

FIGURE 12. Variation by month in thermoregulatory requirement of Black-billed Magpies. Shaded area, no thermoregulatory requirement; hatched area, minimal thermoregulatory requirement; and clear area, absolute thermoregulatory requirement.

Even by selecting only the coldest days, the thermoregulatory contribution (Table 13) for any one composite day was small (1.7 to 4.4% of H_{TD} ; Tables 11 and 12; Fig. 11). January had a two-week cold spell when on a typical night T_e averaged -19.4°C for 15 hours, and during a typical daytime period there was a 3.2-hour span when T_e averaged -7°C (see Fig. 5). No behavioral data were gathered during these cold days, but if the activity level remained the same as for the December birds, the thermoregulatory requirement would have comprised about 17% of H_{TD} . During the remainder of the winter, however, with its milder temperatures, thermoregulation was not a large component of the magpie's daily energy expenditure.

DISCUSSION

The microclimates of the study area imposed only small or negligible thermoregulatory requirements (Table 13), and food never appeared to be in short sup-

TABLE 13
ESTIMATED NUMBER OF HOURS PER COMPOSITE DAY DURING WHICH BLACK-BILLED MAGPIES HAD
A THERMOREGULATORY REQUIREMENT

Phenological event	Month	Nocturnal		Diurnal			
		Roosting	T_r^a	Clear day	T_r^a	Cloudy day	T_n^a
Nonreproductive period							
Molt	July	—	—	—	—	—	—
	Aug.	—	—	—	—	—	—
	Sept.	—	—	—	—	—	—
Nonmolt	Oct.	12.5	2.8	—	—	—	—
	Nov.	14.2	-1.7	1.8	0.0	4.8	3.5
	Dec.	15.1	0.6	2.9	0.0	8.9	2.5
Reproductive period							
Egg laying	Mar. (♀)	11.2	1.1	0.8	2.5	10.8	2.5
	Mar. (♂)	10.8	1.1	1.2	2.5	11.2	2.5
Incubation	Apr. (♀)	8.9	2.8	—	—	—	—
	May (♂)	8.9	2.8	—	—	—	—
Nestling	June (♀)	—	—	—	—	—	—
	June (♂)	—	—	—	—	—	—

^a Average equivalent blackbody temperature (°C) for the indicated number of hours.

ply. Therefore, this investigation provides a description of time and energy budgeting for adult magpies under what may be considered as "base line conditions" of minimal thermal and trophic stress. While the observed pattern of time and energy budgeting may be optimal for these conditions, it may need to be modified in other parts of the range to meet the demands imposed by a more severe climate and/or distribution of food resources. The major stimuli identified in this investigation were changing daylength, the productive demands of ovogenesis and molt, and changing social demands. Variation in H_{TD} during the course of the year (Tables 11 and 12; Fig. 11) was related almost entirely to changes in the per-hour cost of diurnal activity (Figs. 10 and 11). Although the maximum H_{TD} observed was moderate ($2.08 \times H_{ab}$) compared with estimates made for other species of birds (2.3 to $7.2 \times H_{ab}$; Table 18) it should be recognized that this may simply reflect a lack of strong environmental stress on this population (pointing up a potential reserve capacity for existence under more rigorous conditions), and/or overestimates of H_{TD} by other investigators.

THERMAL TOLERANCE AND GEOGRAPHIC DISTRIBUTION

Linsdale (1937) points out that the range of the Black-billed Magpie in North America is restricted to the climate type designated by Russell (1931) as Cold Type Steppe Dry Climate. The range of the magpie extends beyond this climate type to the north into Canada and southern Alaska, but does not extend beyond it to the south or east (Linsdale 1937). The southern and eastern limits of this magpie's distribution have recently been reexamined on the basis of several climatic variables by Bock and Lepthien (1975). They found that the distribution appeared to be limited by increasing summer temperatures to the south, and increasing summer humidity and precipitation to the east on the central plains.

Therefore, it seems that cool-to-cold, dry macroclimates are a major selective factor in the geographic distribution and thermal adaptation of this species.

Macroclimatic categories, however, provide only a gross and indiscriminating index of the potential limits to avian distribution. Within any macroclimatic category, microclimatic sets are a source of environmental variation that can be exploited behaviorally by a species to minimize thermoregulatory stress. In terms of thermal tolerance alone, the geographic range of a species will be fixed ultimately by its physiological capacities and behavioral options in relation to the available array of thermal steps within its own microclimatic set (Brown 1968, Porter and Gates 1969, Gates 1970, Calder 1973, Smith 1974). Black-billed Magpies in southeastern Washington completely avoid, or at least minimize, thermal stress by both obvious and subtle exploitation of their climatic set as well as by an adaptive partitioning of the annual cycle that minimizes the overlap of thermal and trophic stresses.

Habitat use, therefore, can be viewed as a series of movements between distinct thermal steps. Within a step, smaller adjustments by posture or position allow the bird to sample a smaller sliding scale of conditions. Thermal stress within a step may be minimized or even avoided by these postural adjustments, but once the bird can no longer do this, the only way stress can be further reduced or avoided is by moving to a new thermal step. If it is occupying the most favorable thermal step available at that time, then the animal has maximized its behavioral options, and if that step is thermally stressful it must activate physiological mechanisms to maintain heat balance.

The microclimatic analysis demonstrated that during warm months in the northwestern segment of the Black-billed Magpie's range, T_e 's $> T_b$ occurred in the open at ground level for several hours on each clear day, but that on even the hottest days, T_e 's in the shade were always lower than T_{uc} (Fig. 4; Mugaas 1976). To avoid the danger of heat stress, birds limited foraging and other activities on open ground during those hours, and either retreated into the shade for long periods or limited their exposure to open ground by shuttling between it and cooler thermal steps (shade or fence tops). During the winter months, when T_e 's were below T_{lc} (5°C), the cold could not be avoided and metabolic heat production had to increase to offset increased heat loss. It seems reasonable to assume, therefore, that for this magpie, selective pressures have favored physiological adaptation to cold. Contrary to *a priori* expectations, therefore, it is evident that hot days hold greater potential for thermal stress and are more limiting to behavior than cold days. While it is misleading to consider an organism's distribution as being fixed by a single variable, this analysis does reveal that high ground-level temperatures could be limiting to this magpie, particularly when coupled with other unfavorable abiotic and biotic variables. But, in terms of thermal conditions alone, if the macroclimate does not contain microclimates suitable for retreat from high temperatures, or if retreat is possible but necessary for such long periods that it significantly interferes with foraging or other ground level activities (particularly during reproductive or molt periods), then overall fitness in that area would be reduced and the distribution limited.

THE BOUT AS AN INDEX OF BEHAVIOR

The description of behavior used in this investigation is unlike that of most others (Greenlaw 1969, Utter and LeFebvre 1970, Schartz and Zimmerman 1971,

Stiles 1971, Utter 1971, Wolf and Hainsworth 1971, Custer and Pitelka 1972, Verbeek 1972a, Wiens and Innis 1973, Wolf 1975, Wolf et al. 1975), and it may be argued the "traditional" behavioral categories used in these other investigations (foraging, flying, preening, bathing, courtship, territorial defense, nest building, resting, laying, incubating, brooding, storing food, drinking, sunbathing, etc.) provide an ecologically more relevant description of a bird's behavior. However, there were several overwhelming advantages associated with describing the magpie's behavior in terms of Bouts and activities.

Some "traditional" behaviors are composed of both postural and locomotor components, while others are mostly postural changes that occur while the bird is standing or perched, making it impossible to assign to them a realistic energy equivalent. In addition, there is often considerable overlap between the performance of one of these behaviors and another, making it difficult to resolve their separate time and energy requirements. The description used in this investigation did not require the observer to interpret behavior and resolve the time and energy overlaps of complex social events. The activities performed in each Bout are the basic energy-requiring movements, and because they were continuously recorded during each period of visual contact, there was no confusion involved in making a realistic estimate of the cost of activity at any level of resolution (the activities themselves, Bouts, or an entire day). It was also possible to distinguish between energetically expensive and inexpensive behavior and resolve the energetically important from unimportant shifts in the allocation of time and energy. In addition, the use of Bouts as major categories of behavior greatly facilitated the analysis of the spatial and microclimatic context of behavioral events.

By describing behavior in terms of activities (Table 1) it was possible to estimate a maximum and a minimum energy cost for each Bout. For example, the activities associated with Ground Bouts are standing, walking, hopping, and running, which have estimated energy equivalents of 1.7, 2.0, 2.0, and $2.1 \times \dot{H}_b$, respectively. If a magpie spent all of its time running when performing Ground Bouts, it would incur an expense of $2.15 \times \dot{H}_b$, and if it spent all of its time standing the cost would be $1.7 \times \dot{H}_b$. But since the bird spent time performing all four types of activities (regardless of the "traditional" behaviors being performed) and the most time and energy on the least expensive activity, the actual cost of the Bout for each composite day was closer to the minimum than the maximum (1.77 to $1.83 \times \dot{H}_b$; Table 14). With the exception of Air Bouts, Table 14 shows a similar pattern of cost for each of the other Bouts on each composite day. Air Bouts are quantitatively different from other Bouts because of their high energetic cost, and qualitatively different in that more time and energy were spent on the most expensive of the two types of flight, so their actual cost approximated the maximum. In addition, Air Bouts are essentially single-purpose in function (moving the bird from place to place over various distances), while the other bouts are multipurpose and represent the places where most of the business of life is conducted.

If the Bout, as defined in this investigation, was considered the most basic unit of resolution in describing the allocation of time and energy, then behavioral modifications to accommodate changing energy requirements would involve both inter- and intrabout variations. While the goal of a bird's behavior may be altered significantly by changes in activities within Ground, FTBR, and Bush Bouts, the energetic cost of these will be small because the total variation possible is small

TABLE 14
 MAXIMUM AND MINIMUM ENERGY COSTS POSSIBLE FOR BLACK-BILLED MAGPIES DURING EACH BOUT, AND ACTUAL CALCULATED COSTS OF THE BOUTS DURING THE ANNUAL CYCLE EXPRESSED AS A MULTIPLE OF \dot{H}_b

Time of year	Bout			
	Ground	FTPR	Bush	Air
Nonreproductive period				
July	1.81	1.70	1.34	10.84
Aug.	1.83	1.74	1.35	10.20
Sept.	1.78	1.70	1.39	10.37
Oct.	1.81	1.70	1.51	10.47
Nov.	1.80	1.82	1.72	10.97
Dec.	1.81	1.69	1.71	10.31
Minimum ^a	1.70	1.70	1.27	6.00
Maximum ^a	2.15	2.00	2.00	11.0
Reproductive period				
Egg laying ^b				
♀	1.77	1.69	1.65	10.12
♂	1.77	1.67	1.70	9.98
Incubation ^c				
♀	1.79	1.71	1.27	10.00
♂	1.78	1.71	1.61	10.56
Nestling ^d				
♀	1.78	1.70	1.59	9.72
♂	1.80	1.71	1.75	10.40
Minimum ^a	1.70	1.70	1.27	6.00
Maximum ^a	2.15	2.00	2.00	11.00

^a Minimum and maximum energy costs, and activities for respective Bouts were: Ground, stand and run; FTPR, alert perch and hop; Bush, rest perch and hop; and Air, flight ≤ 3 sec. and flight > 3 sec.

^b Late March.

^c Late April.

^d Early June.

(Table 14). For the same reason, interbout variation between these three will have little effect on total energy expenditure. However, interbout variation between these three and Air Bouts can have a large effect on total energy expenditure. For example, if a July female performed each of the four Bouts for one hour at the July cost per Bout, the total cost for a four-hour period would be 87.86 kJ (Table 15). If the bird was always running when performing Ground Bouts, hopping during FTPR and Bush Bouts, the cost of the four-hour period would increase from 87.86 kJ to 95.14 kJ, a change of 7.7% from the July value (Table 15). If the bird was standing during Ground Bouts, alert perching during FTPR Bouts, and rest perching during Bush Bouts, the cost of that four-hour period would be reduced from 87.68 kJ to 86.91 kJ, a decrease of 1.1% from the July value (Table 15). The total range of variation possible by altering intrabout activity is 8.23 kJ, equivalent to about 8 minutes of flight. If the multiples of \dot{H}_b for the July data are used, but the time spent on each Bout is varied, a much larger range of energy expenditure is possible. If time spent flying is increased to two hours, and each of the other Bouts reduced by 20 minutes, the cost of activity is increased from 87.86 kJ to 139.44 kJ, an increase of 51.58 kJ or 58.7% over the

TABLE 15
CONSEQUENCES OF VARIATION IN INTRA- AND INTERBOUT ACTIVITY ON METABOLIC COSTS OF
ACTIVITY OF BLACK-BILLED MAGPIES

	Bout				Totals
	Ground	FTPR	Bush	Air	
July Female ^a					
Activity ($\times \dot{H}_b$)	1.81	1.70	1.34	10.84	
Time (h)	1.0	1.0	1.0	1.0	4.0
Energy (kJ)	10.14	9.52	7.50	60.70	87.86
Possibility I					
Maximum variation					
Activity ($\times \dot{H}_b$)	2.15	2.00	2.00	10.84	
Time (h)	1.0	1.0	1.0	1.0	4.0
Energy (kJ)	12.04	11.20	11.20	60.70	95.14
Minimum variation					
Activity ($\times \dot{H}_b$)	1.70	1.70	1.27	10.84	
Time (h)	1.0	1.0	1.0	1.0	4.0
Energy (kJ)	9.52	9.52	7.17	60.70	86.91
Possibility II					
Activity ($\times \dot{H}_b$)	1.81	1.70	1.34	10.84	
Time (h)	0.66	0.66	0.66	2.0	4.0
Energy (kJ)	6.69	6.28	4.95	121.52	139.44

^a Female $\dot{H}_b = 5.6 \text{ kJ h}^{-1}$; all calculations based on this value.

July value (Table 15). This is equivalent to a magpie running 4.3 hours. The total range of variation possible (212.8 kJ) with this sort of behavioral adjustment ranges from a low of 30 kJ if only Bush Bouts were performed to a high of 242.8 kJ if the bird flew for the entire four hours.

Thus, the behavior associated with Ground, FTPR, and Bush Bouts can be altered substantially and have little impact on the total cost of activity, while moderate variations in the time spent flying have a marked effect on the cost of activity. Therefore, when assessing the cost of a behavior, or the impact of a change in behavior on the total energy expenditure of a bird, the most important element to consider is the change in time spent flying. This also suggests that in terms of optimizing time and energy expenditure over a day, time spent on Air Bouts will have the greatest influence in determining whether the return from all other activity is maximized.

ANNUAL CYCLE OF ENERGY EXPENDITURE

The feeding cycles of animals can be divided into search, approach, capture, and ingestion phases (de Ruiter 1967). Many authors have used these in concert with breadth of diet, "strategies" of movement, and use of patchy food sources to develop mathematical models for predicting foraging efficiencies or optimal foraging patterns (e.g., Emlen 1966; Schoener 1971; Charnov 1973, 1976; Pyke et al. 1977). These investigators have used the premise that animals are "efficient" in their foraging activities (Charnov 1976), and the resulting models all assume that the fitness of a foraging animal is a function of the efficiency of foraging and use energy as the common currency. Thus, natural selection should

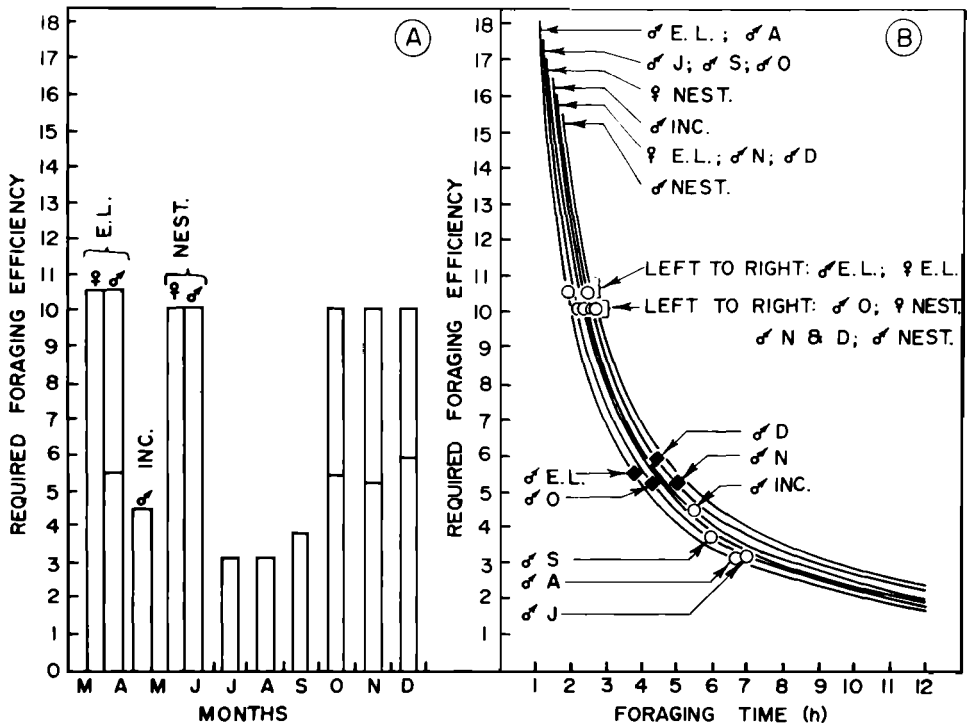


FIGURE 13. A. Required foraging efficiency of Black-billed Magpies during each composite day. Only males are represented from July through December, but both sexes are represented for reproductive stages. B. Required foraging efficiency of Black-billed Magpies as a function of time spent foraging (h), and H_{TD} of each composite day. Months from July through December are represented by the letters J, A, S, O, N, and D, respectively. The η_{RF} calculated for each composite day is plotted on the appropriate curve as an open circle. Values uncorrected for time spent storing food are plotted as solid diamonds. All other abbreviations are as in Figure 8.

favor those foraging patterns that, for a given food resource, provide the largest return for the time and energy invested.

Wolf et al. (1975) used required foraging efficiency (η_{RF}) to determine the effect foraging efficiency would have on the required foraging times of nectar-feeding birds. Required foraging efficiency is expressed as

$$\eta_{RF} = H_{TD}/H_{TF} \tag{12}$$

where H_{TD} is as defined earlier, and H_{TF} is the daily cost of foraging (kJ). The daily cost of foraging is the product of the unit cost of foraging (\dot{H}_{uf} , determined by the activities used in foraging) and the time spent foraging (t_f). H_{TD} represents the smallest amount of energy that must be assimilated across the gut to maintain energy balance. For magpies, Ground Bouts primarily represent time and energy spent foraging, and therefore, offer a first-order estimate of H_{TF} . The histogram in Figure 13A shows η_{RF} 's calculated for male magpies from July through December and both sexes where appropriate for the reproductive stages. This figure shows that η_{RF} occurred at two distinct levels during the year. The derivation of these values is discussed in more detail later.

Achieved foraging efficiency (η_{rf}) which is the ratio of the quantity of energy actually swallowed to cost (Wolf et al. 1975) could not be estimated for the magpie because (1) energy content of individual food items was not known, (2) not all food items swallowed were identifiable, and (3) not all food items handled were swallowed (some were partially eaten, then hidden; others were hidden intact shortly after initial discovery).

The relationship between η_{rf} and the time spent foraging approximates a hyperbolic curve. Curves relating η_{rf} to the time required for foraging are presented in Figure 13B for the H_{TD} 's peculiar to composite days for males from July through December, and for both sexes where appropriate for the reproductive stages. At any particular H_{TD} , η_{rf} increases, as time spent foraging decreases, and as H_{TD} increases at any particular foraging time so does η_{rf} . The η_{rf} 's for the composite days are plotted as open symbols on the appropriate curves in Figure 13B. The low values (3.2 to 4.5) fall on that region of the curves where a small change in η_{rf} produces a large change in foraging time while the large values (10.1 to 10.5) fall where a large change in η_{rf} produces little change in foraging time. Thus, the extent to which foraging time will be decreased or increased will depend on the foraging efficiency a bird can achieve, which in turn is a function of the characteristics of the food supply. The very short foraging times associated with η_{rf} 's of about 10.1 to 10.5 occurred when food items were large and the rate of energy intake was rapid. Longer foraging times and lower η_{rf} 's (3.2 to 4.5) occurred when small food items were being utilized and the rate of energy intake was low.

Since the \dot{H}_{uf} varied little during the year (1.77 to $1.83 \times \dot{H}_b$; Table 14), the major factors determining H_{Tf} were the characteristics of the food being utilized and the time required to exploit it. Coupled with these are the temporal variation in T_c at ground level that will have some influence on when foraging will occur, and what will be available. These factors will be the focal point in the following discussion, which examines the adaptive features of changing activity patterns during various periods of the magpie's annual cycle.

Reproductive period.—The largest productive demand during reproduction is ovogenesis (King 1973, Ricklefs 1974), and combined with all other costs of existence during egg laying, it accounted for 23% of each day's H_{TD} (Fig. 11). This was the only time during the annual cycle when the influence of productivity was nearly as great as that of activity. During this time the female spent little time on Air Bouts (Table 12) so that even with the increased productive demand, her total H_{TD} was less than $2.0 \times H_{ib}$. This implies that there may have been a compensation of the energy of activity for the energy of production. The female also reduced the time spent on Ground Bouts to about 2.5 hours a day, yielding an η_{rf} of 10.5 (Fig. 13A). This drastic change in behavior occurred at a time when freezing and near-freezing temperatures accompanied by snow or rain squalls were not uncommon (Mugaas 1976) and there was no flush of insect prey available to support increased energy demands. The food resources at this time, however, consisted of large earthworms, *Lumbricus terrestris*, and large pieces of carrion, or commercial dog and cat food (from nearby Veterinary School kennels) that the birds found on the ground near and within the nesting territory. Many of these were so large (including the earthworms) that when they were uncovered, they were only partially consumed and then cached. This food resource represented

a concentrated assemblage of large food items that satisfied the energy requirements of egg production with a minimum of ground activity. How much of the carrion and pet food was stored on and near the nesting territory prior to egg laying is not known, but should be investigated since it suggests a way in which these birds could artificially develop a high quality readily accessible food source to be utilized during the egg-laying period. Nor is it known to what extent storing food on or near the territory may influence the onset of egg laying. Late winter breeding of nutcrackers (*Nucifraga* spp.) and perhaps other corvids in snow-covered regions is possible as a result of prior caching of food (Turček and Kelso 1968, Balda and Bock 1971).

During the egg-laying phase the male was also very sedentary, with an H_{TD} only slightly over $1.5 \times H_{ab}$ (Fig. 11). The male's low level of activity during this period may have both an energetic and behavioral function. After the eggs are laid, the male is involved in about 40 days of intense activity transporting food to the incubating and brooding female, as well as the nestlings. His inactivity during egg laying may provide a period during which his own energy reserves can be increased in preparation for the oncoming period of increased activity. Copulation and courtship feeding were observed during egg laying, and both appeared to be solicited by the female. By staying relatively sedentary and near the nest, the male not only "saved" energy, but was readily available to the female, who consequently had to spend little of her time or energy in locating him for these activities. Furthermore, courtship feeding may, as Verbeek (1973) predicts for the Yellow-billed Magpie, provide the priming stimulus to ensure that the male will continue feeding her during incubation. The male spent 1.3 hours more than the female on Ground Bouts. The foraging activity of the male at this time involved not only finding and swallowing the necessary quantity of food, but also finding and storing additional food items and in some cases what appeared to be checking items previously stored (perhaps as reinforcement to recollection of their locality). The female also engaged in some of these activities but did so less than the male. The female often flew to the male after he had uncovered a food item, and after displacing him from it, fed on it herself. If she did not entirely consume it she would hide what remained at a different spot before retiring to a tree or bush. This behavior undoubtedly played a role in exposing stored food and making it available to the female, but it is not known what fraction of her total energy requirement was supplied in this way. Calculating η_{Rf} for the male by assuming that total ground time represented his H_{Tf} yielded a value of 5.5. However, since both birds were feeding on the same food items, and the female's feeding time mostly involved finding and swallowing what was needed, it is reasonable to assume the η_{Rf} for the male, exclusive of time spent storing food, was also about 10.5. Solving Eq. 12 for t_f and using an η_{Rf} of 10.5 for the male, [$t_f = 232.3 \text{ kJ}/(11.15 \text{ kJ h}^{-1} \times 10.5)$], yields 1.98 hours as the time he would require, given the existing food supply, simply to find and swallow what he needed to balance his energy demands. This leaves 1.82 hours, or almost half the time spent on the ground available for food storing activities. By spending the additional time on the ground in augmenting stored food supplies the male insures the continuation of a high rate of energy intake and a reduction in the cost of activity for both himself and the female. The behavior also produces no obvious penalty to the male's allocation of either time or energy to other activities because (1) the

\dot{H}_{uf} is low so the difference in H_{TD} produced by foraging beyond the time required to simply find and swallow what was needed is slight, and (2) the activity was performed on or very near the nest territory so the male was still readily available to the female; consequently the time involved did not detract from that required for reproductive behavior.

During egg laying, the female roosted out of sight within the nest. She presumably sat on the eggs at this time, so nocturnal incubation actually started as the eggs were being laid. Once the clutch was complete, diurnal incubation also started and the male began feeding the female on the nest. This undoubtedly contributed to her high degree ($\approx 93\%$) of diurnal nest attentiveness. The observed male spent more time (8.65 hours; Tables 9 and 10) and energy (96.91 kJ; Tables 11 and 12) on Ground Bouts than was observed for this group of magpies at any other time. He usually transported food directly to the female in the nest, although she occasionally emerged from it as he approached and received the food some distance away from the nest. His flying time (0.93 hours; Table 10) was more than three times that for the male observed during egg laying and the calculated H_{TD} for this male was $1.82 \times H_{fb}$ (Fig. 11). Since he was also feeding the female, the total energy requirement of this stage is represented by the sum of the H_{TD} 's for both the male and the female. The cost of foraging, however, is represented only by the Ground Bout activity of the male. Using these assumptions, η_{Rf} for the incubating stage as a unit is 4.5 [$\eta_{Rf} = (161.6 \text{ kJ} + 275 \text{ kJ}) / (11.21 \text{ kJ h}^{-1} \times 8.65 \text{ h})$]. The simplest assumption leading from this is that he has two η_{Rf} 's; one for feeding himself and one for feeding his mate, and since he probably fed her the same things he ate, the \dot{H}_{uf} (11.21 kJ h^{-1}) and η_{Rf} (4.5) should be the same for both efforts. The details of this male's foraging were harder to follow because he foraged further from the nest territory, but it appeared that he was much less involved in either finding previously stored food or storing new food. The η_{Rf} of 4.5, therefore, may be close to what the bird was actually experiencing and may be a reasonable value to use in calculating the time he had to spend foraging to satisfy the energy requirement of both himself and his mate. The calculation predicts that the male would have had to devote 3.2 hours [$t = 161.6 \text{ kJ} / (11.21 \text{ kJ h}^{-1} \times 4.5)$] of his foraging time gathering food for the female, and 5.4 hours [$t = 275 \text{ kJ} / (11.21 \text{ kJ h}^{-1} \times 4.5)$] gathering food for himself. This result indicates that under the given foraging conditions he spent 2.2 more hours per day satisfying his energy requirement than hers. Any improvement in food abundance or distribution that would increase his rate of energy intake would raise the η_{Rf} and shorten the required foraging times. Any factor that minimizes the female's H_{TD} will reduce the time the male must spend foraging for her. For example, in harsher climates, the thick, well-insulated nest characteristic of these magpies would reduce the female's thermoregulatory costs, and her high degree of nest attentiveness would reduce the cost of her activity. Both factors minimize her H_{TD} and the time required to find the food to feed her. In this study, both thermoregulatory and activity costs were negligible for the female, and her H_{TD} was about as low as could be expected ($1.2 \times H_{fb}$; Table 12; Fig. 11). Therefore, the foraging time imposed on her mate represents an absolute minimum for the given characteristics of the food supply.

In addition to some unidentifiable items picked off the ground, the incubation-stage male also captured small flies by nabbing them out of the air with his beak.

When this male, and one other who was also feeding an incubating female, were captured during this interval, they both had a bolus of small flies in the gular area under their tongues. The bolus, when removed from the mouth, was wet with saliva and very compact. This suggests that Black-billed Magpies may use saliva, as Dow (1965) has reported for the Gray Jay (*Perisoreus canadensis*), to produce large energy-rich pellets from small individual items. When the bolus reached a suitable size, it could be taken to the female (thus increasing the efficiency of transporting food to her, or later on to the chicks), or stored for later use.

No quantitative observations were made during the brooding phase of the nestling period, but it was qualitatively noted that brooding females were very attentive to new hatchlings and spent much time at the nest. Erpino (1968) also reported this for female magpies near Laramie, Wyoming. Consequently, the female's H_{TD} is probably increased only slightly by the transition from incubating to brooding, while the male's should remain high and perhaps even increase, since he may feed the female as well as the nestlings at this time.

The female of the pair observed during the late nestling period fed herself, and appeared to take an active role in transporting food to the young. However, she still spent most of the daytime in the nest tree (9.02 hours; Table 10). Most of the increase in her H_{TD} , over that of the incubating female, therefore, was due to increased flight time associated with transporting food to the nestlings. During this time the male foraged farther from the nest than the female and accumulated the bulk of the nestlings' food requirement. Although insects were abundant (qualitative observation) and were obviously being utilized, the male also often brought large food items back and deposited them on the ground near the nest tree (scraps from hawk kills, unidentified material from animal pens, and some commercial dog and cat food). He and the female then alternated in tearing up these large scraps and transporting them to the nest. Data from Johnson (1972) indicate that the diet of late nestling magpies near Pullman was composed by volume of 31.9% arthropods (29.0% insects), 20.8% earthworms, 28.1% carrion, 14.3% chordates, 3.9% commercial dog and cat food, 0.5% molluscs, 0.4% plant material, and 0.1% unknown objects. A similar variety of foods was found for nestling Black-billed Magpies in other regions of the United States (Kalmbach 1927, Owen 1956, Jones 1958). This variety indicates that during the late nestling stage, at least, parent Black-billed Magpies are opportunistic in foraging for their nestlings and take both large and the most abundant items as encountered.

The η_{RF} of the nestling stage as a unit is represented by the total energy requirement (H_{TD} of the male + H_{TD} of the female + the combined H_{TD} 's of the six nestlings) divided by the combined foraging costs of the male and female. Daily energy expenditures of the male and female (314.5 kJ and 235.0 kJ, respectively) are given in Table 12, as are their respective foraging costs (87.2 kJ and 38.4 kJ). Even though it is an underestimate, H_{TD} of each nestling during the observation period was assumed to be equivalent to its weight-dependent \dot{H}_b as calculated from Aschoff and Pohl's (1970) equation for passerines. Since these nestlings were about to fledge, a cost increment was not estimated for growth requirements. The values for the six chicks are given in Table 16, and total 715 kJ for the nest. The η_{RF} calculated for the nestling stage is $(314.5 \text{ kJ} + 235 \text{ kJ} + 715 \text{ kJ}) / (87.2 \text{ kJ} + 38.4 \text{ kJ}) = 10.1$, which is very close to that calculated for the female during egg laying. If we assume that the diet was the same for the male, female, and

TABLE 16
 METABOLIC RATES PREDICTED FOR SIX BLACK-BILLED MAGPIE NESTLINGS AT ABOUT DAY 21 OF
 THE NESTLING STAGE

Nestling number	Wt. (g) ^a 30 May	Wt. (g) ^b 7 June	Metabolism ^c kJ day ⁻¹
520	135.5	146.1	118.8
521	140.0	150.6	121.3
522	149.0	159.6	126.4
523	140.0	150.0	120.9
530	123.1	133.7	111.3
525	131.6	142.2	116.3
Total for the nest			715.0

^a Nestlings 14–15 days old when weighted at the nest. At this age they are just at the end of the linear growth phase.

^b Weight predicted by adding the mean weight change between nestling days 14 and 22 (10.6 g \pm 2.8; estimated from growth curves of 10 nestlings) to the weights measured on 30 May.

^c Calculated from the Aschoff and Pohl (1970) equation for passerines, kcal h⁻¹ = 0.0317 m^{0.726} where m is body weight (g). [(kcal h⁻¹) (24 h) (4.184 kJ kcal⁻¹) = kJ day⁻¹]

nestlings, then the calculated η_{Rf} should be the same for each parent and that segment of the parents' time devoted to foraging for the nestlings. Since no food storing was observed by either the male or the female during this period, it will be assumed that this element was not a part of the foraging time and that the calculated η_{Rf} represents an optimization of the short-term foraging effort. With this assumption, Eq. 12 can be solved for t_f to calculate the foraging time required for each adult, and by subtracting this from the total Ground Bout time for each adult, the time allocated to foraging for the nestlings can be determined. These calculations indicate that the female required 235 kJ/(9.97 kJ h⁻¹ \times 10.1) = 2.33 hours to feed herself, leaving 1.53 hours of her ground time to forage for the nestlings, and the male required 314.5 kJ/(11.34 kJ h⁻¹ \times 10.1) = 2.74 hours to feed himself, leaving 5.14 hours of his ground time to forage for the nestlings. Solving Eq. 12 for H_{TD} using the \dot{H}_{uf} for the male (11.34 kJ h⁻¹), the η_{Rf} of 10.1, and the time devoted by the male to foraging for the nestlings (5.14 hours) gives the amount of energy crossing the nestlings' gut that can be attributed to food transported to the nest by the male. This calculation yields 588.7 kJ [H_{TD}] = (11.34 kJ h⁻¹ \times 5.14 h \times 10.1)], and represents about 82% of the estimated nestling energy requirement (715 kJ; Table 16). These calculations, while being based on some tenuous simplifying assumptions, nonetheless allow one to determine the foraging commitment of each parent to itself and to the nestlings.

Another alternative would be to assume that the female contributed essentially nothing to feeding the nestlings, so that her Ground Bouts (3.86 hours) represented the time she took to feed herself at an η_{Rf} of 6.1. This would leave the energy requirement of the nestlings entirely up to the male, elevating his η_{Rf} from 10.1, as calculated above, to 11.8. While this is a rather substantial change in η_{Rf} (1.7 units), the time required to satisfy his own energy requirements at this higher η_{Rf} is 2.35 hours, just 0.39 hours less time than in the first case. It is difficult to know what a change of 1.7 η_{Rf} units means in terms of how the quality of the food source must change to allow it, but because of its position on the η_{Rf} curve (Fig. 13B) it may represent something that is ecologically impossible. On the other hand \pm 0.39 hours of foraging time is insignificant to the bird in terms of

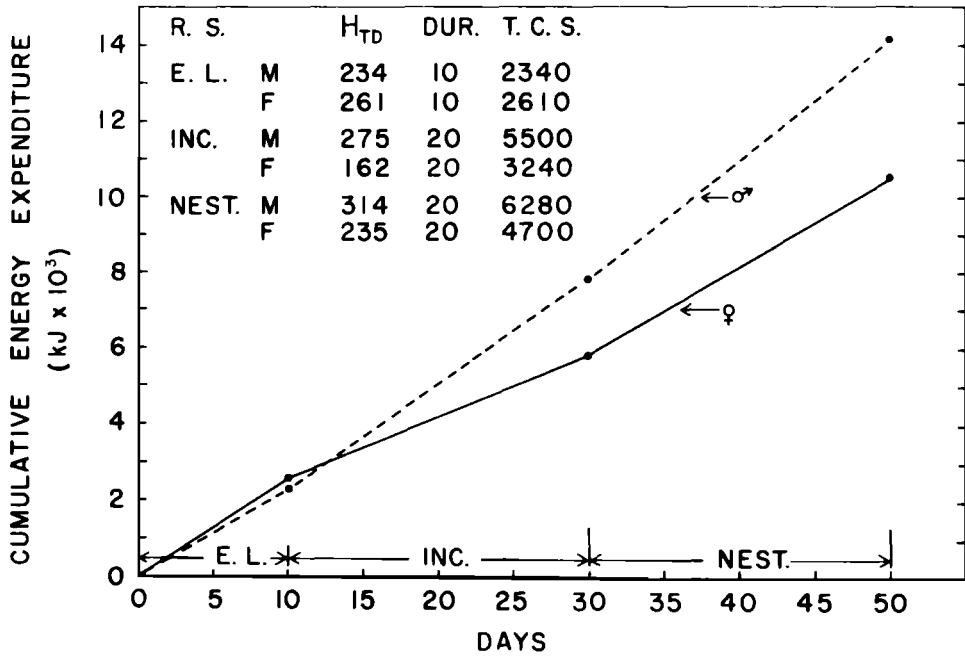


FIGURE 14. Cumulative energy expenditure ($\text{kJ} \times 10^3$) for Black-billed Magpies during various reproductive stages as a function of days during which these expenditures were incurred. The solid line represents the female, the dotted line, the male. R. S. = reproductive stage; DUR. = duration of the stage in days; T. C. S. = total cost of stage; M = male; F = female; and all other abbreviations are as in Figure 8.

either time or energy. Therefore, it seems that the first case is the more realistic of the two alternatives presented.

The cumulative energy cost of reproduction for both females and males is presented in Figure 14, where the estimated H_{TD} for each sex (Table 12) is plotted on a daily basis for each stage of the reproductive period. No adjustment has been made for the potentially lower cost of the female's brooding activity during the first part of the nestling stage, and consequently, her cumulative total is probably overestimated. By the end of the nestling stage, the cumulative total for the male exceeds that of the female by 3570 kJ.

Trivers (1972), in a discussion on the role of parental investment in sexual selection, predicts that (1) where females invest much more than males, polygamous breeding will occur, (2) where the male invests more than the female, sex-role reversal and perhaps polyandry will occur, and (3) where investment by each sex is about equal, monogamy should occur. The Black-billed Magpie is clearly monogamous, and may even mate for life (Bendire 1895, Linsdale 1937, Johnson 1972), or at least for more than one breeding season. Consequently the parental investment for each sex should, according to the Trivers concept, be about the same. Trivers (1972) rigorously defines parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parents'

ability to invest in other offspring." He places further limits on the definition by stating that parental investment can include metabolic investment in the primary sex cells, and any investment that benefits the young (feeding, guarding, etc.), but not in finding a member of the opposite sex, or subduing a member of one's own sex to obtain a member of the opposite sex. And he concludes, "Energy investment may be a good approximation of parental investment, but it is clearly sometimes a poor one. An individual defending its brood from a predator may expend little energy in the process, but suffers a high chance of mortality; such behavior should be measured as a large investment, not a small one as suggested by the energy involved."

In the case of the Black-billed Magpie, while the male expends more energy in raising the young, the female cares for and incubates the eggs, broods, and gives other forms of attention to the young, and is the more aggressive and the leader of the pair in defense of the nest from both predators and other magpies. So even though the total energetic cost of the female's activities is lower than the male's, they require considerable fidelity in their execution; therefore, their importance in terms of parental investment must be measured, as Trivers (1972) suggests, in other than energetic terms. From this point of view, the relative investments of the two sexes may not be so different, but cannot be rigorously compared until all investment costs have been expressed in a common set of units.

Molt.—Molt in the magpie is sequential through the flight feathers, and requires about 77 days. By extending the molt over a long period of time, each day's energy increment is much less than if it were performed simultaneously over a shorter time (King 1974, Ricklefs 1974, Chilgren 1975). Various investigations have shown that the total daily intake of food during the molt may be the same as in a nonmolting bird (Davis 1955), or only slightly increased (West 1960, 1968; Blackmore 1969; Chilgren 1975). Thus, even if each day's increment of cost is small, the fact that food intake increases only slightly, if at all, suggests a compensatory shift in the partitioning of energy expenditure (King 1974).

Energy for growing new feathers appeared to come primarily from feeding on the abundance of grasshoppers present during the molt. Flight times were very low (indicating that the grasshoppers were ubiquitous and could be exploited with a minimum of flying) and the greatest expenditures of time and energy were on Ground Bouts, followed closely by rest perching during Bush Bouts (Tables 9 and 11; Figs. 9 and 11). The η_{RF} 's calculated for these months (3.23 to 3.77; Fig. 13A) were the lowest for the year. Food-storing behavior was not observed, so the times associated with Ground Bouts must represent time required to exploit the grasshoppers. The low η_{RF} 's and long foraging times also indicate that the rate of energy intake was low as a result either of the low energy content of each grasshopper and/or of the low rate of capture.

July and August had mostly clear days (Fig. 2) with ground level T_c 's exceeding T_b during midday (Fig. 4; Mugaas 1976). Foraging, therefore, was mostly restricted to the cooler morning and late afternoon periods, with rest perching occupying most of the midday. Molt of the body feathers, with its accompanying exposure of patches of skin, probably reduced the insulative value of the plumage, but the warm temperatures, particularly in July and August when body molt was heaviest,

would have eliminated or at least minimized any thermoregulatory demand. Thus, it was estimated that molt was accomplished with H_{TP} 's of only 1.70, 1.61, and $1.69 \times H_{ob}$ for July, August, and September, respectively (Table 11).

The August H_{TP} is a composite of data gathered during the first half of that month, which corresponds to the period of heaviest body molt. It was at this time that energy expended on activity was lowest (Fig. 11). This suggests that there was a steady decrease in activity from the onset to the heaviest phase of the body molt, followed by a steady increase in activity to the end. This is similar to the activity pattern observed during the postnuptial molt in captive White-crowned Sparrows, *Zonotrichia leucophrys gambelii* (Chilgren 1975). The eastern White-crowned Sparrow, *Zonotrichia leucophrys leucophrys*, the White-throated Sparrow, *Zonotrichia albicollis*, and the Slate-colored Junco, *Junco hyemalis hyemalis*, have also shown a decrease in locomotor activity in cages during molt (Eyster 1954). Field data from several other species indicate that inactivity during molt is not uncommon (Blanchard 1941, Davis 1945, F. S. L. Williamson 1956, K. Williamson 1957, Zimmerman 1965, Newton 1966, Dolnik and Blyumenthal 1967, Penny 1967, Mewaldt et al. 1968, Haukioja 1971) but this is the first study that describes the behavior associated with this inactivity in more than a qualitative way.

Since the caloric value of typical food items, and the rate of capture and intake were not measured, it is not possible to determine whether or not the total daily food intake of these magpies was increased during the molt. The decrease in activity, however, indicates that the total energy intake could have remained the same throughout the molt and still allowed the bird to maintain its energy balance.

Nonproductive period.—During October, November, and December there were no productive demands on the birds, but the length of the diurnal period was progressively shortening (Figs. 8 and 9), constraining the time available for obtaining energy. As daylength decreased, flight time increased and the tempo of the birds' diurnal activity showed a steady increase from October through December (Figs. 10 and 11). The diurnal activity pattern at this time included flying relatively long distances from place to place, and then spending a short period of time on the ground before flying again. Flying, therefore, became the most expensive diurnal activity (Table 11), but it allowed the birds to exploit widely scattered patchy food sources. Under these conditions the intensity of activity increased as less and less time was available each day for either visiting known food patches or exploring the wintering area for new ones.

This pattern of activity was energetically expensive (Fig. 10) and produced high H_{TP} 's (Fig. 11) but the food patches obviously held large, high-quality food items that supported this energy demand with a minimum of foraging time. The birds were often observed finding large food items, feeding on them awhile, and then storing whatever remained before moving on. The source of all these large items is not known, but at least some of them came from carrion (hawk or owl kills, road kills, and butchering activities around the animal pens), commercial dog and cat food, and vegetable matter left in gardens (potatoes, pumpkins, squash, tomatoes, and mushrooms softened after the first frosts appeared to be favorites) that the birds themselves stored around the area. Food hiding by European Magpies, *Pica pica*, has been described by Hayman (1958), Butlin (1971), and Henty (1975) and is a trait also common to other corvids. (For a review, see Turček and

Kelso 1968; also more recently Salfeld 1969, Balda and Bock 1971.) But for the Black-billed Magpie, it would be interesting to know (1) how much time each day was spent checking foods already hidden, (2) how much stored as opposed to newly found food was eaten each day, (3) how much of the food stored by an individual was actually reclaimed by that individual, and (4) how much of the food stored by one individual was found by others. This aspect of the magpie's winter behavior and ecology merits further study.

Since some of the foraging time (Ground Bouts) involved food storing, η_{rf} 's calculated using the total time spent on Ground Bouts to estimate H_{rf} (5.28, 5.19, and 5.99; Fig. 13B) are lower than if only the time involved in finding and swallowing food were used in making the calculations. The very short amounts of time (4–5 hours; Fig. 9) spent on Ground Bouts indicates that the food items being swallowed allowed for a rapid rate of energy intake. Consequently, it may not be far wrong to assume that the η_{rf} , exclusive of food storage time, was about the same as that calculated for the egg-laying female, or the nestling-stage adults (10.1 and 10.5; Fig. 13A). Using this assumption, and the lower of the two possible η_{rf} 's (10.1) in solving Eq. 12 for t_f , it is possible to estimate that finding and swallowing required 2.36, 2.59, and 2.58 hours, while finding and storing occupied 2.15, 2.45, and 1.78 hours of the total Ground Bout time for October, November, and December, respectively.

During this three-month interval the time devoted to Ground Bouts remained fairly constant (4–5 hours), while time allocated to flight increased and that devoted to Bush and FTPR Bouts decreased. This behavior preserved ground foraging time in the face of a steadily decreasing number of daylight hours. The allocation of more time to Air Bouts, even though time spent on Ground Bouts was stable could imply: (1) the frequency of visits to each food patch was increased, (2) less time was spent on old patches and more on searching new areas (perhaps looking for new food items to store on known food patches), or (3) the number of food patches utilized increased. Since the time spent on Bush and FTPR Bouts did decrease directly with the decrease in the number of daylight hours (Fig. 9) it may be fair to speculate that they represent a reserve of time that could be allocated to additional flying and/or foraging if needed, as predicted by the "principle of stringency" (Wilson 1975).

Recapitulations.—An organism's food and feeding habits have a primary influence on the type of activity it will perform (Linsdale 1937). The foraging behavior of the Black-billed Magpie appeared to be regulated by the size and distribution of the food items being utilized. A general qualitative summary of these observations is given in Table 17. Ground time in the table refers specifically to that required by an individual to satisfy its own energy requirement, and is related to the size of the items being utilized. Large food items provided for a high rate of energy intake and a rapid satisfaction of individual energy demands, while use of small items yielded a low rate of energy intake and required a prolonged foraging time to balance the energy equation. Table 17 shows that the time spent on flight is related to the pattern of food distribution (ubiquitous, concentrated in a single patch, or concentrated in several widespread patches) and to behavioral demands (incubation and nestling stages in particular). Except in the case of egg-laying females, the annual variation in H_{rd} (Fig. 11) was due primarily to small changes in the time spent in flight (total variation observed was less than two hours),

TABLE 17
DISTRIBUTION, ABUNDANCE, AND SIZE OF BLACK-BILLED MAGPIE FOOD ITEMS IN RELATION TO
BEHAVIORAL CHARACTERISTICS USED IN EXPLOITING THEM

Phenological event	Qualitative characteristics of major food items			Behavioral characteristics					
	Size selected	Energy content	Distribution ^a	Finding and:			Rate of intake	Total time	
				Sw	St	Tr ^b		Ground ^c	Flight
Egg laying									
Male	large	high	COP	+	+	0	fast	short	short
Female	large	high	COP	+	0	0	fast	very short	very short
Incubation									
Male	small + large ^d	low high	U S	+	0	+	slow	very long	moderate
Nestling									
Male	large ^e small ^e	high low	S U	+	0	+	fast	long	long
Female	large ^e small ^e	high low	S U	+	0	+	fast	short	moderate
Molt	small ^f	low	U	+	0	0	slow	long	short
Oct.–Dec.	large	high	CMP	+	+	0	fast	short	long

^a Abbreviations as follows: COP, concentrated in one patch; CMP, concentrated in many patches; S, scattered; U, ubiquitous.

^b Abbreviations as follows: Sw, swallowing; St, storing; Tr, transporting.

^c This includes the time required to swallow their own energy requirement as well as the time for storing food or finding food for other individuals.

^d While some large items were utilized, the males fed mostly on small items.

^e Any food item encountered, large or small, was utilized.

^f Grasshoppers were the most abundant small item available at this time, and the magpies appeared to feed almost exclusively on them.

which emphasizes the point that because flight time is expensive, it is the critical element in the bird's behavioral repertoire and is used very conservatively.

The basic premise stated by Linsdale has been further refined in the recent literature on feeding theory, which states that foraging behavior and food selection should maximize foraging efficiency and fitness (Schoener 1971, Krebs 1973, Pulliam 1973, Pyke et al. 1977). The η_{RF} 's calculated and predicted for the various composite days in this investigation give qualitative clues about the foraging efficiencies of the magpie at different times during the annual cycle. The calculated values cluster in two groups (Fig. 13A, B). The high group (10.1 to 10.5) would indicate a fast rate of energy intake and a high (perhaps maximized) foraging efficiency. The other group (3.2 to 4.5) indicates a slow rate of energy intake and a low foraging efficiency.

Individuals in the high η_{RF} group were behaving like *time minimizers* (Schoener 1971). This type of foraging is expected when there is a fixed energy requirement, with no gain in fitness being realized if the requirement is exceeded, and there is a time requirement for other activities. Such is the case for magpies during the egg-laying stage, nestling stage, and months of October through December. During these times it appears that foraging efficiency is being maximized, foraging time for individual energy requirements minimized, and time left for other activities maximized. The high η_{RF} 's also reflect the omnivorous nature of the diet and

the ability to capitalize on almost any food encountered, particularly large items that have a high energy content.

The low η_{RF} 's of the incubating stage male, and birds during the molt period, are difficult to place in the context of foraging theory. The evidence indicates that at these times the birds were not behaving like either *time minimizers*, or *energy maximizers* (Schoener 1971). The unavoidable conclusion seems to be that during these times the magpies were simply not maximizing foraging efficiency. Smith and Sweatman (1974) point out that, considering the selective compromises that organisms make in dealing with their environment, there is no need to assume that truly optimal foraging should always be the rule. This leaves us searching for alternative explanations for these situations. Clues for these come from considerations of how "behavior at one point in time *will* affect the optimal behavior at a later point in time" (Pyke et al. 1977), and the advantages of reducing the cost of activity during a prolonged period of productive requirements.

During the nesting period, behavior became focused on an area around the nest and foraging was primarily restricted to that area. This area was actively defended by the pair, particularly the female, from the late stages of nest building up through the nestling stage. During the incubation period, insect prey was becoming more abundant all over the study area, and because the chance of encountering successive hatches of insects should increase as the days continued to warm, they represented a readily available, rapidly renewing resource. The combined energy demand of the male and female was also lower at this time than during either of the other two reproductive stages. It could be, therefore, that since energy requirements were low and the pair had a nearly exclusive bid on the food items within their defended area, the male was "managing" the resources of his restricted foraging area for a "sustained yield" (Pyke et al. 1977) by selecting mostly insects and bypassing most large food items. This would preserve the large items for a time when energy demands became more intense such as during the later nestling stages. The behavior would be particularly beneficial if the rate of renewal of large items was low, or even to some extent dependent on the food-storing activities of the pair. This explanation suggests that behavior in this case is favoring long-term fitness rather than maximizing short-term foraging efficiency (Pyke et al. 1977) and although it is tenuous, it should be testable.

During the molt period the adults became very secretive and essentially divided their time between foraging and perching quietly in the shade. Exploiting the ubiquitous grasshopper population allowed them to minimize the time required to fly from a rest area to a feeding area and completely eliminated the need to fly from food patch to food patch. Thus, by utilizing the grasshoppers and foraging at less than maximum efficiency, flight time and hence H_{Tf} were kept at a minimum. Since the \dot{H}_{uf} is not large in comparison to flight, extending the foraging time has less of an effect on H_{Tf} than a small increase in flight time to explore for large food items. Minimizing H_{Tf} could be particularly important for the molting birds if some of the cost of molt is compensated by a depressed activity budget. There may be, in addition, some nutrient requirement during the molt that favors the use of grasshoppers over other items. Again, the proposed explanation would favor long-term fitness over maximizing short-term foraging efficiency (Pyke et al. 1977).

MINIMIZING H_{TJ} THROUGH ADAPTIVE USE OF TIME AND ENERGY

Many variables contribute to H_{TJ} (Table 2) but they can all be placed into one of two adaptive sets. Variables such as basal metabolism, thermoregulation, and production represent physiological adaptations, that when viewed collectively comprise one set. Because an individual cannot directly control the time and energy requirements of the variables within this set, it may be regarded as the obligatory component of H_{TJ} . Behavioral adaptations comprise the second set. The time and energy requirements associated with this set can be manipulated behaviorally by the individual. Therefore, the set may be regarded as the facultative component of H_{TJ} . In their simplest form, the variables that make up this set can be reduced to the activities performed within each Bout, and their energy requirement amounts to the per-hour cost of behavior.

Since some form of behavior is ultimately involved in obtaining the energy required by the variables in the physiological set, it exerts a driving force on the behavioral set. The degree of flexibility in the behavioral manipulation of time and energy resources, and hence the energetic cost of the behavior, will depend on (1) how stereotyped the behavior pattern may be, and (2) the availability of suitable environmental resources. Therefore, H_{TJ} has some fixed minimal requirement associated with it that will be determined by the variables in the physiological set, and a realized value whose magnitude will be determined by the per-hour cost of activity. The adaptive use of time and energy should allow the animal to integrate its physiological capabilities behaviorally with the biotic and abiotic components of the environment in such a way that, given a particular phenological circumstance, H_{TJ} will be kept as low as possible.

Data for the magpie support this concept. As demands on the resources of time and energy changed during the year so did the cost of activity and the thrust of the birds' behavior (Fig. 11). The data for any one composite day imply that these demands were met with the lowest possible H_{TJ} and that behavioral adjustments were primarily responsible for accomplishing this. These adjustments are summarized below, and their effectiveness was undoubtedly enhanced by the temporal separation of reproduction and molt. (1) Magpies demonstrated the tendency to minimize energy expenditure via the conservation of movement (a habit that is probably common to the entire animal kingdom). Hence, with the exception of Air Bouts, the most time and energy within the various Bouts was allocated to the least expensive activities (Tables 9, 10, and 12). (2) We estimated that the activity having the greatest impact on H_{TJ} was flight. Regardless of changes occurring within or between other Bouts, it was the small amounts of time added to or subtracted from Air Bouts that markedly influenced the per-hour cost of activity and H_{TJ} . By restricting flight time to that which just accomplished the required behavior, H_{TJ} was held to a minimum. (3) During productive periods (egg laying and molt), nonproductive costs were minimized, primarily by keeping the rate of activity down. (4) The \dot{H}_{if} was low and fairly stable throughout the year so that any one day's H_{TJ} was a function of the time spent on the ground finding and swallowing food. The time required to find and swallow the required food in turn was determined by the characteristics of the food resource being utilized. Consequently, η_{if} varied during the year, but always in such a way that long-term fitness seemed to be enhanced. The role that food-storing plays in the overall foraging effort needs to be clarified. (5) Maintaining a territory only during

the reproductive period minimized that responsibility. In addition, territorial disputes were infrequent and brief when they did occur. Pursuit flights were kept to a minimum and much of the disagreement was settled by posturing and calling. (6) Selecting a winter roost that minimized convective and radiative heat loss, and avoiding long exposure to $T_e > T_{uc}$ during the summer, both operated to minimize thermoregulatory demands.

It is, therefore, our prediction that, in general, selection should operate to minimize H_{TD} by minimizing the time-related cost of the variables associated with each adaptive set (integrating the magnitude of the daily energy cost and gross efficiency as it relates to the duration of a process), and that those individuals (or populations) that can realize a given benefit with an H_{TD} that is lower than that of their competitors will have a selective advantage. Theoretically this view is supported by the concept of exploitation efficiency (Fisher 1930, Emlen 1978) which as a generalized expression can be written as

$$\eta_E = B_T/C_T \quad (13)$$

where η_E is exploitation efficiency, B_T is the total of all the possible benefits attained in a given time interval, and C_T is the total of all the costs incurred in that same interval. Some of the benefits and some of the costs can be compared directly using energy as a common currency (energy gains:production::cost of activity:cost of production) but others cannot because their value cannot be gauged only in terms of energy (reproductive success, social position, predator defense, mineral and fluid balance, etc.). Since H_{TD} includes all the costs that can be evaluated using energy as a currency, it represents a prominent component in the denominator of Eq. 13, and should exert considerable influence on η_E . The relationship between η_E and H_{TD} is inverse so that one can predict that for any given phenological event η_E will be enhanced if H_{TD} can be kept at a minimum.

COMPARISON OF TIME-BUDGETS OF BLACK-BILLED AND YELLOW-BILLED MAGPIES

Mating systems, territoriality (defined for both species of magpie as an area around the nest defended against conspecifics), courtship and copulation, nest structure and location, clutch size, incubation, fledging success, flocking, and roosting have been described for the Black-billed Magpie in North America by several authors (Dice 1917; Kalmbach 1927; Linsdale 1937, 1946a; Evenden 1947; Owen 1956; Brown 1957; Jones 1960; O'Halloran 1961; Erpino 1968; Johnson 1972) and for the Yellow-billed Magpie by Linsdale (1937, 1946b), and Verbeek (1970, 1972a, 1972b, 1973). Linsdale (1937, 1946a, 1946b), and, to a greater extent, Verbeek (1970, 1973) have compared the natural histories of these species, and now it is possible also to compare their time budgets. Verbeek (1972a) described the Yellow-billed Magpie's behavior in terms of traditional categories (feeding, resting, preening, bathing, building, flying, incubating, egg laying, brooding, territory defense, drinking, and storing acorns), and presented the data as the percent of the daylight period spent on each behavior in central California. Consequently, the data are not quantitatively comparable with those of this investigation, but some qualitatively important differences and similarities are itemized below.

By mid-September, molt was essentially completed in both species, and it is at this time that Yellow-billed Magpies, but not Black-billed Magpies, increase

the time spent defending their nesting territories (Verbeek 1972a, 1973). The Yellow-billed Magpie defends a breeding territory throughout the year, but most intensely during the fall, winter, and spring. The Black-billed Magpie defends a similar territory but only from about mid-nestbuilding through the nestling stage.

Verbeek (1972a, 1973) reports that the female Yellow-billed Magpie spends most of her time in feeding activity during egg laying (68% of the daylight period) and that the increased food intake supported the cost of egg production. The female Black-billed Magpie spends most of her time during egg laying in Bush Bouts and little on the ground feeding (Table 10). The difference in female patterns between these species is probably related to the type of food being utilized in each place. The Black-billed Magpie's food resources at this time are large items while the Yellow-billed Magpie's food, by contrast, is an invertebrate fauna (primarily insects) that just starts to increase at the onset of egg production (Verbeek 1973). Although this must represent an abundant, ubiquitous food source, each item would be small and contain less energy than the large items used by the Black-billed Magpie. Consequently, the Yellow-billed Magpie would have to spend more time feeding to acquire the extra energy needed for egg production.

Females of both species devoted little time to flying during egg laying (Verbeek 1972a; Table 10), indicating that there is a common behavioral mechanism operating to decrease the cost of activity during egg production. Even though the female Yellow-billed Magpie spent a larger amount of time on the ground feeding, and may have expended more energy in this activity than the female Black-billed Magpie, it is still reasonable to assume that, unless she ran or walked continuously while on the ground, her overall cost of activity and H_{TD} should still have been reduced.

During the late nestling stage, the female Black-billed Magpie observed in this study spent most of her time in the nest bush perched near the nest (Table 10), while the male was more wide ranging in his activities and often flew off the nesting territory in search of food. In contrast to this, Verbeek (1973) reports that it is the female Yellow-billed Magpie that is more far ranging and forages off the territory during the nestling stage.

Verbeek's (1970) investigation indicates that his study population of Yellow-billed Magpies fed primarily on ground-dwelling invertebrates and had a much more restricted diet than we qualitatively observed for the Black-billed Magpie. The milder climate associated with the Yellow-billed Magpie's distribution would make invertebrates, especially insects, abundant over longer periods of time, and the birds in California obviously take advantage of this. Kalmbach (1927) also reported a greater use of invertebrates (especially insects) by the Yellow-billed than the Black-billed Magpie. While the above comparisons suggest the Yellow-billed Magpie may be more of a food specialist than the Black-billed Magpie, the data are too limited to establish this point. More comparative work needs to be done on the food habits of these two species, particularly with respect to how they may be responsible for interspecific differences in time and energy budgeting.

COMPARISONS OF H_{TD} FOR SEVERAL SPECIES OF BIRDS AND THE TECHNIQUES USED IN ESTIMATING THEM

The cost of existence has been estimated for a number of species of birds by a variety of techniques, and these have been reviewed by Utter (1971), Gessaman

(1973), and King (1974). In a more recent review, Walsberg (In press) has calculated regression equations for H_{TD} as a function of body mass for all species considered,

$$\log H_{TD} = \log 11.87 + 0.608 \log m \quad (14)$$

for those that feed in flight,

$$\log H_{TD} = \log 13.64 + 0.663 \log m \quad (15)$$

and those that do not feed in flight,

$$\log H_{TD} = \log 8.96 + 0.653 \log m \quad (16)$$

where H_{TD} is as described above and m is body mass (g). The data from which these equations were developed are heterogeneous with respect to methods used in obtaining them and were treated to average out variation due to multiple estimates for species, seasonal variation, and body mass for sexually dimorphic species (Walsberg In press). Nonetheless, they indicate that H_{TD} does not parallel basal metabolism as a function of mass (reflecting a greater intensity of activity in small birds), and H_{TD} averages about 57% greater for small (<80 g) birds that feed on the wing than for those that do not. In addition, Walsberg (In press) found no difference in separate regressions for passerines and nonpasserines. However, because these equations were developed from such a heterogeneous body of data, and because H_{TD} shows considerable annual variation (this investigation and Walsberg 1977), the values predicted by these equations may not be a good yardstick upon which to judge the accuracy or inaccuracy of any one estimate. But since the reliable modeling of energy flow through populations depends on reasonably accurate estimates of H_{TD} , it is important to know what constitutes a good estimate.

Turnover rates of D_2O^{18} in body water were used to estimate CO_2 production, and consequently H_{TD} in free-living Mockingbirds, *Mimus polyglottos* (Utter 1971), Purple Martins (Utter and LeFebvre 1970), and House Martins (Hails and Bryant 1979). Because validation studies of this technique by Hails and Bryant (1979), and other investigators (Lifson et al. 1955; McClintock and Lifson 1957, 1958a, 1958b; Lee and Lifson 1960; Lifson and Lee 1961; LeFebvre 1964; Mullen 1970, 1971a, 1971b) have shown close agreement (5–10% between CO_2 output calculated from isotope turnover, and that actually collected, the estimates for the Mockingbird, Purple Martin, and House Martin may be the best from which to begin evaluating others. In addition, the measurements for Purple Martins, Mockingbirds, and House Martins are directly comparable because in each case they are for birds experiencing reproductive (exclusive of egg laying) but not thermoregulatory demands above a basal level. Values for the Mockingbird range from 1.35 to $2.10 \times H_{ab}$ and may represent the range to be expected for a species that does not feed on the wing. Values for the Purple Martin ranged from 2.30 to $3.70 \times H_{ab}$, and those for the House Martin from 2.22 to $5.27 \times H_{ab}$ (with means of 3.1 and $3.3 \times H_{ab}$ for males and females, respectively). The values for the latter two species may be representative of birds that do feed on the wing (Table 18; see also Walsberg In press).

Utter (1971) also estimated H_{TD} for Mockingbirds and Purple Martins using the TAL method, and these values are presented for comparison with the D_2O^{18} values in Table 18. In both species, the TAL estimates tend to be higher than

TABLE 18
SELECTED H_{70} VALUES

Species	Body wt. (g)	Conditions	H_{70} (kJ day ⁻¹)	H_{70}/H_{60}	Method ^a	Source
<i>Buteo regalis</i> ♀	1983 ^b	Ida., nestlings	1110	1.9	D	Wakely 1978
<i>Buteo regalis</i> ♀	1983 ^b	Ida., nestlings	1233	2.0	D	Wakely 1978
<i>Buteo regalis</i> ♂	1237 ^b	Ida., nestlings	1381	3.3	D	Wakely 1978
<i>Buteo regalis</i> ♂	1237 ^b	Ida., nestlings	1566	3.8	D	Wakely 1978
<i>Branta leucopsis</i>	1550	Neth., winter	857.7-1000	2.0	H	Ebbinge et al. 1975
<i>Eudocimus albus</i>	881	S. Fla., late nestlings	688.7	1.9	E	Kushlan 1977
<i>Buteo platypterus</i>	473	N. Y., incubating	430	1.3	H	Mosher and Matray 1974
<i>Asio Flammeus</i>	406	Ill., winter	787	5.4	A	Graber 1962
<i>Recurvirostra americana</i> ♀	316	Ore., prenesting	623	4.6	D	Wiens and Innis 1973
<i>Recurvirostra americana</i> ♀	316	Ore., incubating	542	4.0	D	Wiens and Innis 1973
<i>Recurvirostra americana</i> ♀	316	Ore., nestlings	467	3.5	D	Wiens and Innis 1973
<i>Recurvirostra americana</i> ♀	316	Ore., fledglings	408	3.0	D	Wiens and Innis 1973
<i>Recurvirostra americana</i> ♂	316	Ore., prenesting	623	4.6	D	Wiens and Innis 1973
<i>Recurvirostra americana</i> ♂	316	Ore., incubating	456	3.4	D	Wiens and Innis 1973
<i>Recurvirostra americana</i> ♂	316	Ore., nestlings	461	3.4	D	Wiens and Innis 1973
<i>Recurvirostra americana</i> ♂	316	Ore., fledglings	406	3.0	D	Wiens and Innis 1973
<i>Asio otus</i>	252	Ill., winter	665	6.1	A	Graber 1962
<i>Elanus caeruleus</i>	243	S. Africa, nonbreeding	411	3.2	D	Tarboton 1978
<i>Zenaidra macroura</i>	120	N. Dak., autumn	297	4.7	B	Schmid 1965
<i>Agelaius acadicus</i>	96	Ill., winter	247	3.4	A	Graber 1962
<i>Progne subis</i> ♀	47.3	Minn., nestlings	203	3.4	C	Utter and LeFebvre 1970
<i>Progne subis</i> ♀	48.1	Minn., nestlings	182	3.0	C	Utter and LeFebvre 1970
<i>Progne subis</i> ♂	48.8	Minn., nestlings	139	2.3	C	Utter and LeFebvre 1970
<i>Progne subis</i> ♂	51.8	Minn., nestlings	159	2.5	C	Utter and LeFebvre 1970
<i>Progne subis</i> ♀	47.7	Minn., nestlings	207	3.4	D	Utter 1971
<i>Progne subis</i> ♀	47.7	Minn., nestlings	227	3.7	D	Utter 1971
<i>Progne subis</i> ♂	50.3	Minn., nestlings	162	2.6	D	Utter 1971
<i>Mimus polyglottos</i> ♀	50.9	N.J., incubating	114 ^c (115) ^d	1.8 ^b (1.9) ^d	C,D	Utter 1971
<i>Mimus polyglottos</i> ♀	47.4	N.J., nestlings	176 ^c (121) ^d	3.0 ^c (2.0) ^d	C,D	Utter 1971
<i>Mimus polyglottos</i> ♀	48.2	N.J., disrupted cycle	124 ^c (118) ^d	2.1 ^c (1.9) ^d	C,D	Utter 1971

TABLE 18
CONTINUED

Species	Body wt. (g)	Conditions	H_{70}^b (kJ day ⁻¹)	H_{70}/H_{mb}	Method ^a	Source
<i>Mimus polyglottos</i> ♂	44.5	N.J., nestlings	73 ^c (106) ^d	1.3 ^c (1.7) ^d	C, D	Utter 1971
<i>Mimus polyglottos</i> ♂	49.5	N.J., nestlings	119 ^c (147) ^d	1.9 ^c (2.4) ^d	C, D	Utter 1971
<i>Mimus polyglottos</i> ♂	44.8	N.J., nestlings	116 ^c (113) ^d	2.0 ^c (1.8) ^d	C, D	Utter 1971
<i>Mimus polyglottos</i> ♂	46.3	N.J., unmated	125	2.1	D	Utter 1971
<i>Mimus polyglottos</i> ♂	46.3	N.J., preincubation	127	2.1	D	Utter 1971
<i>Mimus polyglottos</i> ♂	46.3	N.J., incubation	130	2.1	D	Utter 1971
<i>Mimus polyglottos</i> ♂	46.3	N.J., nestlings	126	2.1	D	Utter 1971
<i>Mimus polyglottos</i> ♂	46.3	N.J., fledglings	141	2.3	D	Utter 1971
<i>Mimus polyglottos</i> ♂	46.3	N.J., fledglings	124	2.0	D	Utter 1971
Several	6.6-47.0	Alas., breeding	—	2.0	E	West and DeWolfe 1974
<i>Spiza americana</i> ♂♂	35.0	Kans., breeding	100	2.4	C	Schartz and Zimmerman 1971
<i>Passer domesticus</i>	29.0	Ill., Jan.	117	3.2	E	Kendeigh 1973
<i>Passer domesticus</i>	29.0	Ill., Aug.	83	2.3	E	Kendeigh 1973
<i>Calcarius lapponicus</i> ♂♂	28.6	Alas., breeding, early	167	4.6	D	Custer and Pitelka 1972
<i>Calcarius lapponicus</i> ♂♂	28.6	Alas., breeding, late	105	2.8	D	Custer and Pitelka 1972
<i>Calcarius lapponicus</i> ♀♀	25.4	Alas., egg laying	134	4.0	D	Custer and Pitelka 1972
<i>Phainopepla nitens</i> ♂♂	24.0	Calif., nestlings	89.2 ^c	2.8 ^c	D	Walsberg 1978
<i>Phainopepla nitens</i> ♀♀	24.0	Calif., nestlings	89.0 ^c	2.8 ^c	D	Walsberg 1978
<i>Anthus spinoletta</i>	22.0	Eng., winter	50.0	1.6	G	Gibb 1956
<i>Parus major</i>	19.4	Eng., winter	94.0	4.5	F	Gibb 1957, 1960
<i>Spizella aborea</i>	18.0	Alas., breeding	84-105	1.8-2.1	E	West 1973
<i>Delichon urbica</i> ♂	17.8	Eng., nestlings	79.4 ^f	3.1 ^f	D	Hails and Bryant 1979
<i>Delichon urbica</i> ♀	17.8	Eng., nestlings	86.2 ^g	3.3 ^g	D	Hails and Bryant 1979
<i>Nectarina famosa</i>	13.5	Kenya, breeding	71	3.4	D	Wolf 1975
<i>Oreotrochilus estella</i> ♀	8.1	Peruvian Andes, incubating	77	4.9	D	Carpenter 1976
<i>Oreotrochilus estella</i> ♀	8.1	Peruvian Andes, late nestling	102.1	6.5	D	Carpenter 1976
<i>Oreotrochilus estella</i> ♂	8.1	Peruvian Andes, winter with torpor	35.7	2.3	D	Carpenter 1976
<i>Oreotrochilus estella</i> ♀	8.1	Peruvian Andes, winter with torpor	51.9	3.3	D	Carpenter 1976
<i>Colibri coruscans</i> ♀	7.6-8.7	Peruvian Andes, nestlings or fledglings	58.1 ^h -48.0 ^h 56.0 ⁱ -39.1 ⁱ	5.6 ^h -7.2 ^h 3.7 ⁱ -5.4 ⁱ	D	Hainsworth 1977

TABLE 18
CONTINUED

Species	Body wt. (g)	Conditions	H_{np}^{in} (kJ day ⁻¹)	H_{np}/H_{mb}	Method ^a	Source
<i>Calypte anna</i> ♂♂	4.8	Central Calif., breeding, 21 Jan.	28	3.0	D	Stiles 1971
<i>Calypte anna</i> ♂♂	4.8	Central Calif., breeding, 22 Mar.	33	3.6	D	Stiles 1971
<i>Calypte anna</i> ♂♂	4.8	Central Calif., feeding territory	29	3.2	D	Stiles 1971
<i>Calypte anna</i> ^j ♂	4.8	Central Calif., feeding territory	30 ^h -22 ⁱ	3.2 ^h -2.4 ⁱ	D	Calder 1975
<i>Calypte anna</i> ^k ♂	4.8	Central Calif., breeding, Jan.	34 ^h -24 ⁱ	3.7 ^h -2.6 ⁱ	D	Calder 1975
<i>Calypte anna</i> ^k ♂	4.8	Central Calif., breeding, Mar.	37 ^h -28 ⁱ	4.1 ^h -3.1 ⁱ	D	Calder 1975
<i>Calypte anna</i> ♀	4.8	Ariz., incubating, 17 Feb.	26	2.9	D	Calder 1975
<i>Calypte anna</i> ♀	4.8	Ariz., brooding, 22 Feb.	31	3.4	D	Calder 1975
<i>Calypte anna</i> ♀	4.8	Ariz., brooding, 24 Feb.	30	3.2	D	Calder 1975
<i>Calypte anna</i> ♀	4.8	Ariz., incubating, 30 Apr.	22	2.4	D	Calder 1975
<i>Stellula calliope</i> ♀	3.2	Wyo., incubating, July	31	5.2	D	Calder 1971

^a A, pellet analysis; B, crop contents; C, doubly labeled water; D, time-activity laboratory; E, extrapolations from laboratory data; F, extrapolations from food consumption of captives; G, observation of feeding rate and excretory rate; H, observation of feeding rate; I, observation of feeding rate combined with laboratory data.

^b Weights used by Wakely (1978) represent the means for three adult females and two adult males by Imler (1937).

^c Based on a respiratory quotient of 0.8.

^d Concurrently determined time-activity laboratory estimate.

^e Averages calculated from Walsberg (1978).

^f Average of 10 males.

^g Average of 16 females.

^h Nighttime, homeothermic.

ⁱ Nighttime, torpid.

^j Recalculated by Calder from Pearson (1954).

^k Recalculated by Calder from Stiles (1971).

D_2O^{18} estimates (calculated using a respiratory quotient of 0.8) made at comparable stages of the reproductive period. The differences between the two methods are greatest for Mockingbirds. Utter (1971) "lumped" all nonflight activities from his behavioral observations together, and assigned them an energy equivalent of $2.0 \times \dot{H}_b$. This is equivalent to deciding that when the birds were not flying, they were hopping or walking, which overestimates H_{TD} , especially for the Mockingbird where about 64% of the daylight period was spent in nonflight activities, as compared with about 15% for the Purple Martin. When Utter (1971) corrected the Mockingbird's H_{TD} by assigning an energy equivalent of $1.6 \times \dot{H}_b$ to nonflight activity (which is what Kale 1965 measured for nonflight activity in the Long-billed Marsh Wren, *Telmatodytes palustris griseus*), there was close agreement between the TAL and D_2O^{18} estimates. This illustrates that reasonably accurate estimates of H_{TD} can be made with the TAL method if the time budget is accurately known, if measured energy equivalents can be assigned to behaviors, and if thermal conditions surrounding a bird are known.

Stiles (1971), and Calder (1971, 1975) have both used the TAL method to estimate H_{TD} for the Anna Hummingbird, *Calypte anna*, (Table 18). Both authors made careful time-activity budgets for the birds, and then estimated energetic costs using Lasiewski's (1963) measurements of the costs of perching, flying, and torpor in Anna Hummingbirds. Consequently, their estimates are probably reasonably accurate. Likewise, TAL estimates for the Malachite Sunbird, *Nectarina famosa* (Wolf 1975), an Andean hummingbird, *Oreotrochilus estella* (Carpenter 1976), a Peruvian hummingbird, *Colibri coruscans* (Hainsworth 1977), and the Phainopepla, *Phainopepla nitens* (Walsberg 1978) are also probably realistic (Table 18) because these factors were also accounted for in these investigations.

Calder (1975) also used the TAL method to estimate the H_{TD} of an incubating Calliope Hummingbird, *Stellula calliope*, near Moran, Wyoming (Table 18). But, unlike the data for the incubating Anna Hummingbird, he made no correction for the effective insulation of the nest during the cold (4.4°C) nighttime period of incubation and believes that the estimate is too high. TAL estimates made for the Lapland Longspur, *Calcarius lapponicus* (Custer and Pitelka 1972), Dickcissel, *Spiza americana* (Schartz and Zimmerman 1971), Black-shouldered Kite, *Elanus caeruleus* (Tarboton 1978), Ferruginous Hawk, *Buteo regalis* (Wakely 1978), and American Avocet, *Recurvirostra americana* (Weins and Innis 1973) are also probably too high (Table 18) because of the magnitude of the equivalents assigned to various complex behaviors and/or the manner in which the thermoregulatory requirements were evaluated.

Estimates of H_{TD} based on measurements of existence energy (Table 18, Ken-deigh 1973, West 1973, West and DeWolfe 1974, Kushlan 1977) are difficult to evaluate because of the practice of including an arbitrary term in the energy equation that is supposed to account for the cost of free existence. Inclusion of this term is based on the assumption that free-living birds are more active than caged birds. This seems tenuous at best, however, for two reasons. First of all a captive bird may actually spend more or even less time hopping and fluttering in a cage than in freedom, so there is no way to relate the cost of nonflight activity in cages to nonflight activity in freedom, and secondly, the energy equivalent that is used for calculating the value of this term is arbitrarily determined. It would seem most reasonable when using this method to eliminate the term for free

existence and simply add increments for flight and production to the basic existence energy measurement. But even then, there would be no way of knowing whether one were overestimating or underestimating the cost of non-flight activity, and there would still be some difficulty in evaluating the reliability of the estimate.

Gibb (1956) observed feeding and excretion rates of Rock Pipits, *Anthus spinoletta*, on the coast of Cornwall during the winter, and estimated H_{TD} from the observed gross energy intake minus the observed excretory loss. The resulting estimate of $1.6 \times H_{tb}$ (Table 18) seems too low for a bird of that size exposed to an average daily temperature of 4.5°C. This value could be better assessed, however, if the r_b of these pipits and their daily time budget were known. An elegant study using the same technique on wintering Barnacle Geese, *Branta leucopsis* (Ebbinge et al. 1975), yielded an estimate of $2.0 \times H_{tb}$ (Table 18). These investigators thought their estimate was too low because they had not accounted for the effect of the geese selecting food having a lower fiber content than the samples they analyzed.

Mosher and Matray (1974) measured digestive efficiency, existence energy, and the average energy composition of prey for the Broad-winged Hawk, *Buteo platypterus*. Then by observing the daily food intake of an incubating female, they calculated an H_{TD} for her of $1.3 \times H_{tb}$ (Table 18). This value agrees well with the estimate made in this investigation for an incubating magpie (Table 12).

Some other techniques that have been used to estimate H_{TD} are pellet analysis (Graber 1962), crop contents (Schmid 1965), and extrapolations from the food consumption of captives (Gibb 1957, 1960). In spite of the fact that these estimates were made during the fall and winter (Table 18) when there would have been a thermoregulatory requirement associated with them, they all seem too high, suggesting problems with the techniques.

Of the methods used to date, it is apparent that TAL estimates, if performed properly, provide an inexpensive and reasonably good estimate of H_{TD} . Although all the variables required for this type of analysis are subject to error, especially since they are often extrapolated or predicted from values for other species, it is the cost of activity that provides the greatest potential for confusion. This is unfortunate because, as has been demonstrated in this investigation and others (Walsberg In press), activity costs are most responsible for variations in H_{TD} . The problem can be minimized, however, if behavior is described using activities for which energy costs have been measured. The system used in this investigation illuminates some helpful suggestions and the validity of some simplifying assumptions:

(1) Variations in the cost of nonflight daytime activity are small, so unless the data are wanted for some other purpose, it is probably not necessary to detail all of this activity. An adequate estimate could be made using an "average" multiple of \dot{H}_b derived from short samples of the activities performed during nonflight periods. Exceptions to this of course would occur when a significant part of the nonflight daytime period is spent doing something unusual like sleeping or running, in which case an "average" multiple would miss the mark.

(2) As this and other TAL investigations have shown, small variations in flight time produce large variations in H_{TD} . Therefore, it is more important to measure variation in flight time accurately than variations in other activities.

(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.