximum at the lower limit of the zone of thermal neutrality, the lower critical temperature. At environmental temperatures lower than this, thermal balance is maintained by increasing heat production.

By use of a simple physical model and by careful analysis of data on insulation and on the relationship between metabolism and environmental temperature in a number of homeotherms, Scholander and his associates (1950*a*) have shown that the difference between central body temperature and the lower critical temperature, the critical gradient $T\Delta_c$, is proportional to the basal rate of heat production and to the maximum value for overall insulation. Likewise they have also shown that the heat production below thermal neutrality is proportional to the temperature difference between body and environment, in accordance with Newton's Law of Cooling. It is assumed that the slope of the curve relating metabolism and temperature below thermal neutrality is related to the maximal overall insulation—the greater the insulation the more shallow the slope.

The observed relation between metabolism and temperature for the Evening Grosbeak conforms quite well to the generalizations previously outlined. We do not regard the gradual transition from regulation of body temperature through control of heat loss to regulation by adjustment of heat production as a serious deviation. Heat production below thermal neutrality is proportional to the temperature difference between body and environment, as indicated by the linear relation between oxygen consumption and environmental temperature below thermal neutrality, and by the fact that the regression line fitted to the data between −13°C. and +10°C. extrapolates to zero rate of metabolism at a temperature falling within the normal range of body temperature for this species. This implies that the insulation of the grosbeaks does not change below thermal neutrality (see "Results") and that a single constant, that for the slope of the regression line, can be used as a basis for calculation of heat loss incurred with overall insulation at a maximum, per unit of body surface (we have employed the formula $m^2=0.1\ Kg^{2/3}$ for estimating the surface area), per degree of temperature difference between the core of the body and the environment, per unit of time. We shall refer to the heat loss expressed in these terms as the thermal conductivity of the Evening Grosbeak, in line with the usage of Morrison and Tietz (1957). It amounts to 1.8 kcal. $m^{-2}\ {}^\circ C.^{-1} hr.^{-1}$ in this bird. This value is only about two-thirds those reported by Morrison and Ryser (1953), for the thermal conductivity of two Wisconsin mammals of comparable size, a vole (*Microtus*), and a weasel (*Mustela*).

Behavior and ecology.—In view of the heightened energy requirements of the Evening Grosbeak in the cold, it is important to review those aspects of its behavior and ecology which facilitate procurement and storage of food during the short days of the northern winter, or those which tend to reduce the impact of the winter environment. It will also be appropriate in this review to consider pertinent information on other members of the subfamily Carduelinae.

The social foraging habits and strong flight of carduelines facilitate discovery of food afforded by fruiting conifers and other trees, which often occur in widely scattered groups. These birds feed in well-integrated flocks, which habit tends to miminize dispersal of individuals away from good food sources. Feeding birds regularly will call to passing flocks comprised of individuals of the same species, which thus gain an opportunity to share in the food. The nomadic wanderings in winter of many carduelines, including the Evening Grosbeak, regularly involve distances of hundreds of miles, and apparently represent an effective means of enhancing discovery and exploitation of food.

The Evening Grosbeak and other carduelines are capable of storing relatively large amounts of food in the crop, which is well developed in them and small or absent in birds of related groups. Such storage capacity must be of considerable importance in allowing the birds to maintain an elevated metabolic rate overnight in the cold. The storage capacity of the crop is augmented in the breeding season in certain species by the development of buccal pouches, which have been reported in *Leucosticte tephrocotis* (Miller, 1941), *L. atrata,* and *Pinicola enucleator* (French, 1954).

We attempted to measure the crop capacity of Evening Grosbeaks by sacrificing captive birds at dusk and weighing crop contents. Two birds examined on May 14 without any preliminary period of fasting had nearly empty crops and were very fat (75.5 and 76.8 grams). We then starved a male, but provided it with water, for eight days, in order to induce it to fill its crop with sunflower seeds. After a feeding period of an hour, its crop contained 12 sunflower seeds weighing 1.85 grams which occupied a volume equivalent to approximately ⅘ the total capacity of this structure. Sunflower seeds consist of 28 per cent fat, 19 per cent protein, and, presumably, about 44 per cent carbohydrate, judging from figures given in "The Handbook of Biological Data." The total combustion of these materials in 2.3 gm. of sunflower seeds, which should approximate the crop capacity of the individual referred to above, could be expected to yield about 12.7 kcal. If the net energy of this amount of sunflower seeds is assumed to be 50 per cent of the combustion value, as seems reasonable from various studies of nutrition (Brody, 1945), this would provide the bird with approximately 6.4 kcal. At an environmental temperature of −9°C., the heat production of a fasting grosbeak would amount to approximately 1.3 kcal./hr. At this rate the 6.4 kcal. would be expended in slightly less than 5 hours. The remaining energy to carry the bird through the night would have to come from food in other portions of the digestive tract at nightfall and from body reserves of carbohydrate, fat, and perhaps protein. The crop capacity of the Evening Grosbeak may be greatly exceeded by that of certain other carduelines; a Pine Grosbeak weighing 81 gm. was observed to have nearly 6 gm. of staminate catkins from jack pine (*Pinus banksiana*) in its crop (Butsch, 1957).

Many small birds wintering in the north appear to evade winter conditions at the extreme by roosting in sheltered places. The use of holes in trees by chickadees (*Parus*) and nuthatches (*Sitta*) is an example. Little is known of the roosting habits of carduelines, but roosting sites are probably in thick vegetation. Mrs. Doris H. Speirs tells us that she has seen Evening Grosbeaks leaving a dense clump of conifers very early in the morning. Judging by the behavior of captive birds, crossbills (*Loxia*) may roost in thick terminal clusters of pine needles (Tordoff, 1954:350). The amount of protection afforded by these roosting places has not been measured, but it must be considerable.

Several features of the breeding biology of carduelines seem favorable to existence in 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 warm nest temperatures despite near-freezing air temperatures noted in the redpoll (*Acanthis*), for one, by Irving and Krog (1956). The capacity of the young to thrive on vegetable matter provided them through regurgitation by the parent is also of interest here, for it makes the breeding of members of this group largely independent of a supply of insects, which may be scarce or lacking in cold weather. In at least some species of carduelines, breeding seems primarily keyed to the availability of seed crops, irrespective of the time of year. Crossbills appear to provide the best example of this. The breeding of these birds seems wholly independent of day length, taking place when adequate concentrations of food, usually pine seeds, are found. Nesting of this species has been reported for every month of the year in such widely separated places as Maine and Colorado. In Colorado, the peak of nesting is often in midwinter. The success of this species in solving its energy problems in cold weather is eloquently demonstrated by its ability to reproduce successfully during the shortest days of the year, at temperatures ranging from 7°C. to −23°C., with up to several feet of snow on the ground (Bailey, Niedrach, and Baily, 1953:24, 33).

Carduelines offer intriguing opportunities for studies of cold adaptation, for they possess many attributes which seem to make them, as a group, better adjusted to cold than related passerines.

SUMMARY

This study of the effects of temperature upon oxygen consumption and body and skin temperatures of the Evening Grosbeak was undertaken in an effort to learn how small birds cope with extreme cold in nature. The basal metabolic rate for this bird, 2.5 cc. 0_2/gm./hr., is similar to those of other passerines of comparable size (50–65 gm.). The grosbeak can through adjustment of its overall insulation maintain heat loss equal to its minimal heat production at environmental temperatures down to 16°C. which has been designated its lower critical temperature. Below 16°C. heat loss increases and normal body temperature can only be maintained by elevation of heat production from the minimal level at the rate of 1.8 kcal. per m^2 of body surface per degree lowering of environmental temperature per hour. This rate is only about two-thirds those noted for mammals of similar size, which indicates that the grosbeak surpasses them in the effectiveness of its overall insulation. Cooling of peripheral tissues does not appear to contribute significantly to this insulation, for skin temperature of this bird was maintained within 3°C. to 6°C. of body temperature even at subfreezing environmental temperatures.

The fact that the lower critical temperature of the Evening Grosbeak is well above the temperatures it regularly encounters in nature during winter means that it must in its temperature regulation resort to augmentation of its heat production at this season. This requires increased food intake when food is likely to be in shortest supply and the daylight hours for feeding most limited. A number of aspects of the behavior and ecology of the Evening Grosbeak, and of other carduelines as well, seem well suited for allowing them to contend with this situation. The social foraging habits and strong flight of these birds must facilitate location and exploitation of food. Their well developed crops must enable them to store prior to nightfall relatively large quantities of food. They may evade the full impact of their environment at night by utilizing various types of shelter. The capacity of young carduelines to thrive on vegetable matter makes them largely independent of a supply of insects, which might be scarce or lacking in the cold weather in which some species, notably crossbills, have been observed to breed.

LITERATURE CITED

Bailey, A.M., Niedrach, R. J., and Baily, A. L.
1953. The red crossbills of Colorado. Denver Mus. Nat. Hist., Mus. Pictorial No. 9, 64 pp.
Brody, S.
1945. Bioenergetics and growth (Reinhold Publ. Corp., N.Y.).
Butsch, R. S.
1957. Notes on the winter birds of Sugar Island, Michigan. Jack-Pine Warbler, 35:14–19.
Dawson, W. R.
1958. Relation of oxygen consumption and evaporative water loss to temperature in the cardinal. Physiol. Zool., 31:37–48.
Depocas, F., and Hart, J. S.
1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open-circuit systems and in a short-lag, closed-circuit apparatus. Jour. Appl. Physiol., 10:388–392.
French, N. R.
1954. Notes on breeding activities and on gular sacs in the pine grosbeak. Condor, 56:83–85.
Fry, F. E. J.
1958. Temperature compensation. Ann. Rev. Physiol., 20:207–224.
Gelineo, S.
1955. Tempèrature d'adaptation et production de chaleur chez les oiseaux de petite taille. Arch. Sci. Physiol., 9:225–243.

Hart, J. S.
1957. Climatic and temperature induced changes in the energetics of homeotherms. Rev. Can. Biol., 16:133–174.
1958. Metabolic alterations during chronic exposure to cold. Fed. Proc., 17:1045–1054.
Hart, J. S., Heroux, O., and Depocas, F.
1956. Cold acclimation and the electromyogram of unanesthetized rats. Jour. Appl. Physiol., 9:404–408.
Heroux, O., Hart, J. S., and Depocas, F.
1956. Metabolism and muscle activity of anesthetized warm and cold acclimated rats on exposure to cold. Jour. Appl. Physiol., 9:399–403.
Irving, L., Krog, H., and Monson, M.
1955. The metabolism of some Alaskan animals in winter and summer. Physiol. Zool., 28:173–185.
Irving, L., and Krog, J.
1956. Temperature during the development of birds in arctic nests. Physiol. Zool., 29:195–205.
King, J. R.
1957. Comments on the theory of indirect calorimetry as applied to birds. N.W. Sci., 31:155–169.
Miller, A. H.
1941. The buccal food-carrying pouches of the rosy finch. Condor, 43:72–73.
Morrison, P. R., and Ryser, F. A.
1953. Temperature and metabolism in some Wisconsin mammals. Fed. Proc., 12:100–101.
Morrison, P. R., and Tietz, W. J.
1957. Cooling and thermal conductivity in three small Alaskan mammals. Jour. Mamm., 38:78–86.
Peters, J. P., and Van Slyke, D. D.
1946. Quantitative clinical chemistry. 2nd ed. (William and Wilkins Co., Baltimore).
Scholander, P. F.
1955. Evolution of climatic adaptation in homeotherms. Evolution, 9:15–26.
Scholander, P. F., Hock, R., Walters, V., and Irving, L.
1950*a*. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull., 99:259–271.
Scholander, P. F., Hock, R., Walters, V., Johnson, F., and Irving, L.
1950*b*. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull., 99:237–258.
Sellers, E. A., Scott, J. W., and Thomas, N.
1954. Electrical activity of skeletal muscle of normal and acclimatized rats on exposure to cold. Amer. Jour. Physiol., 177:372–376.
Spector, W. S. (ed.)
1956. Handbook of biological data (W. B. Saunders Co., Phila.).
Steen, J., and Enger, P. S.
1957. Muscular heat production in pigeons during exposure to cold. Amer. Jour. Physiol., 191:157–158.
Tordoff, H. B.
1954. Social organization and behavior in a flock of captive, nonbreeding red crossbills. Condor, 56:346–358.

Department of Zoology and Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, April 17, 1959.