

(3) Bouts as defined in this investigation are valuable aids in describing and cataloging the position of a bird in its habitat (which is important to know when linking activity to the thermal environment), and the basic energy-requiring activities within a Bout (walking, running, standing, perching, etc.) describe the cost of its activity whether the bird is feeding, courting, or defending a territory. The elements that distinguish these other "traditional" behaviors from each other are the smaller, and energetically less costly vocal and postural elements, and these will have little effect on the total H_{TD} . So unless a record of them is needed for some other purpose they can be ignored in estimating the cost of activity.

(4) Ambient air temperatures in the shade, on cloudy days, or at night are reasonably good measures of the thermal environment provided the animal is sheltered from convective and radiative losses. In sunlight, however, ambient air temperature is a poor measure of the thermal environment and, if used, can lead to a misinterpretation of behavioral and physiological responses. For example, Lustick et al. (1978) describe Herring Gulls, *Larus argentatus*, panting in direct sunlight at T_a of 12°C and interpret this as a downward shift of the birds' T_{uc} (30°C without sunlight). The T_{uc} did not shift, but the sunlight changed the characteristics of the physical environment and produced an equivalent blackbody temperature in excess of the Herring Gulls' T_{uc} . Other examples of animals panting or experiencing heat stress in direct sunlight at low T_a 's are not uncommon, and are usually misinterpreted as indicating an unusually low T_{uc} for the animal involved. Use of T_e in characterizing the thermal environment allows the investigator to avoid such misinterpretations, and accurately assess the thermoregulatory requirements of the animal in question.

SUMMARY

Thermal energy exchange and equivalent blackbody temperature (T_e) analyses were used to describe the Black-billed Magpie's microclimatic set, the thermal steps within it, and the potential thermoregulatory demands of those steps during one annual cycle in southeastern Washington. This analysis revealed:

1. In the microclimatic set of the magpie there were four distinct thermal steps: a) open ground, b) fence top high or higher in the open, c) in the shade within or under dense foliage shielded from the sky, and d) in the shade but exposed to the sky.

2. Because of the relationship between radiation absorbed and windspeed, postural changes alone, under some conditions, altered the value of T_e within a thermal step by as much as 11°C.

3. From late April through September, T_e 's at ground level (9 cm) exceeded the magpie's upper critical temperature (T_{uc}) for several hours during mid-day (up to as high as 56°C), fence tops offered a more moderate range of T_e 's (usually not greater than the bird's T_b), and in the shade T_e 's were always below T_{uc} .

4. From October through April, if there was sunshine, T_e 's at ground level were usually above the lower critical temperature (T_{lc}), even if air temperature (T_a) was not. In general, therefore, open ground during the daylight hours provided a comfortable thermal environment during these cold months, particularly if the birds could avoid strong winds.

5. The winter roost was selected to minimize convective and radiative heat loss.

6. The magpie could always avoid heat stress by sitting in the shade, but when T_e was below T_{lc} metabolic heat production had to be increased. It was suggested, therefore, that selective pressure has favored physiological adaptation to cold over heat, and that heat stress is more limiting to this species than cold.

Productive events were found to be partitioned adaptively, both with respect to each other and the physical environment:

1. The period of reproductive stress (late January to mid-June) preceded the months of potential heat stress when ground level activities (particularly food gathering for nestlings) could be limited.

2. There was no apparent overlap between the reproductive (late January to mid-June) and molt (mid-June to mid-September) cycles.

3. The costs of maintaining a territory were reduced by limiting that activity to a part of the reproductive period (nest building through the nestling stage).

Daily energy expenditure (H_{TD}) was estimated using the time-activity laboratory method. H_{TD} was expressed as a multiple of the daily basal metabolic requirement ($\dot{H}_b \times 24 \text{ hours} = H_{db}$) and showed considerable variation throughout the annual cycle:

1. The lowest estimates ($1.20 \times H_{db}$) were made for the incubating female.

2. Other low estimates, varying between 1.56 and $1.70 \times H_{db}$, were associated with the male during egg laying and with both sexes during the molt.

3. The highest estimate ($2.08 \times H_{db}$) was made for a male feeding nestlings.

4. Other high estimates, varying between 1.75 and $1.98 \times H_{db}$, were associated with the female laying eggs, the male tending the incubating female, the female tending nestlings, and both sexes during October, November, and December.

The time-activity energy budget analysis revealed the source of this variation and several adaptive features of the magpies' behavior:

1. Thermoregulatory demands, when they occurred, were 5% or less of any day's H_{TD} ; molt was estimated at 8% of H_{TD} , and ovogenesis at 23% of H_{TD} . The cost of activity, however, varied from a low of about 25 to a high of about 50% H_{TD} . It, therefore, accounted for most of the variation in H_{TD} during the annual cycle. The mean per-hour cost of activity was expressed as a multiple of \dot{H}_b and showed the following variation: a) the lowest value ($1.35 \times \dot{H}_b$) was estimated for the incubating female, and other low values were estimated for the egg-laying stage, and the molt period (1.75 and $1.89 \times \dot{H}_b$ for females and males, respectively), and b) the highest values were estimated for the nestling stage (2.11 and $2.62 \times \dot{H}_b$, respectively).

2. Magpies demonstrated a tendency to minimize energy expenditure via the conservation of movement. Over the period of a day, the least amount of time (0.10 to 1.71 hours) was devoted to Air Bouts, which are the most expensive. Small changes in the time devoted to Air Bouts made large changes in the per-hour cost of activity and hence H_{TD} . By restricting flight time to that which just accomplished the required behavior, H_{TD} was held to a minimum. When magpies performed Ground, FTPR, and Bush Bouts, the most time and energy within each Bout were spent on the least expensive activity.

3. During productive periods (ovogenesis and molt), nonproductive costs were minimized by reducing the per-hour cost of activity. This was reflected in the fact that during these periods the time devoted to Air Bouts was held to a minimum (0.18 to 0.62 hours), as compared with times of 1.22 to 1.71 hours during the

October to December interval or 0.93 to 1.58 hours for a male tending his incubating female and, later, his nestlings.

4. This led to the hypothesis that selection should operate to minimize H_{TD} , and since changes in behavior are the greatest source of variation in H_{TD} , selection should favor those behaviors that maximize the return on the investment of time and energy in activity.

The cost of foraging, and the required foraging efficiency (η_{Rf}) for any one day depended on the characteristics of the food resource being utilized. Consequently η_{Rf} varied during the year, but always in such a way that long-term fitness seemed to be enhanced when 1) individual food items were large, finding and swallowing time was short, rate of energy intake high, and η_{Rf} was high (10.1 to 10.5) and 2) individual food items were small, finding and swallowing took longer, the rate of energy intake was low, and η_{Rf} was low (3.2 to 4.5).

The time-activity laboratory method used in this investigation was evaluated and shown to provide inexpensive, reasonably accurate estimates of H_{TD} , provided that measured energy equivalents can be assigned to the behaviors being described and that thermoregulatory demands are adequately determined.

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LITERATURE CITED

- ASCHOFF, J., AND H. POHL. 1970. Rhythmic variations in energy metabolism. *Fed. Proc.* 29:1541-1552.
- BALDA, R. P., AND W. J. BOCK. 1971. Ecology and morphology of food storage in the Clark's Nutcracker. *Abstr. 89th Stated Meeting, A. O. U. Seattle, Washington.*
- BALDA, R. P., M. L. MORRISON, AND T. R. BEMENT. 1977. Roosting behavior of the Piñon Jay in autumn and winter. *Auk* 94:494-504.
- BARTHOLOMEW, G. A. 1958. The role of physiology in the distribution of terrestrial vertebrates. Pp. 81-95 in C. L. Hubbs (ed.), *Zoogeography*. Publ. No. 51, Amer. Assoc. Advan. Sci., Washington, D. C.
- BENDIRE, C. H. 1895. Life histories of North American birds. *U.S. Natl. Mus., Spec. Bull.* 3:1-518.
- BERGER, M., AND J. S. HART. 1974. Physiology and energetics of flight. Pp. 415-477 in D. S. Farner and J. R. King (eds.), *Avian biology*. Vol. IV. Academic Press, New York.
- BERNSTEIN, M. H., S. P. THOMAS, AND K. SCHMIDT-NIELSEN. 1973. Power input during flight of the Fish Crow, *Corvus ossifragus*. *J. Exper. Biol.* 58:401-410.