

phoricarpus albus, spirea, *Spirea betulifolia*, and service berry, *Amelanchier alnifolia*).

About 36 adult magpies occupied this area during the investigation. Six of them, previously marked with colored bibs bearing an identifying number, had been used by Johnson (1972) in an earlier investigation. When Johnson marked these birds (1970–1971), juvenals (birds yet to complete their first molt) received red bibs, and adults yellow bibs. Therefore, when field observations first started (April 1973) the three birds with red bibs were two to three years old, and the three with yellow bibs were more than three years old. Johnson had also marked magpie populations in adjacent drainages, and during the winter when these joined with ours in a communal roosting flock, several other birds with bibs were seen. In the spring of 1974, only two red-bibbed and one yellow-bibbed birds were breeding in the study area. The other three either had been assimilated into another population during the winter flocking, had lost their bibs, or had been eliminated entirely. Therefore, it appears that the adult individuals in the observed population were resident not only to the Pullman area in general, but perhaps specifically to the study area. This population remained within a home range area as a loose flock, except during the reproductive season, when the adults dispersed over that same area as pairs on nesting territories.

RATIONALE AND METHODS OF THERMAL ANALYSIS

The thermal environment is the milieu in which all activity takes place. It is therefore one of the major selective forces in an organism's environment, and while there are many laboratory investigations describing physiological, morphological, and behavioral adjustments of birds to various thermal regimes (see Dawson and Hudson (1970) and Calder and King (1974) for recent reviews), few describe the set of thermal conditions available to an animal in its natural environment or the extent to which an animal may utilize a set of microclimatic differences to extend the full range of variation identified in the laboratory. For an animal as mobile as a bird there are several different thermal conditions available to it at any time, and it is important in evaluating time-activity and energy budgets not only to determine the character of these on a temporal basis but also to determine which of them are actively sought and occupied at certain times of the day or year. The ability to accept or reject various thermal environments may allow an animal to "assemble the environmental conditions necessary for survival and reproduction out of remarkably unlikely arrays of environmental factors" (Bartholomew 1958). It is in this context that the analysis of thermal energy exchange between organisms and their environment becomes important and makes it possible to quantify the relative roles of physiological, morphological, and behavioral adaptations in determining an animal's temporal spacing of activities (daily and seasonal), daily energy requirements, distribution within its habitat, and perhaps geographic distribution.

Winslow et al. (1936a, 1936b, 1937) made fundamental pioneering studies of "partitioned calorimetry" in a controlled laboratory environment and estimated the radiative, evaporative, and convective heat transfer terms separately for men under a wide variety of thermal conditions. They (Winslow et al. 1937) described their controlled laboratory environment in terms of a single "operational tem-

perature" which took into account the combined contributions of radiation and air temperature in creating a specific thermal environment. Since then, methods have been developed for describing the thermal energy budgets of plants and animals under uncontrolled field conditions (Gates 1962, Geiger 1965, Birkebak 1966, Monteith 1973, Campbell 1977) with concomitant efforts to bridge the gap between field and laboratory studies of thermal balance. A seminal step in bridging this gap was the development of the "climate space" concept by Porter and Gates (1969). From its location on a climate space diagram, a particular set of microclimatic conditions can be reduced from real expressions of radiation, wind, and air temperature to a single "lumped" variable, the equivalent blackbody temperature (T_e), which can be directly equated to a blackbody cavity (Morhardt 1971, Morhardt and Gates 1974). Laboratory data describing thermoregulatory responses of animals are usually gathered in controlled thermal environments that also approximate blackbody cavities. Therefore, by comparing thermal environments in terms of equivalent blackbody cavities, it is possible to completely bridge the gap between the field and the laboratory, and to predict appropriate thermoregulatory responses for animals in the field from estimates of T_e . This assumes that thermoregulatory responses are the same to equivalent thermal environments even though the relative contributions of the physical variables may differ between the two.

The equivalent blackbody temperature, used as an index of the thermal environment in this investigation, is given by Eq. 1,

$$*T_e = T_a + (R_{abs} - \epsilon\sigma K_a^4)/\rho_a c_p (1/r_a + 1/r_r) \quad (1)$$

where T_e is the equivalent blackbody temperature ($^{\circ}\text{C}$), T_a is air temperature ($^{\circ}\text{C}$), K_a is air temperature in degrees Kelvin, R_{abs} is the flux density of absorbed radiation (W m^{-2}), ϵ is the emissivity of the animal's surface (0.98), σ is the Stephan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ }^{\circ}\text{K}^{-4}$), ρ_a is the density of air at 20°C (1.2 kg m^{-3}), c_p is the specific heat of air ($10^3 \text{ J kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$), r_a is boundary-layer thermal resistance [s m^{-1} ; $r_a = K(d/u)^{0.5}$; where u is wind velocity (m s^{-1}); d is the characteristic dimension of the bird; and K is a constant (310) for laminar flow over a flat plate; Robinson et al. 1976], and r_r is the radiative resistance (s m^{-1} ; $r_r = \rho_a c_p / 4\epsilon\sigma T_a^3$; Monteith 1973). Derivation of Eq. 1 comes from the climate space of Porter and Gates (1969) and is given in detail by Robinson et al. (1976) and Campbell (1977).

The equivalent blackbody temperature describes one end of the thermal gradient for heat gain or heat loss between the animal and the environment. It is used in Eq. 4 of Robinson et al. (1976) to describe the physiological response of an animal to its thermal environment through an energy budget,

$$\dot{H}_m - \lambda E = [\rho_a c_p / (r_b + r_e)](T_b - T_e) \quad (2)$$

where \dot{H}_m is the flux density of metabolic heat at the skin surface (W m^{-2}), λE is latent heat flux density (W m^{-2} ; $\lambda = \text{heat of vaporization} = 2.43 \text{ MJ kg}^{-1}$; $E = \text{total evaporative water loss} = \text{g m}^{-2} \text{ s}^{-1}$), r_b is whole body thermal resistance [s m^{-1} ; equal to tissue resistance (r_t) plus coat resistance (r_c)], T_b is body temperature ($^{\circ}\text{C}$), and the other terms are as defined above.

* See p. vi for list of symbols.

The validity of this approach in describing thermal environments and predicting physiological responses to them is supported by the investigations of both Robinson et al. (1976) and Mahoney and King (1977), who demonstrate good concordance between theoretical and empirical estimates of \dot{H}_m using T_e as a measure of the environmental end of the thermal gradient.

NONMETEOROLOGICAL VARIABLES

Values for the various nonmeteorological variables associated with Eqs. 1 and 2 were estimated as extrapolations from literature values, measured on live magpies and study skins, or evaluated from an appropriate equation.

Surface area.—If the tail, head, and legs are excluded, the silhouette of a bird's body has the shape of a prolate spheroid, while the head minus the beak can be considered a hemisphere. Therefore, the area of the external surface involved in radiative exchange with the physical environment can be estimated from the sum of the areas of these two solids as given in Eq. 3,

$$A_t = [2\pi b^2 + (2\pi ab/e) \sin^{-1}e] + 6.285 r^2 \quad (3)$$

where a , b , and e are the major axis, minor axis, and eccentric, respectively, for a prolate spheroid, and r is the radius of the hemispherical head. Measurements were made at the feather surface of head circumference, body circumference at its widest point, and body length from the middle of the neck to the base of the tail on six live male and four live female magpies. These measurements were then used in calculating the external surface areas for these birds. Walsberg and King (1978c) have subsequently demonstrated with empirical measurement that the external feather surface is on the average 23% less than the skin surface area beneath the plumage and point out the necessity of using the former for estimates of heat transfer in birds. Their allometric equation for external surface area ($S_{ext} = 8.11 m^{0.667}$; where S_{ext} is the external surface area in cm^2 , and m is body mass in grams) predicts values for female (242 cm^2) and male (261 cm^2) magpies that conform closely (-8.0 and $+0.7\%$ difference for females and males, respectively) to those calculated geometrically (Table 4).

The projected surface area normal to the direct solar beam (A_p) is the area of a shadow cast by the bird on a surface that is normal to the solar beam. Eq. 4 gives the A_p/A_t ratio for a prolate spheroid (Campbell 1977, pers. comm.)

$$(A_p/A_t) = \frac{[1 + (x^2 - 1)\cos^2\theta]^{\frac{1}{2}}}{2x + (2 \sin^{-1}\sqrt{1 - x^2}/\sqrt{1 - x^2})} \quad (4)$$

where x is the ratio of the minor to major axis of the spheroid (b/a , representing the bird's body), and θ is the angle between the solar beam and the major axis.

Absorptivity.—Through the courtesy of Dr. Warren Porter, Department of Zoology, University of Wisconsin, reflectance measurements were made of the black back, black chest, and white belly plumage of three magpie study skins. Reflectance was measured at 5 to 60 nm intervals over the spectral range from 295 to 2500 nm. Each reading was corrected to correspond to the reflectance of the energy present in that wavelength of the solar spectrum as seen on a clear day at 12:00 hours on 1 July at 46°N . These values were then integrated over the corresponding solar spectrum to give an average reflectance for each of these

plumage areas. The corresponding average absorptivity was calculated from the equation $1 = \alpha + \tau + \rho$, where α is the absorptivity, τ is the transmissivity (assumed to be zero), and ρ is the reflectivity.

Physiological variables.—The physiological variables required in energy budget analysis are body temperature, metabolic rate, rate of latent heat loss, lower critical temperature (T_{lc}), upper critical temperature (T_{uc}), and whole body resistance. These variables were not measured directly during this investigation but were taken from the literature or estimated from accepted equations. Values for T_b were taken from Stevenson (1971) who found that Black-billed Magpies show a diurnal variation in T_b of about 3.5°C, ranging from 39°C while roosting to 42.5°C while active. Basal metabolic rate (\dot{H}_b ; 70 W m⁻²), T_{lc} (5°C), and T_{uc} (35°C) were also taken from Stevenson (1971). The proportion of metabolic heat lost via evaporative cooling at various air temperatures under laboratory conditions was estimated from Eq. 56 in Calder and King (1974). Whole-body thermal resistance was calculated by solving Eq. 2 for r_b . The maximum and minimum values for r_b bounding the thermoneutral zone (T_n) were then obtained by substituting the T_{uc} and T_{lc} for T_e in the equation.

Characteristic dimensions.—The characteristic dimension d used in estimations of r_a refers to the orientation of the bird with respect to the direction of the wind. For a bird whose long axis is parallel to the wind, d is the straight line length from the base of the beak to the base of the tail, and for a bird whose long axis is normal to the wind, d is the body diameter at the widest point. These measurements were obtained from six male and four female magpies and averaged separately for the sexes to estimate d .

METEOROLOGICAL VARIABLES

The required meteorological variables were measured in the field at localities occupied by the birds. During any period of measurements (except at night) a transect was established so that several (3 to 5) localities could be sampled. A typical transect would sample the shade of a grove of trees, an open bottom area, and a hillside or hill crest, or a north-facing slope and south-facing slope. Each locality was then sampled once each hour during the entire measurement period. A complete diurnal record was generally not made on any one day, but a composite day was constructed for each month. Measurements were made for at least four hours at different times on two to four different days, so that by the end of the time required to complete the series, a complete dawn-to-dark record was available for each position along the transect. The location of the transect varied from season to season as the birds changed their pattern of distribution over the study area. Nighttime measurements were made within the roost sites of the population, which changed with season. Portable, battery-operated meteorological instruments were mounted on a pack frame and carried along the transects, or placed within the roost site for these measurements.

Radiation measurements.—Shortwave radiation was measured with a Moll-Gorczyński solarimeter (Kipp and Zonen, Delft, Holland, manufacturer). The sensor was mounted on the end of a 60-cm-long tube and held 80 cm above the ground with a tripod. A 4-cm-diameter aluminum disk, suspended 12 cm above the sensing surface on a thin wire, was used to shade the sensor surface in order to measure scattered shortwave radiation. The surface of the disk facing the

sensor was painted with flat black Krylon. All measurements were made with the radiation sensor in a horizontal position, facing upward for global and scattered radiation, and downward for reflected radiation. The value for the direct beam was calculated from Eq. 5,

$$S_p = (S_{Tt} - S_s) / (\cos \beta \cos \delta \cos h + \sin \beta \sin \delta) \quad (5)$$

where S_{Tt} is global radiation, S_s is scattered radiation, β is the latitude of the study area ($46^{\circ}37.5'$), δ is the solar declination taken from the ephemeris for the day in question, and h is the hour angle of the sun (List 1971).

Longwave sky radiation was estimated in three ways. On clear days or days with scattered clouds, longwave sky radiation was estimated from the Idso-Jackson (1969) equation for atmospheric radiation and corrected for cloud cover (Monteith 1973). On some days, sky temperatures were measured with a Wahl Heat Spy radiation thermometer (Model HSA-120, William Wahl Corporation, Los Angeles, California, U.S.A.) and converted to irradiance using $\epsilon = 1.0$ for sky emmissivity. On completely overcast days, or within a shady canopy, or within the roosting grove at night, longwave ground and sky radiation were estimated from measurements of total incoming radiation (Q) made with a modified Moll-Gorczyński solarimeter fitted with a polyethylene dome and a thermocouple thermometer on the cold junction of the sensor's thermopile (Mugaas 1976, Campbell et al. 1978). The longwave component was then estimated by subtracting the total shortwave reading (S_{Tt}) from Q .

Air and ground temperatures.—Air temperature was measured with a 26 ga copper-constantan thermocouple shaded from sky radiation with an aluminum foil shield. Measurements were made at 9 cm (mid-height on a bird standing on the ground) and 160 cm (fence-post height) above the ground. Ground temperatures were measured with this same thermocouple by pulling the aluminum shield back from the junction and laying the junction on the ground. In all cases of air and ground temperature, the maximum and minimum temperatures observed for a one-minute period were recorded and the average of these used in data presentation. Ground temperature was also used to calculate longwave terrestrial radiation.

Windspeed.—A Hastings model RB-1 anemometer with an omnidirectional probe was used to measure windspeed. Measurements were made at 9 cm and 160 cm above the ground for a period of one minute at each height and the maximum and minimum values recorded for that interval. The average of these was used as the mean windspeed.

RATIONALE AND METHODS OF TIME-ACTIVITY AND ENERGY BUDGET ANALYSIS

BEHAVIORAL CATEGORIES

Behavior was described in units called Bouts. Bouts (Table 1) defined an individual's position within the habitat, and the length of a Bout was determined by the amount of time spent in that position. For example, a Ground Bout started when a bird landed on the ground and ended when it left it. Fence, Telephone Pole, and Roof Bouts were combined into a single Bout abbreviated FTTPR. Within each Bout, the basic energy-requiring movements, called activities, were quan-