

TIME AND ENERGY BUDGETS OF THE MOCKINGBIRD (*MIMUS POLYGLOTTOS*) DURING THE BREEDING SEASON

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ABSTRACT.—A time and energy budget of male and female Mockingbirds (*Mimus polyglottos*) in six phases of their breeding cycle was completed using the equivalent temperature model to predict perching metabolic rates. Recorded time-budget behaviors included perching, bipedal locomotion, flight, and the time spent in the sun and shade. Over the total study period, males and females spent an average of 92.3% and 92.8% of their active day perched, 2.4% and 1.6% in bipedal locomotion, and 5.3% and 5.6% in flight, respectively. *BMR* plus thermostatic requirements averaged, seasonally, 78.1% of *DEE_{tot}* in males and 76.1% in females. The choice of shaded or exposed microhabitats made very little difference in energy expenditure. *DEE_{tot}* varied from 96.9 kJ in males with incubating females to 113.0 kJ in males caring for fledglings, and from 75.1 kJ in incubating females to 113.2 kJ in females caring for fledglings. Unmated, pre-nest-building, and incubating birds spent significantly less energy than did birds caring for nestlings ($P < 0.05$) or birds caring for fledglings ($P < 0.05$). With the exception of the nest-building phase, when females are producing eggs, and the incubation phase, when females gain insulation from the nest, male and female *DEE_{tot}* closely paralleled each other throughout the season. The large amount of predation that occurred at the study site suggests that birds may allocate time to perching to minimize the probability of predation on themselves or their offspring. Received 26 February 1982, accepted 4 October 1982.

A VIABLE approach to ecological and evolutionary problems is available through the use of time- and energy-budget analysis. Because time and energy are resources common to all organisms, this approach can serve both to quantify the diversity of interactions between an organism and its environment (a functional problem) and to decipher evolutionary trends and their causes (Porter and Gates 1969, King 1974). This is the key to the vitality of the approach: functional and evolutionary problems can be addressed simultaneously (Mayr 1961). As more comparative time and energy data are gathered and analyzed, ecological and phylogenetic correlates of life history elements (e.g. energy invested per egg, energy invested in offspring, time and energy devoted to offspring by males and females) will emerge, increasing our power to discriminate ecological problems and the modes in which natural selection attempts to solve them. But this is not all that the technique does for us. When we

enter the Hutchinsonian "ecological theater" (Hutchinson 1965) armed with time and energy concepts, we come out with a more thorough understanding of the proximal elements linking organisms to their environments. We become sensitive to the energetic patchiness of an organism's environment and may visualize it as a series of microhabitats in which biological and physical factors interact to determine whether an organism experiences net energy gains or losses. We are granted a clearer understanding of the reasons for the distribution of organisms within habitats.

The habits of the Mockingbird (*Mimus polyglottos*) make it an ideal species of which to analyze time and energy budgets. Individuals nest in semi-open habitats, which facilitates behavioral observations; they are highly territorial; and their home ranges are sufficiently small that they can be covered rapidly by a person on foot. In this report I present time and energy budgets for Mockingbirds during a single breeding season in Davis, California. The major goals were to discern the dynamics of time and energy expenditure of males and females throughout the reproductive cycle, to investigate the role that microhabitat selection

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plays in determining energy expenditure, and to compare the time budgets of this Mockingbird population with those collected by Utter (1971) on Mockingbirds in New Jersey.

METHODS

The activity patterns of Mockingbirds were studied in riparian and urban habitats near the veterinary medical complex of the University of California at Davis, Yolo County, California. The study lasted from 2 February 1978 to 6 June 1978. The habitat of most birds consisted of fallow fields with patches of asphalt parking lots and expanses of lawn. Oaks (*Quercus ilex* and/or *Quercus agrifolia*) were scattered over most birds' home ranges. Pyracantha (*Pyracantha* sp.) was commonly available, and its fruits were used by birds in all phases of the breeding cycle.

Five Mockingbirds were mist-netted, weighed, and color-banded in January 1978. The sexes of the birds were determined by subsequent observations of behavior (singing, displays, etc.). The mean weight of the birds was 54.8 g (range, 48.9–59.3 g). The only positively identified female in the sample also weighed 54.8 g, so I assume that there is no weight dimorphism.

The duration of three types of activities and the time spent in the sun and in the shade were quantified using a panel of four stopwatches. Data were primarily recorded in hourly periods. At the end of each hourly period, air temperature and the percentage of cloud cover were recorded, and windspeeds were measured in the sun and shade in microhabitats similar to the ones that the bird had occupied. Windspeed was measured with a Thermometrics series 100 hot wire anemometer. Data on total short-wave radiation per hour were obtained from the meteorological station at the University of California at Davis, located 400 m from the study site.

Activity categories included perching, flying, and bipedal locomotion. Bipedal locomotion (*BPM*) was restricted to the actual moments when locomotion occurred. The *BPM* category does not represent time spent foraging. The open habitat allowed me to monitor the birds' behaviors continuously. In the rare instances that birds were lost during observation periods, the data for that period were excluded unless visual contact was regained in less than 2 min.

The birds' seasonal cycle was divided into six data-collection phases: unmated, pre-nest-building, nest-building, incubation, nestling care, and fledgling care. Data were collected throughout the day and several times at night. Male and female power-consumption data were pooled in each phase for statistical analysis.

Home ranges were estimated from behavioral observations several times during the study. Home

ranges were traced on scale photographs (1" = 100') obtained from the Department of Architects and Engineers at the University of California at Davis. Areas were then calculated from these photographs.

CALCULATION OF ENERGY EXPENDITURE

An energy budget for an animal under steady-state conditions with its environment, where conduction is not important, can be written

$$MR - \lambda E = [\rho c_p / (r_b + r_e)] (T_b - T_e) \quad (1)$$

where *MR* is metabolic rate ($W \cdot m^{-2}$), λE is latent heat loss ($W \cdot m^{-2}$), r_b is whole-body thermal resistance ($s \cdot m^{-1}$), r_e is equivalent resistance, T_b is body temperature ($^{\circ}C$), T_e is equivalent temperature, and the product of the density (ρ) and the specific heat of air (c_p) is a constant ($1,200 J \cdot m^{-3} \cdot K^{-1}$ at $20^{\circ}C$) (Mahoney 1976, Campbell 1977). This equation was used to predict the metabolic rates of perching Mockingbirds during their activity phase whenever environmental conditions were such that *MR* exceeded the metabolic rate predicted by the Aschoff and Pohl (1970) (A/P) diurnal equation for passerines, multiplied by a factor of 1.2 [the factor 1.2 corrects for illumination under diurnal conditions (Mahoney and King 1977)]. Such conditions existed when $35^{\circ}C \leq T_e \leq 14^{\circ}C$.

To compute a metabolic rate with equation 1, it is necessary to measure or calculate values for several bird and environmental parameters. Environmental parameters include short-wave (SW) radiation, long-wave (LW) radiation, windspeed, and ambient temperature. A bird's SW radiation environment was determined from measured values of total SW radiation using the technique of Campbell (1977: table 5.1, equations 5.7 and 5.8; 1981: equations 1.5, 1.6, 1.9). The LW radiation environment was calculated from equation 11 in Unsworth and Monteith (1975) and equation 5.13 in Campbell (1977). Bird parameters incorporated in equation 1 include the characteristic dimension (d), the SW absorptivities of the back and belly, the amount of area exposed to different types of SW radiation, various resistances to heat transfer, and evaporative water loss. The characteristic dimension was measured, and the absorptivities of the birds' backs and bellies (0.6 and 0.51, respectively) were estimated by comparing Mockingbird plumage to bird plumages that were similarly colored and the absorptivities of which were known. The ratio of the area exposed to perpendicular SW radiation over the total area of the bird was estimated as 0.21 (Mugaas 1976). It was also assumed that the upper half of the bird's total area was exposed to scattered SW radiation, while the lower half was exposed to reflected SW radiation (Mahoney 1976). Maximum total resistance was calculated from $r_t = 283m^{0.21}$, where m is the bird's mass (g) (Robinson et al. 1976). The max-

imum value that r_e could attain was $158 \text{ s} \cdot \text{m}^{-1}$ or 24% of the maximum total resistance (Mahoney and King 1977). Maximum body resistance, r_b , max, during the day was calculated to equal $423 \text{ s} \cdot \text{m}^{-1}$ by equations given in Robinson et al. (1976). Using this value as a peak for r_b and the shape of Fig. 2 in Mahoney and King (1977), I derived body resistances at other equivalent temperatures. Evaporative water loss (E) was calculated from data from the Pyrrhuloxia (*Cardinalis sinuatus*) and the Northern Cardinal (*C. cardinalis*) (Hinds and Calder 1973). They give an equation for water loss between 20°C and 32.5°C : $E(\text{g/day}) = 0.48m^{0.545}$, where m is body mass (g). This equation was used to calculate evaporative water loss in the range of 20°C – 32.5°C . Below 20°C , the graph was drawn to 0.5% body mass evaporated per hour at 13°C (in accordance with their data) and then was further extrapolated to 7°C , the lowest T_e that occurred during my study. At 45°C the data of Hinds and Calder give unreasonably low results for a Mockingbird's total metabolic rate. For this reason, I assumed that evaporative water loss is equivalent to metabolic heat production at an equivalent temperature equal to the birds' body temperature (42°C), and I set both equal to $105 \text{ W} \cdot \text{m}^{-2}$ at this temperature. For equivalent temperatures greater than 35°C , this approximation yields the following equation: $E(\text{W} \cdot \text{m}^{-2}) = 10.2 T_e(^\circ\text{C}) - 324.2$.

Calculation of hourly metabolic rates.—Two equivalent temperatures were determined for each observation period: one for conditions of full sunlight and one for conditions in the shade. A metabolic rate was determined for each equivalent temperature. The metabolic rate was then recalculated to represent the proportion of each hour spent in the sun and shade.

The costs of bipedal locomotion and flight were considered to be independent of environmental conditions. The cost of bipedal locomotion (*BPM*) was assumed to be 1.5 times the cost of perching in the thermal neutral zone, and the cost of flight was calculated as equal to 9.4 times the metabolic rate calculated from the Aschoff and Pohl (1970) equation for passerines resting at night (Hart and Berger 1972).

The final cost of an hourly period for a nonreproducing bird was the sum of the cost of each behavior ($\text{J} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$), times the fraction of the hour spent in that behavior, multiplied by the surface area of the bird (m^2). Plumage surface areas were determined from $SA = 7.81(m)^{0.667}$ (Walsberg and King 1978a), where m is bird mass (g) and SA is surface area (cm^2).

Nighttime energy expenditure.—Hourly nighttime energy expenditure in the thermal neutral zone (TNZ) (22.5 – 35°C) was calculated from $114.8 M^{0.726}$ (M in kg) (Aschoff and Pohl 1970). The range of environmental temperatures that delimits the TNZ was calculated for the lower critical temperature from $T_{l,c} = T_b - 6.98m^{0.266}$, where m is mass (g) (Calder and King 1974). The upper critical temperature was assumed to equal 35°C . Because no windspeed or LW radiation data

were collected at night, when temperatures dropped below the TNZ, Kendeigh's (1969) equation, $H(\text{kcal/day}) = 4.769m^{0.417}$ [where m is mass (g)], was used to calculate a metabolic rate at 0°C , and metabolism was computed based on the assumption that it decreases linearly as temperature increases from 0 to 22.5°C . A single temperature (the mean nighttime temperature) was used to calculate hourly energy expenditure.

Incubating birds.—The modeling procedure for incubating birds was the same as for nonincubating birds except for periods when birds were on the nest. Because birds nested in heavy vegetation where little or no light penetrated, SW radiation fell to $0 \text{ W} \cdot \text{m}^{-2}$ under these conditions. The model assumed that 10% of the incubating bird's surface area was covered by the brood patch, that 40% of its surface was exposed, and that 50% of its surface area was in the nest (excluding the brood patch). The resistance for a 1.9-cm-wide egg (Bent 1948) was set at $41.9 \text{ s} \cdot \text{m}^{-1}$; the brood patch resistance was set equal to $45 \text{ s} \cdot \text{m}^{-1}$; body resistance was approximated as $423 \text{ s} \cdot \text{m}^{-1}$ (max. night); and nest resistance was set equal to $300 \text{ s} \cdot \text{m}^{-1}$ (values estimated in the manner of Walsberg and King 1978b). The characteristic dimension for the nest with the bird was approximated as 15 cm. All other facets of this model were similar to the analysis by Walsberg and King (1978b). In this phase of the cycle, the calculated metabolic rates for birds on the nest during the day were compared to the Aschoff and Pohl (1970) resting equation. If predicted metabolic rates on the nest during the day dropped below this value, they were set equal to it. During the night, incubating birds' metabolic rates were set equal to 82% of a nonincubating bird's metabolic rate under similar temperature conditions (Walsberg and King 1978b).

Egg formation.—Egg formation was assumed to take 5 days, and the cost of forming 1 g of egg, at an efficiency of 70%, was estimated as 6.28 kJ (King 1973). Because a single Mockingbird egg weighs 3.75–4.25 g (Hanna 1924), a total cost of 25.1 kJ per egg was assumed. Because clutch size near Davis ranged from 3 to 4 eggs ($n = 8$), the total costs to form 3 eggs in 7 days and 4 eggs in 8 days were both calculated. I chose the mean of these two values, $468 \text{ J} \cdot \text{h}^{-1}$, to add to the hourly expenditure of egg-producing females. Nest-building females were the only group of birds to have this cost of production added to hourly expenditure.

Converting hourly data to daily energy expenditure.—To convert energy expenditure per hour to daily energy expenditure (DEE_{tot}), a mean value of hourly expenditure was calculated for each bird in that particular phase, and then a mean of these means was calculated. This value was used for a bird during waking hours (from 15 min before civil twilight in the morning to 15 min after civil twilight in the evening). DEE_{tot} includes the costs of basal metabolism,

TABLE 1. Sensitivity of DEE_{tot} to errors in model parameters at $T_a = 10^\circ\text{C}$, $T_g = 12^\circ\text{C}$.^a

Variable ^b and % change	Radiation ($\text{W}\cdot\text{m}^{-2}$) and wind-speed ($\text{m}\cdot\text{s}^{-1}$)			
	50, 0.5	880, 0.5	50, 5	880, 5
Mass				
+10%	+5% ^c	+5%	+5%	+5%
-10%	-5%	-5%	-5%	-5%
Perching^d				
+25%	+21%	+21%	+21%	+21%
-25%	-21%	-21%	-21%	-21%
Flight^e				
+25%	+4%	+4%	+4%	+4%
-25%	-4%	-4%	-4%	-4%
Surface area				
+25%	+7%	+2%	+8%	+8%
-25%	-6%	-5%	-9%	-6%
r_b				
+25%	-2%	-1%	-5%	-2%
-25%	+9%	+2%	+11%	+11%
Night metabolism				
+10%	+4%	+4%	+4%	+4%
-10%	-4%	-4%	-4%	-4%

^a Values given are the percentage increase or decrease in DEE_{tot} due to the change in the parameter indicated, under the total short-wave radiation and windspeed conditions specified.

^b Other variables tested and their deviations included $T_a \pm 1^\circ\text{C}$; $T_g \pm 10^\circ\text{C}$; $T_b \pm 2^\circ\text{C}$; albedo, A_p/A_t , A_{bl}/A_t , d , E , r_{e1} , and the cost of BPM, all varied by 25%; and back and belly absorptivities $\pm 10\%$. All variations led to less than a 2% change in DEE_{tot} .

^c The standard DEE_{tot} 's for the conditions of total short-wave radiation and wind given are 50, 0.5: 108.2 kJ; 880, 0.5: 107.1 kJ; 50, 5: 112.3 kJ; and 880, 5: 108.8 kJ.

^d Costs include BMR plus TR and encompass the total 24-h period.

^e Costs include BMR.

thermoregulation, production, and activity. DEE_{tot} values could be in error if there were trends in energy expenditure throughout the activity period, but no daily trends were apparent when the data were analyzed separately in four activity periods: before 0900, 0900–1200, 1200–1700, and after 1700.

SENSITIVITY ANALYSIS

Because it was necessary to estimate many parameters in the DEE model, the effects on outcomes of the model were analyzed by varying each parameter by 10–25%. These sensitivity analyses were run under four conditions of radiation and wind, and at three different combinations of air and ground temperatures (Tables 1, 2). The DEE values produced by the model were compared to a matching standard, which had identical SW radiation and windspeed values. Because the model used to calculate DEE varied with environmental conditions (i.e. the metabolic rate calculated from the Aschoff and Pohl equa-

TABLE 2. Sensitivity of DEE_{tot} to errors in model parameters at $T_a = 25^\circ\text{C}$, $T_g = 27^\circ\text{C}$ and $T_a = 30^\circ\text{C}$, $T_g = 32^\circ\text{C}$.^a

Variable ^b and percentage change	Estimated DEE_{tot} ($\text{kJ}\cdot\text{h}^{-1}$)	Percentage deviation from original estimate
Mass + 10% ^c	117.2	+ 6% ^d
Perching cost + 25% ^c	124.3	+13%
Flight cost + 25% ^e	115.9	+5%
Surface area + 25%	116.4	+5%
Nighttime metabolism + 10%	113.6	+3%

^a Under all radiation ($\text{W}\cdot\text{m}^{-2}$) and windspeed ($\text{m}\cdot\text{s}^{-1}$) conditions specified, the results were identical.

^b Variables tested were identical to those at $T_a = 10^\circ\text{C}$. All other variables led to less than a 2% change in DEE_{tot} .

^c Changes in the minus direction mirrored changes in the positive direction for all variables in the table.

^d The standard DEE_{tot} under all conditions of radiation and wind is 110.4 kJ.

^e Costs include BMR.

tion multiplied by 1.2 was compared to that produced by the T_e model, and the higher value was used in calculating a perching metabolic rate), some outputs were asymmetrical in the analyses (e.g. r_b and surface area at $T_a = 10$; $T_g = 12^\circ\text{C}$). The percentage that input parameters were varied represents probable maximal errors in these values.

For nonincubating birds at $T_a = 10, 25$, and 30°C , the model is most sensitive to changes in the values of the cost of perching, the mass of the bird, the surface area of the bird, and the cost of flight. At $T_a = 10^\circ\text{C}$, the model is also highly sensitive to changes in body resistance. Variation of other variables, to the degree indicated in Table 1, led to less than a 2% change in DEE_{tot} under all conditions specified.

Errors in the cost of perching can have a large impact on DEE due to the large fraction of time occupied by this activity (Ettinger and King 1980). A 25% error in the value of perching metabolic rate at $T_a = 25$ or 30°C leads to a 13% change in DEE_{tot} under all radiation and wind conditions, while at $T_a = 10^\circ\text{C}$ a similar error leads to a 21% error in DEE_{tot} . A 10% change in mass with $T_a = 25$ or 30°C caused a 6% increase in DEE_{tot} , while for $T_a = 10^\circ\text{C}$ the increases and decreases were 5%. Errors in DEE_{tot} resulting from 25% errors in surface-area approximations produced a change in $DEE_{tot} \leq 9\%$ (Tables 1, 2). Flight occupied a small percentage of the day but was an energetically expensive behavior. A 25% change in the cost of flight caused a 5% change in DEE_{tot} at 25 and 30°C and a 4% change in DEE_{tot} at $T_a = 10^\circ\text{C}$. A 25% decrease in r_b at 10°C caused an 11% increase in DEE_{tot} at high windspeeds and a 9% increase in

DEE_{tot} under low windspeeds and low radiation. r_b was utilized only when T_e 's were below 14°C , and this occurred commonly only during the unmated and pre-nest-building phases (less than 7% of all other phases combined had unshaded T_e 's below 14°C). Therefore, these are the only phases of the study that could be much affected by errors in r_b .

The major value of such sensitivity analyses is to indicate which variables need to be measured with the greatest accuracy under specified environmental conditions. To set confidence limits on model outputs of DEE_{tot} when all errors are combined is more difficult. The probability of all errors being simultaneously additive is scant, however (some will cancel others of opposite sign), so a probable 95% confidence limit should lie in the range of $\pm 5\%$ of the DEE predicted by the model.

RESULTS AND DISCUSSION

BASAL AND THERMOSTATIC EXPENDITURE

The percentage of the total daily energy expenditure devoted to basal and thermostatic requirements (BMR and TR , respectively) ranged from 67%, in females caring for fledglings, to 86%, in incubating females. BMR plus TR averages, seasonally, 78.1% of DEE_{tot} in males and 76.1% in females. Only 12% (range 5.5–19%) of DEE_{tot} is consumed by thermoregulation in males and 9.6% (range 5.5–15.3%) by thermoregulation in females. Approximately 99% of the thermoregulatory costs accrued at night, as daytime temperatures rarely fell below 14°C . A comparison of these data on the percentage of power consumption due to BMR plus TR with extant data shows my values to be the highest yet known. Kendeigh's range of estimates for House Sparrow (*Passer domesticus*) (67–80%) BMR plus TR comes closest to the Mockingbird values (Kendeigh 1972).

The large fraction of DEE_{tot} accounted for by basal and thermoregulatory power consumption in this model, relative to previous models, probably stems primarily from the limits of our knowledge on the energetic costs of behaviors. This model assumes that, under a given set of environmental conditions, all daytime activities in nonincubating birds, other than bipedal locomotion and flight, cost a constant amount. Previous models (e.g. Mugaas 1976, Walsberg 1978, Ettinger and King 1980) have assumed that nonflight activities (e.g. perching, singing, foraging) other than BPM are more costly, which decreases the fraction of DEE_{tot} due to BMR plus TR .

In general, energy devoted to maintenance was obligatory, but, when ambient temperature was below 14°C , birds could modify this expenditure through the differential utilization of microhabitats. T_a 's below 14°C occurred during 26 of 40 sampling bouts involving nonmated males, in 7 out of 29 bouts with males in the pre-nest-building phase, and in 4 out of 28 bouts dealing with pre-nest-building females.

To investigate the role that microhabitat choice played in determining TR requirements during each of these phases, I determined the mean fraction of time spent in the shade and sun for each phase during periods when T_a was less than 14°C . A metabolic rate for each bird in the sun and in the shade for each of these hourly periods was then calculated. The lower of these two values was used to determine a minimum rate of energy expenditure, and this was compared to the actual rate of energy expenditure the bird experienced. An average value of potential energy savings was then obtained for each phase. Unmated and pre-nest-building males could have saved 119.2 and 53.7 $\text{J}\cdot\text{day}^{-1}$, respectively, by utilizing the physical environment in such a way as to minimize energy expenditure, while pre-nest-building females could have saved 1,110 $\text{J}\cdot\text{day}^{-1}$.

The ecological significance of these potential energy savings can be investigated by converting these energy equivalents into food resources. *Pyracantha* berries were commonly utilized on many territories during these phases and have a mean energy content of 1.24 $\text{kJ}\cdot\text{berry}^{-1}$ ($n = 2$; $\bar{x} = 18.4 \text{ kJ}\cdot\text{g}^{-1}$, $s = 0.20$). Thus, under these environmental circumstances microhabitat choice for energy savings is of little importance. Nevertheless, the insights into the within-habitat distribution of endotherms gained by breaking the climate space of Porter and Gates (1969) into compartments corresponding to regions within the thermoneutral zone and outside the thermoneutral zone are potentially great, as a similar approach (that of measuring functional-response rates for a wide variety of traits at different temperatures, identifying peak response temperatures for each trait, and searching for temperatures that maximize the number of traits whose peaks overlap) has proven to be for ectotherms (Brett 1971, Huey and Stevenson 1979).

VARIATIONS OF ACTIVITY AND DEE BETWEEN AND WITHIN REPRODUCTIVE PHASES

Ordering the data according to reproductive phase allows the detection of energetic correlations among reproductive, other biotic (e.g. predation and food resources), and abiotic factors. Those phases imposing the strictest limitations on time budgets and requiring the greatest mobilization of resources can thus be revealed. Using phases of the breeding cycle as standards for data collection also allows for precise comparative studies within a taxon that may reveal life-history or behavioral adaptations, allow them to be correlated with habitat changes, and suggest causes for adaptation (Lack 1968).

Unmated phase.—During this phase males spent relatively little time in flight (Table 3). Foraging was restricted to fruits available within the territories, and males generally hopped or ran from bush to bush. Aggressive displays toward robins (*Turdus migratorius*) were common. Because of the low tendency to fly, the small home range sizes, and the short active daylength (Table 4), DEE_{act} [DEE_{act} includes the costs of production and activity alone (Ettinger and King 1980)] for the males reached a seasonal low during the nonmated phase.

Pre-nest-building phase.—Birds first formed a pair bond on 10 January. Quantitative observations of this phase were made between 19 February and 26 May. Several birds moved into this phase more than once during this study. Male home-range sizes were of intermediate values, and time spent in flight slightly increased over that of unmated males, primarily due to the exploration of surrounding areas (Table 3, 5). Increasing temperatures compensated for increasing active daylength and the increased percentage of time spent in flight, so that males' DEE_{tot} remained constant between these two phases (Tables 3, 4). The females' range in energy expenditure was more tightly clustered than that of the males (4.0–4.8 $\text{kJ} \cdot \text{h}^{-1}$ to 3.9–6.4 $\text{kJ} \cdot \text{h}^{-1}$, respectively). Females did not explore surrounding areas during this phase.

Nest-building birds.—Nest building required 2 days for the three pairs of birds observed. Nest construction began on 20 February. Time-budget observations in this phase were made on a single mated pair. The male spent more time in *BPM* during this phase than in any other phase of the study (Table 3), mostly in

TABLE 3. Mean^a percentage of the active day spent in three activities, and mean energy allocation and expenditure (DEE_{em}) for Mockingbirds in all phases of the study.

Phase	Minutes of data	Number of birds	Percentage of active day spent			DEE ($\text{kJ} \cdot \text{day}^{-1}$) spent				Total	
			Perching	BPM	Flight	BMR + TR	Perching ^b	BPM	Flight		Egg production
Unmated	1,768	6	94.5 (94.2) ^c	2.3 (2.2)	3.2 (3.6)	85.1	6.5	0.5	8.1	—	100.2
Pre-nest-building (♂)	1,646	3	94.0 (93.3)	2.0 (2.4)	4.0 (4.3)	79.7	8.0	0.6	11.9	—	100.2
Pre-nest-building (♀)	1,422	3	94.5 (95.0)	2.8 (2.4)	2.7 (2.6)	79.9	8.1	0.8	8.1	—	96.9
Nest-building (♂)	372	1	91.3 (91.3)	4.5 (4.5)	4.2 (4.2)	80.2	6.5	1.1	10.6	—	98.4
Nest-building (♀)	347	1	93.7 (93.7)	1.8 (1.8)	4.5 (4.5)	80.3	6.7	0.4	11.2	11.2	109.8
Incubation (♂)	136	2	95.0 (93.6)	2.0 (2.5)	3.0 (3.9)	78.8	8.4	0.6	9.1	—	96.9
Incubation (♀)	1,183	3	96.1 (96.1)	1.0 (0.9)	2.9 (3.0)	64.8	1.3	0.3	8.7	—	75.1
Nestlings (♂)	1,100	3	91.7 (90.4)	1.3 (1.5)	7.0 (8.0)	75.8	8.4	0.4	22.6	—	107.2
Nestlings (♀)	1,170	3	90.9 (91.0)	2.1 (1.8)	7.0 (7.2)	75.5	8.3	0.6	22.6	—	107.0
Fledglings (♂)	1,228	2	90.6 (90.9)	1.2 (1.3)	8.2 (7.8)	77.6	8.3	0.3	26.8	—	113.0
Fledglings (♀)	759	2	89.7 (88.1)	1.1 (1.2)	9.2 (10.7)	76.4	8.0	0.3	29.2	—	113.2

^a Values are the mean of all individual birds' means.
^b Perching, BPM and flight values are for the amount of power consumption above BMR plus TR.
^c The bracketed numbers are actual mean values; the unbracketed numbers are the means of the means.

TABLE 4. Calculation of mean DEE_{tot} for each phase of the study.

Date	Phase of cycle	Daytime expenditure ($J \cdot h^{-1}$)	Day hours available	Night-time expenditure ($J \cdot h^{-1}$)	Night hours available	DEE_{tot}
10 February	Unmated	4,422	12.0	3,930 ^b	12.0	100.2
15 April	Pre-nest-building (δ)	4,594	14.6	3,532	9.4	100.2
15 April	Pre-nest-building (φ)	4,364	14.6	3,532	9.4	96.9
1 May	Nestbuilding (δ)	4,652	15.2	3,142	8.8	98.4
1 May	Nestbuilding (φ)	5,131 ^c	15.2	3,610 ^c	8.8	109.8
5 May	Incubation (δ)	4,381	15.3	3,434	8.7	96.9
5 May	Incubation (φ)	3,307	15.3	2,816	8.7	75.1
21 May	Nestlings (δ)	5,149	15.8	3,142	8.2	107.2
21 May	Nestlings (φ)	5,138	15.8	3,142	8.2	107.0
24 May	Fledglings (δ)	5,356	15.9	3,434	8.1	113.0
12 May ^d	Fledglings (φ)	5,538	15.6	3,284	8.4	113.2

^a Activity begins 15 min before civil twilight in the morning and ends 15 min after civil twilight in the evening.

^b Nighttime temperatures were as follows: 10 February, 5.5°C; 15 April, 10.0°C; 1 and 21 May, 14.4°C; 5 and 24 May, 11.1°C; 12 May, 12.8°C.

^c Includes 468 $J \cdot h^{-1}$ production.

^d Female data collected for this phase were centered around 12 May; male data around 24 May.

collecting twigs. He contributed 4–6 twigs per hour, compared to the female's range of 0–1 twigs per hour. Females increased power consumption substantially during this phase due to egg formation (Table 3). Except for this expense, the female's time and energy budget was essentially identical to the male's.

Incubation phase.—Incubation lasted approximately 13 days in the one nest observed in detail. Similarly, Laskey (1962) found incubation periods from 12 to 12.5 days in 18 nests. Male Mockingbirds neither incubated nor fed the female at the nest. Both male and female power consumption reached a seasonal low during the incubation phase (Table 3). Females actually flew for a slightly greater percentage of time in this phase than they did in the pre-nest-building phase, but increasing temperatures, combined with the large amount of time spent on the well-insulated nest (mean for active portion of the day = 78.2%), led to an overall decline in DEE_{tot} . This decline is in accordance with the theory of Walsberg and King (1978b) that the incubation phase is a period of reduced power consumption because of shifts within the entire time/energy budget.

Birds with nestlings.—The nestling period lasts 12 days. All nests contained two young. Average male and female time/energy budgets during this phase were virtually identical (Table 3). Males and females substantially increased the percentage of the active day spent in flight. Males devoted a greater percentage

of their flight time to predator defense, however, while females generally used flight as a means to reach a broader range of foraging habitats.

The ranges in the mean values of daytime energy expenditure were large for both males and females (4.0–8.2 $kJ \cdot h^{-1}$ and 3.9–7.9 $kJ \cdot h^{-1}$, respectively). Males varied greatly in the amount of time devoted to feeding offspring and predator defense. Observations of male 1 suggest that he fed nestlings more frequently (4 times in 1 h) than did male 3 (who fed nestlings but 7 times in 18 h of observation). Male 3 spent a large amount of energy fending off potential predators. He attacked crows, (*Corvus brachyrhynchos*), American Kestrels (*Falco sparverius*), dogs, and a Northern Harrier (*Circus cyaneus*) during the observation periods. The variation in female values was caused by differences in foraging ranges. Female 2 utilized a large home range and spent a mean of 11.2% of her active day in flight, whereas female 1 spent a mean of only 3.9% of her active day in flight while utilizing a smaller home range. For females, an increase of time in flight did not reflect a greater number of feedings at the nest. Female 1 fed her young 6 times in 1 h. Female 2 fed her young in 11 of 12 h of observation, with a mean of 3.6 items (fruits or insects). Females apparently feed young at greater rates than males during the nestling phase (this study, Utter 1971).

Fledgling phase.—Only pair 1 raised an off-

TABLE 5. Home-range sizes.

Bird	Phase of cycle	Date(s)	Area (ha)
Male 1	Pre-nest-building, nest-building, nestlings	8 February–11 April	0.58
	Pre-nest-building	12 April	1.63
	Fledglings	10 May	1.66 ^a
	Fledglings	26 May	1.33
Male 2	Pre-nest-building	21 April	1.96
	Nestlings	20 May–26 May	2.92
	Nestlings	27 May	5.28
	Nestlings	3 June	7.06
Male 3	Pre-nest-building	22 April	4.73
	Nestlings	22 May–26 May	7.76
	Pre-nest-building	27 May	11.00
Male 4	Unmated	18 February–19 February	0.42
Male 5	Unmated	3 February–7 February	0.11

^a Also includes a 415-m flypath to a small grove of trees.

spring that survived. This bird left the nest on 10 May and was still being fed by the parents when the study was terminated on 16 June.

Males and females reached peaks in seasonal values of DEE_{tot} and DEE_{act} during this phase (Table 3). The relatively long active daylengths and the increase in the percentage of the active day devoted to flight combined to produce this effect (Tables 3, 4). Both males and females fed the young. The male of pair 1 fed the young very little early in the phase (1 time in 7 h). During the same time span, the female fed the two offspring a mean of 6.1 fruits or insects per period ($n = 18$). Ten days after nest departure, the male bird started constructing another nest and simultaneously slowly began to take over the feeding of the fledged offspring. By the time incubation was initiated by the female, the male had taken over the feeding of the fledgling completely, providing a mean of 6.5 fruits or insects per hour ($n = 9$).

INTERPHASIC COMPARISONS AND TRENDS

Unmated and incubating birds spent significantly less energy than birds caring for nestlings ($P < 0.05$) or birds caring for fledglings ($P < 0.01$) (t -test, Steele and Torrie 1960). Incubating birds also spent significantly less energy than pre-nest-building birds ($P < 0.05$). Pre-nest-building birds spent significantly less energy than either birds caring for nestlings ($P < 0.05$) or birds caring for fledglings ($P < 0.05$). No statistical tests were attempted on nest-building birds because of the small sam-

ple sizes. Statistical comparisons of DEE_{act} yielded similar results.

The pattern of interphasic variation in DEE_{tot} almost certainly does not reflect an ultimate pattern of time and energy expenditure evolved by these birds. More likely, it is produced by variations in a particular set of proximal factors in the birds' environments. Major proximal factors that have the potential of varying between phases are social structure (territory attainment and defense, pair-bond formation), daylength, the physical environment, the demands of eggs or young, predator pressure, and resource abundance.

Unmated males showed extreme territorial aggression in January and February when breeding territories were being obtained. Pair-bond formation did not increase energy expenditure over that of territorial defense alone (compare unmated and pre-nest-building males; Table 4), and even the additional demand of building a nest while holding a mate and a territory did not increase the amount of energy devoted to activity.

Increasing daylengths allow more young to be produced, but it is the production of young that causes the energy requirements to change, not increases in daylength. A comparison of BMR plus TR costs between phases shows that the physical environment's impact on variation between phases was small (Table 3). The energy demands of production (eggs, then maintenance and growth of young) increase as the phases progress (Ricklefs 1974). This causes the total energy demands of parents and young to

TABLE 6. Total energy expenditure (DEE_{tot}) and energy expenditure in activities above the basal and thermostatic requirements (DEE_{act}) during the time period required to raise young to a state of free existence. In the mid-fledgling phase, females begin a second brood, while males care for fledglings of the first brood.

Phase	Days	kJ · phase ⁻¹			
		Male		Female	
		DEE_{tot}	DEE_{act}	DEE_{tot}	DEE_{act}
Pre-nest-building	5.5	551	113	595	155 ^a
Nest-building	2.0	197	36	220	59
Incubation	12.0	1,163	217	901	124
Nestlings	12.0	1,286	377	1,284	378
Fledglings	37 ♂♂, 13 ♀♀	4,181	1,310	1,481	478
Nestling/egg formation	7.5	—	—	933	360 ^a
Incubation	12.0	—	—	901	124
Nestling	4.5	—	—	482	142
Total, kJ		7,378	2,053	6,797	1,820
Mean kJ · day ⁻¹		108	30	99	27

^a In the model, egg formation occurs during the last 5.5 days of the pre-nest-building phase, so 11.2 kJ · day⁻¹ have been added to values from Table 3 when appropriate.

increase throughout the season. Further energy demands are elicited by the increase in the number of potential predators, which occurred with the start of the incubation phase and extended to the fledgling period (eggs, nestlings, and fledglings are assumed to have higher probabilities of being preyed upon than adults). As adults moved into these phases their devotion of time and energy toward potential predators increased (Utter 1971, this study). Data collected show that unmated and pre-nest-building birds occasionally attack Scrub Jays (*Aphelocoma coerulescens*), but do not attack American Crows; nest-building and incubating birds attack jays and crows but not cats or dogs; birds with nestlings display agonistic behaviors toward crows, cats, dogs, and hawks; and birds with fledglings assaulted crows, cats, and dogs during the time that their fledglings were alive. The extra energy demands imposed by predators differ from the increased demands due to development of young in that they can vary from habitat to habitat or even territory to territory.

When food abundance increases, extra energy demands do not necessarily lead to increases in energy expenditure in obtaining food. Energy expenditure did increase as the phases progressed, however, largely as a result of increases in flight time due to predators and home-range expansion (Tables 3, 6). Home-range expansion allowed birds to forage in additional areas and suggests that food supply

and/or quality did not increase commensurately with energy demands.

A large percentage of time was devoted to perching during all phases. This seems to be a regular feature of avian lifestyles (Ettinger and King 1980). At least a portion of this perching time is not involved with foraging. Ettinger and King (1980) have suggested that Wilson's (1975) "principle of stringency" may account for the evolution of this portion, which they have termed the "loafing" component. In the population that I studied, and for passerines in general, this is probably not the case. It is improbable that birds would decrease their fitnesses by foraging for greater periods of time when conditions were favorable because later they might have to contend with an unpredictable event such as cold weather, rain, or snow that would reduce the food supply. Birds have, no doubt, evolved life-history traits in response to this type of environmental unpredictability, but a behavior such as time devoted to foraging should be more proximally flexible than a life-history trait (Warner 1980). Predation pressure is probably a primary selective force determining the "loafing" component. Utter (1971) found that alert perching by Mockingbird males reached a maximum during the nestling phase and was at a seasonal minimum when the birds were unmated. He too felt that this "perching" or "loafing" component was ultimately determined by predation pressure. Furthermore, predation on pas-

serine eggs and nestlings is common in many temperate-zone species (36.2% of eggs laid are prevented from developing into adults due to predation; Ricklefs 1969), and it is a common assumption, although difficult to prove, that organisms occupied with tasks (e.g. mating, foraging) experience higher predation rates than those perched or sitting. In this study, the number of times that perched birds caught sight of predators before I did suggests that birds that devote more time to perching are better able to protect themselves, and their offspring, from predation.

Between-pair comparisons suggest that variation in territorial quality can have pronounced fitness effects. Pair number 1 were the first to form a pair bond and appeared to have the greatest resource density on their territory. They utilized smaller home ranges, they spent significantly less time in flight than other pairs in the pre-nest-building ($P < 0.05$) and nestling phases ($P < 0.05$) (the only phases where sample sizes were large enough to warrant comparisons), they appeared to make more feeding visits to the nest per unit time, and they were the only birds to raise an offspring that survived after leaving the nest.

SEASONAL SUMMARY OF PARENTAL INVESTMENT

A breeding-cycle summary indicates that males have both a larger total power consumption and a larger power consumption due to production and activity than do females (Table 6). This is caused primarily by the extended period of fledgling care, which elevated male power consumption during times when females incubated.

Parental investment may be defined as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring" (Trivers 1972). Relative parental investment plays a large role in the evolution of mating systems and mating behaviors. In Mockingbirds it can be divided into five components: territorial defense, production of eggs, incubation, protection of offspring, and rates of feeding offspring. Because these components have different units (i.e. time, energy, or risk), it is difficult to distill a single quantitative value for parental investment made by males and females. Nevertheless, there are two approaches that can act as

rough measures: (1) qualitative statements can be made about each component and a balance sheet drawn up, and (2) DEE_{net} , because it contains all production and activity costs, can serve as an index of parental investment.

In Mockingbirds, territorial defense is a male-biased behavior involving primarily the devotion of energy resources and risk; egg production and incubation are done totally by the female, the former requiring energy, the latter, time; the protection of offspring is skewed toward the male and demands the use of energy and involves risk; and the feeding of offspring demands the use of time and energy for prey capture and appears to be female-biased during the nestling phase but male-biased during the fledgling phase. This summary suggests that there is a qualitative balance between parents in parental investment. Males have higher DEE_{net} than females over the total breeding cycle (Table 6). Therefore, males may have a slightly greater energetic investment in offspring than females.

Taken together, these two measures indicate that there is little sexual bias in parental investment (male and female investments are both needed throughout the cycle if offspring are to be raised), and this is a major determinant of the overwhelmingly monogamous mating system of Mockingbirds.

INTERPOPULATION COMPARISONS

The behavioral categories used in this study match well only the flight category in Utter's (1971) study of Mockingbirds. Mockingbirds breeding in California and New Jersey spend similar amounts of time in flight (Table 7). The mean percentage of time that male birds in California spent in flight during the whole cycle was 5.5%, whereas Utter's values for two male populations were 7.3% and 6.0%. A comparison of home-range sizes shows that birds in New Jersey had slightly larger average maximal home ranges (7.9 and 7.6 ha in New Jersey vs. 6.5 ha in California), which may account for the lower flight times of the California population.

A major difference between birds in New Jersey and California is that the changes in time spent in flight between phases do not parallel each other. New Jersey males reached a primary peak with fledglings and a secondary peak while females incubated. In California, flight means peaked with nestlings, and a much

TABLE 7. Interspecific comparison of percentage of active day in flight.

Phase of cycle	Utter's study (1971)		
	This study ^a	Population 1	Population 2
Unmated	3.6	6.1	3.2
Pre-nest-building	4.3	6.5	5.3
Incubation	3.9	7.4	7.8
Nestlings	8.0	6.4	5.3
Fledglings	7.8	10.1	8.3
Mean %	5.5	7.3	6.0

^a Utter used actual means, so I present actual means for comparison.

smaller percentage of time was devoted to flight during incubation ($\bar{x} = 3.9\%$) than was found in New Jersey (7.4 and 7.8%). Ecological causes for these differences remain obscure, as Utter gave no reasons for fluctuations in flight times between phases.

Simpson (1978) also collected data on resting, foraging, and flight for Mockingbirds in Maryland. No numerical results are presented, but time spent resting significantly increased during the fall and winter, while flight time significantly increased during the nestling phase ($P < 0.05$).

Hence, over a broad geographic range Mockingbirds expend greater amounts of energy and time being active in the nestling and fledgling phases than in other portions of the breeding cycle. If increased flight time due to nutritional demands is mandatory, then a greater degree of constraint is imposed on the time budget during these phases. Partitioning the necessary flight time nearly equivalently between the male and the female (Table 3) may be a tactic that minimizes the selective impact of this constraint on the pair.

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