METABOLISM AND SURVIVAL TIME OF GROUPED STARLINGS AT VARIOUS TEMPERATURES¹

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Consider the physiological and behavioral adaptations of Starlings (Sturnus vulgaris), the metabolic rates and survival times in roosting and active states of single, paired, and groups of four birds at an ambient temperature of 24–30 C and at 2–4 C were determined.

PROCEDURE

The respiration chamber used to determine the metabolic rates was an open circuit system modified from Haldane (1892), and described in a previous paper (Brenner and Malin, 1965). The chamber used for measuring roosting metabolism was a black, one-gallon, wide-mouth jar. The respiration chamber for measurement of the active metabolism was constructed from a 12-gallon rectangular aquarium covered with heavy plastic and sealed with one-inch adhesive tape.

The metabolic rates of birds in a roosting and active state at 24–30 C were determined only for single birds. At 2–4 C the metabolic rate was determined for a single bird in an active state and the roosting metabolic rates were determined for a single, paired, and a group of four birds.

The birds fasted for 3 hours at the designated temperature, in light for metabolism of active birds and in dark for metabolism of roosting birds. The birds were tested in the respiration chamber for 3 hours; after which they were removed from the chamber and immediately weighed to the nearest milligram.

The body (cloacal) and surface temperatures were recorded at the beginning and end of each test using a Yellow Springs Instrument telethermometer thermistor unit (accuracy \pm 0.5 C). Probe model 402 was used to determine the body temperature and a surface probe model 408 was used for the determination of the surface temperature. The mean surface temperature was derived from six surface readings taken from different areas of the body. The birds had been exposed to the environmental temperature for 3 hours before the first temperatures were recorded and for 6 hours before the final temperatures were taken.

To determine survival time under these conditions birds were deprived of food and water until death. The birds were checked every 4 hours until midnight and then again at 8:00 AM the following morning, and the hour

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that the birds were found dead was recorded. Four birds were fasted to death at 24–30 C in a roosting state and four birds were fasted to death under each of the following conditions at 2–4 C: roosting singly, in pairs, and in a group of four birds.

The metabolism of roosting birds may be the basal metabolism for a bird; but the birds may not be at complete rest during the fasting period and in the chamber and so "roosting metabolism" is used throughout this paper in place of "basal metabolism."

RESULTS

The mean metabolic rate for 12 birds roosting singly at temperatures between 24 and 30 C was 2.86 ± 0.156 cc O_2/g -hr and was significantly lower than the mean metabolic rate of 4.92 ± 0.774 cc O_2/g -hr for 12 single, active birds at the same temperature (P < 0.01) (Table 1). A mean metabolic rate of 5.83 ± 1.20 cc O_2/g -hr was determined for 15 birds roosting singly at 2-4 C. The mean metabolic rate for 10 single birds in the chamber for measuring active metabolism at 2-4 C was 5.82 ± 0.709 cc O_2/g -hr and was not statistically different from that of birds roosting singly at 2-4 C, indicating that the birds were probably really in a roosting state in the chamber. The metabolic rate for an active bird at the ambient temperature of 24-30 C did not differ statistically from that of a single bird in the chamber for measuring active metabolism at 2-4 C (P > 0.30).

When roosting birds were paired in the chamber the metabolic rate decreased to 3.06 ± 0.63 cc O_2/g —hr and was significantly lower than the metabolic rate for a single bird at 2–4 C. Similarly the metabolic rate of 3.04 ± 1.39 cc O_2/g —hr for a group of four birds roosting at 2–4 C was significantly lower than the metabolic rate of a bird roosting singly at 2–4 C but was not different from the metabolic rate for birds roosting in pairs (P>0.90).

The metabolic rates for birds roosting in pairs at 2–4 C was not statistically different from the metabolic rate for birds roosting singly at 24–30 C (P>0.70). Similarly the rate for birds roosting in a group of four at 2–4 C was not statistically different from the metabolic rate of a bird roosting singly at 24–30 C (P>0.75).

The body and surface temperature decreased for single and paired birds after 6 hours of exposure to an environmental temperature of 2-4 C. The mean body temperature of 15 birds roosting singly at 2-4 C was 39.8 C and the mean surface temperature was 31.7 C which represent a 2.7 degree decrease in body temperature and a 5.7 degree decrease in surface temperature from the birds roosting singly at 24-30 C (Table 1). The mean decrease in body temperature of birds in pairs (total of 24 birds) in the chamber was

TABLE 1

Average Body Weight, Metabolic Rates and Body and Surface Temperatures of Starlings under Various Conditions at 24–30 C and 2–4 C

Temperature	24-30	С	2–4 C				
Condition	Roosting	Active	Roosting	Active	Roosting	Active	
Grouping	single	single	single	paired	four	single	
Tests	12	12	15	12	6	10	
Birds	12	12	15	24	24	10	
Average weight	$69.375 \pm$	$67.692 \pm$	$67.986 \pm$	$69.525 \pm$	$72.852 \pm$	$73.476 \pm$	
	0.942	0.792	3.411	0.653	0.861	2.737	
cc O ₂ /g-hr	$2.86 \pm$	$4.92 \pm$	$5.83 \pm$	$3.06\pm$	$3.04\pm$	$5.82 \pm$	
	0.156	0.774	1.20	0.63	1.37	0.709	
Kcal/24 hr	$17.7 \pm$	$28.7 \pm$	$33.1 \pm$	$17.5 \pm$	$19.8 \pm$	$34.8 \pm$	
	3.7	3.5	4.7	2.4	0.80	3.98	
Body temp. (C)	$42.4\pm$	$42.6 \pm$	$39.8 \pm$	$38.8 \pm$	$41.7 \pm$	$39.3 \pm$	
	0.12	0.16	0.28	0.43	1.02	0.45	
Surface temp. (C)	$38.4\pm$	$36.4\pm$	$31.7\pm$	$32.6 \pm$	$35.3 \pm$	$33.3 \pm$	
	0.22	0.25	0.80	0.75	0.59	0.64	

3.7 degrees and the mean decrease in surface temperature was 4.6 degrees. In the chamber for measuring active metabolism at 2–4 C the mean decrease in body temperature for 10 birds was 4.1 degrees. This decrease in body temperature is a further indication that the birds were in a roosting state in the chamber. The birds which were in groups of four at 2–4 C decreased their body temperature only 0.7 degree and their surface temperature decreased 2.1 degrees. The mean body temperature for 12 birds after 6 hours in a roosting state at 24–30 C was 42.4 C and the mean surface temperature was 38.4 C. Birds in an active condition at 24–30 C had a body temperature of 42.6 C and a mean surface temperature of 36.4 C.

Since their body temperature decreased 2.7 and 3.7 degrees respectively the birds roosting singly and in pairs at 2–4 C were in a state of hypothermia which is defined by Edholm (1961) as a condition in which the body temperature of an organism is lowered substantially below normal, perhaps a minimum of 2–3 C below the lowest temperature generally encountered in the particular species.

The birds that were in a state of hypothermia when placed in a cage with other birds at room temperature ruffled their feathers. The other birds in the cage flocked around the introduced bird. This ruffling of the feathers by a bird in hypothermia could be considered a similar response to piloerection in a cold mammal.

Four birds all of which had been roosting singly for 6 hours at 2-4 C

 $\begin{array}{ccc} TABLE & 2 \\ \\ Comparison of Observed and Calculated Survival Time under Various \\ \hline Metabolic Conditions \end{array}$

Metabolic condition	No.	Mean initial body weight	Mean weight at death	% of initial weight at death	Observed survival time (days)	Calculated survival time	Chi- square
Roosting 24-30 C	4	69.8±	53.3±	76.4±	$1.25 \pm$	2.78±	2.84
		1.61	0.89	1.49	0.19	0.30	
Roosting single 2-4 C	4	$77.0 \pm$	$63.0 \pm$	$81.8 \pm$	$1.00\pm$	$1.63\pm$	1.54
		2.48	4.29	0.78	0.40	0.79	
Roosting paired 2-4 C	4.	$83.0 \pm$	$65.8 \pm$	$79.3 \pm$	$3.08\pm$	$3.31\pm$	0.86
		2.06	1.03	2.34	0.39	0.17	
Roosting 4 birds 2-4 C	4	$72.0 \pm$	$57.3 \pm$	$79.6 \pm$	$3.04\pm$	$2.78 \pm$	0.13
		0.78	1.95	0.98	0.31	0.95	

died within an hour after being removed from the respiration chamber. The mean body temperature was 30.5 C, a decrease of 12.1 degrees from normal (range 35 C-23 C). The mean surface temperature was 21.7, a decrease of 14.7 degrees. The duration of the hypothermic condition may have been the cause of death or the birds may not have been able to recover from such a severe drop in body temperature.

The mean respiratory quotient (RQ) decreased from 0.766 for birds roosting at 24–30 C temperature to a mean of 0.708 for all the different metabolic conditions at 2–4 C. A similar condition of a decrease in RQ occurred when chicks were exposed to cold was reported by Kleiber and Dougherty (1934).

The reserve energy supply and survival time under starvation conditions can be calculated from the formula described by Brenner and Malin (1965). The survival time under any given condition can be calculated from the formula S = F/M, when S = survival time (days), F = available energy in kcal, and M = the metabolic rate in kcal/day. All metabolic rates were calculated from the caloric equivalent of 3.408 kcal of energy per gram of CO_2 produced (Brody, 1945:310).

For the four birds which were fasted until death the calculated survival time did not differ significantly from the observed survival time when tested with a chi-square test (Table 2). The survival time increased as the number of birds increased in the chamber at 2–4 C (Table 2). The mean survival time increased from one day for a bird roosting singly to 3 days for birds roosting in groups.

The metabolic rate and reserve energy supply can also be calculated from the formula S = F/M. The calculated metabolic rates and the reserve energy

Table 3

Comparison between Observed and Calculated Metabolic Rates and Body Fat

Metabolic condition	No.	Observed metabolic rate (kcal/day)	Calculated metabolic rate (kcal/day)	Chi- square	Observed body fat (grams) (0.7W)	Calculated body fat (grams) (S = F/M)	Chi- square
Roosting singly, room temperature	4	17.7	24.1	1.70	5.55	2.82	1.34
Roosting singly 2-4 C	4	33.1	32.4	1.52	6.15	3.92	0.57
Roosting paired 2-4 C	4	17.5	22.6	1.15	6.59	4.95	0.33
Roosting group of four 2-4 C	4	19.8	20.5	0.66	5.71	5.70	0.18
Mean					6.00	4.35	0.45

supply of the birds in the different conditions were not significantly different from the observed values (Table 3).

DISCUSSION

The energy available to birds depends on the body weight. The basal metabolic rate also is dependent on the body weight and increases with a 0.73 power of the body weight (Brody, 1945). The relationship of weight to basal metabolic rate and available energy is also the formula for metabolic body size $W^{\%}$ as described by Kleiber (1932). The energy available to an 80 gram Starling, if 0.7 is used for determination, is 56.0 kcal; if 0.75 is used, the available energy is 60.0 kcal. The small difference of only 4 kcal probably is not a significant influence on the survival time. The survival time may be further influenced by the activity of the bird.

There was an increase in survival time from one day for birds roosting singly to 3 days for birds grouped in fours at 2–4 C. This increase may result from a lower metabolic rate and heat loss per bird when the birds were grouped. In nature, the Starling will roost in conifer plantations, over water, or in the warmer area of cities where lights are on at night. The higher ambient temperature in these areas probably also aids in reducing the metabolic rate. The selection of the roosting area and the flocking behavior together both probably aid in survival during cold weather. Koskimies (1961) reported the swift (Apus apus) roosting in groups during the night in late autumn. Kleiber and Winchester (1933) showed that at 14 C, 3-week-

Table 4
Metabolic Rates Reported for Different Species

Species	Metabolic rate ce O ₂ /g–hr or kcal/day	Investigator		
Brown Towhee	2.8 cc O ₂ /g-hr	Dawson (1954)		
Abert's Towhee	$2.80 \text{ cc } O_2/\text{g-hr}$	Dawson (1954)		
Evening Grosbeak	$2.5~\rm cc~O_2/g{\rm -hr}$	Dawson and Tordoff (1959)		
Cardinal	$2.6~{ m cc}~{ m O_2/g-hr}$	Dawson (1958)		
Red Crossbill	$3.1~{ m cc}~{ m O_2/g-hr}$	Dawson and Tordoff (1964)		
White-winged Crossbill	$2.8~{\rm cc}~{\rm O_2/ghr}$	Dawson and Tordoff (1964)		
Red-winged Blackbird	$2.90~\rm cc~O_2/g{\rm -hr}$	Brenner and Malin (1965)		
Gray Jay	20 kcal/day	Scholander et al. (1950)		
Snow Bunting	15 kcal/day	Scholander et al. (1950)		
House Sparrow	11.7 kcal/day	Kendeigh (1944)		

old baby chicks produced 15 per cent less heat per hour when they were allowed to huddle together than when they were separated. Small mammals also reduce their metabolic heat loss at low ambient temperatures by huddling together (Pearson, 1947; 1960; and Prychodko, 1958). A similar behavior occurs in poikilotherms. Brattstrom (1962) stated that tadpoles in aggregations absorb more radiant heat and dispense less heat to the surrounding water than do isolated tadpoles. The survival value of temperature-controlled aggregations in tadpoles appears to be related to an increase in body temperature.

Birds removed from the 2–4 C environment and placed in a cage at 24–30 C with other birds, ruffled their feathers. The other birds generally flew off the perch and gathered around the newly introduced bird. The other birds flying off the perch and gathering around the cold bird may be a reaction to a bird acting strangely in the cage. The result of the ruffle of feathers may be a reduction of heat loss, stimulation to flocking, or both. Baerends (1959) reported that birds brooding artificially cooled eggs would shiver, pant, and increase or decrease the body surface by erection or sleeking of feathers.

The metabolic rates obtained in this study compare closely with other studies (Table 4). This study also indicates that the thermoneutral range defined as the temperature range at which occurs the lowest metabolic rate for the species of birds may be altered by grouping birds at colder tempera-

tures. The Starling did not enter a torpid state as described for other species, and it is not known if a temperature lower than 2-4 C or a longer exposure to 2-4 C would produce torpidity in the Starling.

These data indicate that the Starling does not possess a physiological adaptation for cold, therefore the species may have evolved a behavioral adaptation of flocking to reduce heat loss and maintain its metabolic rate at the roosting level. Starlings roosting in conifers in the residential area of State College, Pennsylvania, were observed to be huddled together and body contact occurred between individuals. The size of this roost was estimated at over 5,000 individuals roosting in approximately 800 square feet. Emlen (1952) defined a flock as an aggregation of homogenous individuals, regardless of size or density. The flocking may arise as the result of a mutual attraction between individuals. The mutual attraction of flocking during the winter months could be a means of reducing the heat dissipation and metabolic rate. The flocking behavior of birds is probably essential to the survival of the species during cold weather if the species does not have a physiological or other behavioral adaptation to cold.

SUMMARY

The metabolic rates for roosting and active Starlings were determined at an ambient temperature of 24–30 C, and the metabolic rates of birds roosting singly, in pairs, and in groups of four were determined at 2–4 C. The metabolic rate of a bird roosting at 24–30 C was 2.86 ± 0.156 cc O_2/g -hr and was significantly lower than the metabolic rate for an active bird. The metabolic rate of a bird roosting singly at 2–4 C of 5.83 ± 1.20 cc O_2/g -hr was significantly higher than the rate of a roosting bird at 24–30 C and from the metabolic rate of 3.06 ± 0.63 cc O_2/g -hr for birds roosting in pairs and 3.04 ± 1.39 cc O_2/g -hr for groups of four birds roosting at 2–4 C.

The single and paired birds held for 6 hours at 2-4 C decreased their body temperature 2.7 and 3.7 degrees and the surface temperature decreased 5.7 and 4.6 degrees, respectively.

The expected survival time was calculated from the body weight and metabolic rate under various conditions. The observed and expected survival time were not statistically different on the basis of a chi-square test. The survival time increased from one day for a bird roosting singly to 3 days for grouped birds at 2-4 C.

The Starling did not enter a torpid state as described for other species and therefore may have evolved a behavioral adaptation of flocking to reduce heat loss and maintain its metabolic rate at the roosting level. The flocking behavior may be essential to the survival of the species during inclement winter weather.

LITERATURE CITED

BRENNER, F. J., AND W. F. MALIN

1965 Metabolism and survival time in the Red-winged Blackbird. Wilson Bull., 77:282-289.

BAERENDS, G. P.

1945 The ethological analysis of incubation behavior. *Ibis*, 10:357-368. Brody, S.

1945 Bioenergetics and growth. Reinhold, New York.

Brattstrom, B. H.

1962 Thermal control of aggregation behavior in tadpoles. *Herpetologica*, 18:38-47. Dawson, W. R.

1954 Temperature regulation and water requirements of the Brown and Abert Towhees, *Pipilo fuscus* and *Pipilo aberti. Univ. California Publ. in Zool.*, 59:81-124.

1958 Relation of oxygen consumption and evaporative water loss to temperature in the Cardinal. *Physiol. Zool.*, 31:37-48.

DAWSON, W. R., AND H. B. TORDOFF

1959 Relation of oxygen consumption to temperature in the Evening Grosbeak. Condor, 61:388-396.

1964 Relation of oxygen consumption to temperature in Red and White-winged Crossbills. Auk, 81:26-36.

EDHOLM, O. G.

1961 Hypothermia and the effects of cold, Introduction. Brit. Med. Bull., 17:1-4. EMLEN, J. T., JR.

1952 Flocking behavior in birds. Auk, 69:160-171.

HALDANE, J.

1892 A new form of apparatus for measuring the respiratory exchange of animals. J. Physiol., 13:419-430.

KENDEIGH, S. C.

1944 Effect of air temperature on the rate of energy metabolism in the English Sparrow. J. Exp. Zool., 96:1-16.

KLEIBER, M.

1932 Body size and metabolism. Hilgardia, 6:315-353.

KLEIBER, M., AND J. E. DOUGHERTY

1934 The influence of environmental temperature on utilization of food energy in baby chicks. J. General Physiol., 17:701-726.

KLEIBER, M., AND C. F. WINCHESTER

1933 Temperature regulation in baby chicks. Proc. Soc. Exp. Biol. and Med., 31:158-159.

Koskimies, J. Van

1961 Fakultative Kaltelethargic beim Manersegler (Apus apus) im Spatherbst. Die Voglewarte, 21:161-166.

PEARSON, O. P.

1947 The rate of metabolism of some small mammals. Ecology, 28:127-145.

1960 The oxygen consumption and bioenergetics of harvest mice. *Physiol. Zool.*, 33:152-160

PRYCHODKO, W.

1958 Effect of aggregation of laboratory mice (Mus musculus) on food intake at different temperatures. Ecology, 39:500-503.

SCHOLANDER, P. R., V. WALTERS, R. HECK, AND L. IRVING

1950 Body insulation of some arctic and tropical mammals and birds. Biol. Bull., 99:225-236.

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