

# TIME AND ENERGY BUDGETS OF THE WILLOW FLYCATCHER (*EMPIDONAX TRAILLII*) DURING THE BREEDING SEASON

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**ABSTRACT.**—We quantified the time-activity budgets of *Empidonax traillii* in five phases of the nesting cycle during 2 yr and converted the results into energy budgets in order to learn the relative costs of reproductive events and their seasonal correlates. Salient results are: (1) Basal and thermostatic power consumption preempt an average of 43% of the total daily energy expenditure ( $DEE_{tot}$ ) in males and 42% in females; variation of air temperature accounts for about 90% of variation in  $DEE_{tot}$ . (2)  $DEE_{tot}$  in males varies from 54 kJ/day (incubation) to 69 kJ/day (nestling phase) and in females from 52 kJ/day (incubation) to 65 kJ/day (prenesting). (3) The portion of  $DEE_{tot}$  allocated to facultative activities varies only moderately, in males from 31 kJ/day (pre-nesting) to 35 kJ/day (nest-construction phase) and in females from 28 kJ/day (incubation) to 36 kJ/day (prenesting, ovogenesis). (4) Energy allocated to maintenance, production, and facultative activity, respectively, tends to vary reciprocally, minimizing interphasic variations of  $DEE_{tot}$ . (5) We argue that the time budgets of both males and females contain a large fraction of uncommitted or "loafing" time. We interpret this as an expression of Wilson's "principle of stringency," which suggests that selection is episodic and that uncommitted time (and energy) serves as a buffer against unpredictable episodes of "stringency," such as inclement weather and/or food shortage. (6) The grand seasonal mean  $DEE_{tot}$  for males and females (54.5 kJ/day) is 1.6% less than an allometric prediction for free-living birds in general and falls between values for birds of the same body mass as *E. traillii* that feed on the wing (73.2 kJ/day, swallows and hummingbirds) and those that do not feed on the wing (46.9 kJ/day), differing significantly from the former ( $P < 0.05$ ) but not the latter. The foraging routine of *E. traillii* entails no more flight time (and often less) than the routines of ground-foraging birds, and so  $DEE_{tot}$  is substantially less than that of truly aerial insectivores. Received 29 October 1979, accepted 18 February 1980.

OF the many approaches to the analysis of the selective pressures that have affected the diversification of life-history patterns, the quantification of time-and-energy budgets is one of the most discriminating and powerful, because it provides an estimate of the allocation of two basic and potentially limiting resources to various vital functions (for review, see King 1974). Although the results of such analyses are intrinsically interesting in relation to basic questions about a given population or species (e.g. relative parental investment in reproduction, allocation of time and energy in relation to environmental seasonality), their utility is greatly multiplied by the accumulation of comparative data. As is typical in comparative biology, the analytical power of data from diverse species grows rapidly with the size of the sample, with results that are not apparent from the individual parts. An example of this is Walsberg's (in press) analysis showing that birds that forage in flight (swallows and hummingbirds in his sample) spend more energy per day than birds that forage by other methods.

The results thus far of analyses based on activity and energy budgets persuade us that this is a sound approach that merits continuation toward a larger matrix of comparative data that will not only improve the reliability of allometric predictions but also will help to discriminate among subsets of the data that may be related to particular avian life styles (e.g. modes of foraging, parental care, locomotion, and so on). In this report we present an analysis of the time-and-energy budget of a sit-

and-wait predator, the Willow Flycatcher, a species whose mode of foraging has not previously been investigated in this context. The Willow Flycatcher, like its congeners, feeds exclusively while in flight, employing both "hawking" (capture of flying insects) and "aerial gleaning" (capturing an insect from a substrate while hovering). Its reproductive biology (King 1955) and foraging ecology (Frakes 1978) near our study site are already well known, and supplied the background for the design of our program.

#### METHODS

We studied the activity of Willow Flycatcher (*Empidonax traillii brewsteri*) in riparian habitat along Four Mile Creek in the Hudson Biological Reserve, Whitman County, Washington from 4 June to 1 August 1977 and 29 May to 24 July 1978. Their habitat here and in adjacent areas of the Palouse Prairie has been described by King (1955). We captured 13 flycatchers in mist nets and banded them with USF&WS aluminum bands and unique combinations of color bands. We ascertained the sex of each individual when possible by the development of the cloacal protuberance or presence of an incubation patch or, subsequently, by behavior (singing, nest building, incubating). The mean weight ( $\pm$ SE) of the 10 birds that we weighed was  $12.6 \pm 0.23$  g, with no significant difference between the 5 nonovulating females (12.7 g) and 5 males (12.6 g).

We quantified the duration of four types of activities using a panel of stopwatches and subsequently transformed the data into percentages of the observation periods and of the activity day. The activity categories included flying, perching, singing, and nest attendance. During 1978 we counted the numbers of flights on selected days as well as measuring their cumulative duration. We were not able to discriminate foraging flights reliably from other types of flight and so abandoned our initial attempts to do so.

We ascertained time budgets in five phases of the reproductive cycle: arrival of males and establishment of territories, nest-construction period, egg-laying period, incubation period, and nestling period. Efforts to quantify activity accurately during the postfledging period of parental care were frustrated by the extreme furtiveness of the adults, by the apparent departure of at least some males from their territories, and by the difficulty of maintaining visual contact with a chosen bird while territorial boundaries were deteriorating. Except for the postfledging period, we watched a selected bird in a known phase of the reproductive cycle for 20 min of each hour during portions of the early morning, midday, and evening on selected days. We could maintain eye contact with the birds almost continuously through these observation periods from a road or fields bordering their linear territories along the creek. Greenlaw (1969) showed by dividing 180-min periods of activity recording for *Pipilo erythrophthalmus* into subsamples of 15, 20, 30, and 45 min that only the results of the 15-min subsamples differed significantly from the others, and so we regard our 20-min samples as faithfully representing longer sample periods. We constructed composite time budgets for each phase of the cycle from observations spaced through several days of the phase. Six h of sampling time, representing 18 20-min periods of observation (one 18-h day) was the minimum used.

We observed that the birds' activity day began about 30 min before the onset of civil twilight in the morning and extended about 30 min beyond the end of civil twilight in the evening. Daylength including civil twilights was 16.87 h at the beginning of the reproductive cycle and 16.40 h at its end, peaking at 17.11 h on 21 June. Because of the range of day-to-day variability, it was not possible to discern a similar seasonal trend, if any, in the length of the birds' activity day, and so we accepted 18.0 h as a reasonable median estimate. Our energy-budget model is very insensitive to error in this variable (see beyond).

We augmented our direct observations of activity at the nest by means of time-lapse photography at six nests [Kodak Super-8 Analyzer cameras set at exposure intervals of 30 (usually) or 60 s], which we used especially to quantify the time that the female spends on the nest during incubation and the time spent by adults in feeding nestlings. We analyzed the films by counting the number of frames in which the female was on the nest during incubation or the adults were at the nest while feeding nestlings and assumed that the bird was engaged in the same activity in the intervals between photographs as that observed in the photograph. We also assumed that the female's activities while off the nest were the same as those measured by direct observation (Table 3). Because the daily energy expenditure (DEE) computed from activity budgets obtained by direct observation and by time-lapse photography differed by only 3.1%, we pooled the results in Table 3.

We estimated daily energy expenditure (DEE, kJ/day) from this equation:

$$DEE_{tot} = [18(BMR_d + TR)] + [6(BMR_n + TR)] + [1.66t_p + 1.83t_s + 1.48t_n + 7.13t_f], \quad (1)$$

where  $DEE_{tot}$  = total daily energy expenditure, and the other terms are as defined in the text immediately following. The first two sets of bracketed terms concern basal and thermostatic requirements, where  $BMR_d$  = the "basal" or minimal energy requirement during the 18-h day,  $BMR_n$  = the basal requirement during the 6-h night, and  $TR$  = the thermostatic requirement when air temperature is below the lower critical temperature.  $BMR_n + TR$  is estimated as 18% less in incubating than in nonincubating females (Walsberg and King 1978). The basal and thermostatic requirements of the Willow Flycatcher have not been measured directly, and so we estimated them from data for the similar Acadian Flycatcher, *Empidonax vireescens* (Yarborough 1971), in which  $BMR_n$  is 0.638 kJ/h for a 12.6-g individual and is estimated as 24% greater during the day ( $BMR_d = 0.791$  kJ/h), according to Aschoff and Pohl (1970). We calculated the metabolic rate below the lower critical temperature as  $\text{kJ/h} = 1.72 - 0.045T_a$ , as transcribed from Yarborough (1971) for the mean weight of Willow Flycatchers. We computed average air temperature ( $T_a$ ) and equivalent temperature ( $T_e$ , Robinson et al. 1976) from continuous meteorological recordings in the microhabitat of the Willow Flycatcher (Walsberg and King 1978). As the results for the estimation of  $TR$  computed from  $T_a$  and  $T_e$  did not differ when averaged for 24-h periods in 1977, as shown also elsewhere for the White-crowned Sparrow, *Zonotrichia leucophrys* (Mahoney 1976), we used the simpler  $T_a$  to compute  $TR$  in both 1977 and 1978.

The energy requirements for activity ( $DEE_{act}$ ) are included as numerical conversion coefficients (kJ/h) in the third bracketed set in equation (1), each being a multiplier for the time spent (h/day) in the associated activity; alert perching ( $t_p$ ), singing ( $t_s$ ), on the nest incubating ( $t_n$ ), and in flight ( $t_f$ ). The power consumption while perching (1.66 kJ/h) is estimated as  $2.1 \times BMR_d$ , the cost of singing (1.83) as  $1.1 \times$  perching, and the cost of incubating during the day (1.48) as  $0.81 \times$  perching (11% less). Power consumption in flight (7.13) was estimated from equation 2 of Berger and Hart (1974). The rationale for the selection of these conversion factors is discussed in general by King (1974) and in particular for the incubation period of the Willow Flycatcher by Walsberg and King (1978).

An estimate of the energetic cost of egg production, as computed by the method of King (1973), was added to the  $DEE$  for females in this phase of the reproductive cycle. The mean weight of the Willow Flycatcher's egg is about 1.68 g (Hanna 1924, Walkinshaw 1966), the period of follicular growth to the stage of ovulation requires about 4 days, the caloric density of the egg is about 4.40 kJ/g, and the net efficiency of production is estimated as 70%. The mean clutch size observed during this study was 3.2 eggs, and so a clutch of 3 was used in these calculations. The mean clutch size for the region in general (King 1955, plus subsequent data) is 3.4 ( $n = 51$  nests).

North American empidonaces typically undertake their annual molt on the wintering grounds following the autumnal migration. We found no evidence of molt in *E. traillii* captured during this investigation, and so its costs are irrelevant to our energy budgets. We have also excluded the heat increment of feeding ("SDA" or "SDE"), which results from thermodynamic inefficiency in the assimilation of absorbed food—for instance in the daily repletion of fat reserves used in nocturnal metabolism. The heat increment of synthesis represents an added cost of production if it does not substitute for the thermostatic requirement. Whether it does or not is controversial (Calder and King 1974), but we have adopted the conservative course in assuming that it does. For readers who prefer the alternative, we can crudely estimate the heat increment of daily fattening as follows. From data reported later, we first estimate that energy consumption during a 6-h night is about 5.7 kJ. If this energy is supplied by the combustion of fat with a caloric density of 38.9 kJ/g, then 0.15 g of fat will be used. We arbitrarily augment this by 50% to provide a "safety factor," thus requiring the daily synthesis of 0.22 g of fat. If carbohydrate is the precursor, the net efficiency of synthesis is about 0.56 (Brody 1945). The heat liberated by daytime synthesis will therefore total  $(1 - 0.56)(0.22)(38.9) = 3.8$  kJ/day. Readers who prefer this assumption should therefore augment our values  $DEE_{tot}$  by a maximum of about 4 kJ.

#### SENSITIVITY ANALYSIS

The construction of energy budgets from time budgets is subject to error mainly because of the range of uncertainty in selecting the conversion factors for computing the energy equivalents of timed activities, but deterministic energy budgets such as ours have only rarely (e.g. Wiens and Innis 1974, Mahoney 1976, Walsberg and King 1978) been subjected to error analysis to examine their reliability and sensitivity to major variables.

To illustrate the magnitude of error in  $DEE$  associated with error in the quantification of conversion factors, we selected the time budget of a male during the incubation phase (Table 2) and increased each conversion factor by 25%, with results shown in Table 1. The largest error in  $DEE$  (+13.4%) results

TABLE 1. Sensitivity of  $DEE_{tot}$  to error in estimating energy conversion factors for activity (males during the incubation phase,  $DEE_{tot} = 53.9$  kJ/day).

+25% error in conversion factor for:	Estimated $DEE_{tot}$ (kJ/day)	Percent deviation from original estimate
Perching	61.1	+13.4
$BMR + TR$	59.3	+10.0
Flight	54.6	+1.3
Singing	53.9	nil <sup>a</sup>

<sup>a</sup> Slight difference disappears in rounding to tenths.

from error in quantifying the power consumption during perching, because perching strongly predominates in the time budget even though its conversion factor (1.66 kJ/h) is smaller than those for singing (1.83) and flying (7.13). An error this large, however, is very unlikely, because the conversion factor augmented by 25% is equal to  $3.3 \times$  nocturnal  $BMR$ , which is an unrealistic relative power consumption for a quiescent bird (King 1974). We believe that the maximum plausible error in  $DEE$  from this source is about 6%.

The model is next most sensitive to error in the quantification of basal and thermostatic power consumption, which comprises nearly half of the  $DEE$ . A cumulative 25% error due to error in measuring air temperature (unlikely) or in estimating  $BMR$  and  $TR$  produces a 10% error in estimating  $DEE$ . This is probably an overestimate of the maximum probable error. The coefficient of variation is typically about 7–10% in intraspecific measurements of oxygen consumption in small birds, and so about 95% of the estimates (about 2 SD) in a typical sample fall within about  $\pm 20\%$  of the mean. An error as large as 25% in estimating  $BMR + TR$  is therefore possible, but  $P = 0.7$  that the error is no larger than about 10%, producing a 4% error in the estimate of  $DEE$ .

Errors of  $DEE$  resulting from errors in quantifying power consumption during singing and flight are small because of the relative brevity of these activities in the repertoire of the Willow Flycatcher. The effects of reasonable ranges of variation in several other factors affecting the  $DEE$  equation (e.g. body weight, reduction of thermostatic power consumption during incubation, difference in minimal metabolic rate between day and night) all produce errors of about 1% or less in the estimation of  $DEE$  and can be disregarded in this investigation. Finally, a 0.5-h error (an unlikely extreme) in estimating the length of the activity day produces only a slight error (1.8%) in the estimate of  $DEE$ .

In sum, because it is unlikely that errors to which the model is significantly sensitive will all be simultaneously additive (some will cancel others of opposite sign), we believe that our estimates of  $DEE$  are accurate to within about 5% of the true value. Estimates of power consumption or relative power consumption by individual components of the energy budget (as contrasted with total  $DEE$ ) are susceptible to greater error, and so assertions about the allocation of energy to various functions or activities should be tempered by reasonable caution.

## RESULTS AND DISCUSSION

We report here only data that can be correlated exactly with the phases of the reproductive cycle, usually with an error of no more than  $\pm 1$  day within phases. Our data for males are much less abundant than for females, as direct observation of the latter could be augmented by time-lapse photography from the phase of nest-building onward and activity budgets for some males had to be omitted because, by mischance, they could not later be associated with specific mates or known phases of the cycle. This makes some of our samples too small for statistical comparisons. We first examine variation in the obligatory basal and thermostatic power consumption throughout the season, and then turn to variations of activity and its power requirements in the phases of the reproductive cycle.

### BASAL AND THERMOSTATIC EXPENDITURE

The weather on sampling days, and in general, was warmer in 1977 than in 1978, and there were likewise significant differences between sampling days within years.

TABLE 2. Mean percentage of daytime spent in three activities and mean daily energy expenditure ( $DEE_{tot}$ ) by male Willow Flycatchers during the breeding season.

Phase of cycle	Activity			$DEE_{tot}$ , kJ/day		Number of		Minutes of observation
	Perching <sup>a</sup>	Singing <sup>a</sup>	Flying	Mean	Range	Birds	Budgets	
Prenesting <sup>b</sup>	85.0	12.0	3.0	56.2	53.2–57.7	4	5	1,080
Nest construction	92.1	2.9	5.0	61.1	54.8–67.4	2	3	880
Incubation	97.0	0.7	2.3	53.9	51.4–56.4	3	2	740
Nestlings	97.0	0.3	2.7	59.6	—	2	1	360

<sup>a</sup> Singing while perching (the sum of these is the total occupied by alert perching).

<sup>b</sup> Territorial establishment and courtship before nest construction begins.

The effect of this variation of temperature on thermostatic power consumption must be factored out of the energy budget to allow recognition of the variation, if any, in the allocation of energy to various voluntary activities. In phases of the reproductive cycle for which we have adequate samples, we found that mean daily air temperature accounts for 87% ( $r = -0.931$ ) of the variation of  $DEE_{tot}$  of females during the incubation phase and 92% ( $r = -0.960$ ) during the nestling phase. We assume a similar relationship in other phases of the cycle. The residual variation among days and phases is small and indicates that the variation of power consumption by activity is likewise small, as will be shown later.

Obligatory basal and thermostatic power consumption preempt a seasonal average of 42.9% of  $DEE_{tot}$  in males and 42.3% in females, of which an average of 11.5% (range, 6.7–14.3) is consumed by thermoregulation in males and 10.3% (7.0–16.8) in females. Comparative data from other species are scant. In White-crowned Sparrows (*Zonotrichia leucophrys*), the sum of basal and thermostatic demand during the breeding season in three montane or subarctic sites ranged from 46 to 55% of  $DEE_{tot}$ , and thermostatic demand alone was 14–21% of  $DEE_{tot}$  (Mahoney 1976), thus exceeding the fraction consumed by this function in Willow Flycatchers in their warmer habitat. In Phainopeplas (*Phainopepla nitens*), basal and thermostatic demand may be as high as 81% of  $DEE_{tot}$  in incubating males in March and as low as 37% in males feeding nestlings in July (Walsberg 1977). Kendeigh (1972) estimated that basal plus thermostatic demand ("standard metabolism") ranges from 67 to 80% of total energy expenditure in House Sparrows (*Passer domesticus*) during the breeding season in Illinois. Black-billed Magpies (*Pica pica hudsonia*) spend 48–68% of  $DEE_{tot}$  in basal plus thermostatic requirements during the breeding season in eastern Washington except during incubation, when the quiescent female spends 85%. Ther-

TABLE 3. Mean ( $\pm$ SE) percentage of daytime spent in three activities and mean daily energy expenditure ( $DEE_{tot}$ ) by female Willow Flycatchers during the breeding season.

Phase of cycle	Activity			$DEE_{tot}$ , kJ/day	Number		Minutes of observation
	Perching	At nest	Flying		Birds	Budgets	
Prenesting <sup>a</sup>	94.8	—	5.2	65.2	2	2	920
Nest construction and ovulation	51.8 $\pm$ 8.8	45.9 $\pm$ 9.3	2.3 $\pm$ 0.5	58.0 $\pm$ 1.6	5	7	4,230 <sup>b</sup>
Incubation	24.7 $\pm$ 2.2	74.4 $\pm$ 2.3	0.9 $\pm$ 0.1	51.7 $\pm$ 0.6	6	19	8,390 <sup>b</sup>
Nestlings	70.4 $\pm$ 3.5	27.0 $\pm$ 3.6	2.6 $\pm$ 0.2	53.1 $\pm$ 1.1	6	18	6,427 <sup>b</sup>

<sup>a</sup> Courtship, pair-formation, initial nest-site searches.

<sup>b</sup> Includes direct observation and time-lapse photography.

TABLE 4. Mean number of flights per day and mean rate and duration of flights in Willow Flycatchers during the phases of the breeding season.

Phase	Flights/day		Flights/min <sup>a</sup>		Seconds/ flight		Number of budgets	
	Male	Female	Male	Female	Male	Female	Male	Female
Before arrival	1,173	—	1.2	—	1.6	—	1	—
Prenesting and courtship	1,186	696	1.4	0.7	2.0	1.2	2	1
Nest-site selection	1,313	1,313	1.3	1.3	3.5	3.6	1	1
Nest construction	1,349	1,422	1.3	1.4	1.7	2.0	1	1
Incubation <sup>b</sup>	1,100	202	1.0	1.1	1.4	1.1	1	1
Nestlings	1,202	977	1.2	1.5	1.4	1.3	2	4 <sup>c</sup>

<sup>a</sup> Flights/min of perching time.

<sup>b</sup> Midpoint of incubation.

<sup>c</sup> Heterogenous sample from days 3, 5, 8, and 11 (total flights, respectively, 454, 876, 1,117, and 1,463 per day).

mostatic requirements alone are at a maximum of 4.5% of  $DEE_{tot}$  during the egg-laying phase in this well-insulated species and become negligible by the time of the nestling phase (Mugaas 1976).

Estimates of basal and thermostatic demand such as the foregoing could be computed from several other studies if the basic data had been reported in sufficient detail. It is unfortunate that this has not typically been the case, as the fraction of  $DEE_{tot}$  expended in maintenance functions over which an animal has only minor facultative control (through behavioral thermoregulation) may be a limiting factor at the extremes of geographical range; but the significance of this can be discerned only with the aid of comparative data from many species and environments.

#### VARIATIONS OF ACTIVITY AND $DEE$ BETWEEN AND WITHIN REPRODUCTIVE PHASES

*The prenesting phase.*—Male Willow Flycatchers were first detected in the study area on 7 June 1977 and 29 May 1978, when they were already singing intensively and engaged in territorial disputes. Female Willow Flycatchers were not detected until 7 days later when they were already engaged in courtship chases and frequent circuits of their territory while they “tried out” potential nest sites (as described in detail for *Empidonax virescens* by Mumford 1964). Males frequently accompanied their mates on these circuits. Nest construction began about 4 days after the females arrived and required 3–4 days before the first egg was laid. The female continued to mold the rim of the nest during the egg-laying phase and even the first few days of incubation. The male did not assist with nest construction but often accompanied the female during this period of frequent copulation. This accounts for the male's increase of flying time between the prenesting and nest-construction phases (Table 2), as the male's courtship flights were added to those devoted to foraging and territorial patrol, and accordingly accounts for the increase of  $DEE_{act}$  and hence  $DEE_{tot}$  (Table 2, 4).

Because of the large amount of flight devoted to courtship and to nest-site inspection, the female's  $DEE_{tot}$  and  $DEE_{act}$  were, like the male's, at a seasonal maximum during the prenesting phase (Table 3, 4). The male's singing activity diminished sharply after the initial period of territorial establishment and was concentrated in dawn and dusk peaks throughout the season, unlike the patterns in *Empidonax minimus*, *E. virescens*, and *E. difficilis*, which sing intensively only near dawn (MacQueen 1950, Davis 1959, Davis et al. 1963, Mumford 1964).

TABLE 5. Daytime activity and energy allocation by female Willow Flycatchers during nest construction and ovulation.

Day of ovulation cycle <sup>a</sup>	Percent time spent			DEE (kJ/day) spent			DEE (kJ/day)		Total
	Perching	Flying	At nest	Perching	Flying	At nest	Egg production	Activity	
-3	81.1	4.4	14.5	24.2	5.6	3.9	3.6	33.7	65.1
-3	82.8	3.8	13.4	24.7	4.9	3.6	3.6	33.2	60.6
-1	63.3	2.6	34.1	18.9	3.4	9.2	7.1	31.5	55.9
0	35.9	1.5	62.6	10.7	1.9	16.7	6.3	29.3	60.2
0	34.9	1.4	64.2	10.4	1.8	17.1	6.3	29.3	53.0
+1	29.3	1.2	69.4	8.8	1.6	18.5	2.5	28.9	55.2
+1	35.4	1.5	63.1	10.6	1.9	16.8	2.5	29.3	56.2
Mean	51.8	2.3	45.9	15.5	3.0	12.2	4.6	30.7	58.0
SE	8.8	0.5	9.3	2.6	0.6	2.5	0.7	0.8	1.6

<sup>a</sup> Day 0 = day on which the first egg of the clutch is laid.

Our data on the daily numbers, rates, and durations of flights, although sparse, reflect the general activities of the birds during the prenesting phase (Table 4). Females are furtive, typically flitting around in the interior of shrubbery and engaging in briefer and fewer flights at about half the male's rate per hour of perching time. This is followed by a phase of nest-site selection, which we have combined elsewhere with the prenesting phase but present separately here because flight behavior differs so obviously from that of adjacent phases. Our data for the members of one pair (Table 4) are virtually alike (an unlikely result that caused us to double-check the primary data). The total flights per day increase from the preceding phase, and, more conspicuously, the mean duration of flights increases as longer nest-site searches are added to the brief foraging sorties. As already mentioned, the male frequently accompanies his mate in this phase and so also engages in longer flights.

*Nest construction and ovulation phase.*—Activity and power consumption in this phase must be treated separately for females, as the periods of nest construction, ovogenesis, and egg-laying overlap and impose special problems of interpretation. In a small bird laying a 3-egg clutch (one egg per day in Willow Flycatchers), the period of rapid ovarian growth (and hence of increasing power consumption by ovogenesis) begins about 4 days (day -4) before the first egg is laid (day 0), reaches a peak on day -1, and falls to zero on day +2, after the third egg is laid (King 1973). The female is thus simultaneously spending energy on ovogenesis and nest construction, and the dynamics of this phase are particularly difficult to unravel. Our sample of activity budgets is smaller than is fully satisfactory for this purpose, because, in particular, it does not include the terminal day (+2) of the phase. (It was impossible to know which of two or more initial nest-building sites to watch or photograph; some were abandoned, and several sets of observations were therefore aborted.) Nevertheless, the sequence of seven budgets in Table 5 reveals the trends in this phase. On day -3 the female is engaged in constructing the base and bulk of the nest, and so her flying time and flight energy are at a peak in this phase, entailing many flights to collect nesting materials and averaging one flight to the nest each 4.5 min. By day -1, when the energy consumption by egg production is nearing its peak (12.7% of  $DEE_{tot}$ ), her flying time is diminishing, as most of the materials for the nest have already been transported. From this point onward, beginning on day 0, the female spends about two-thirds of the daytime at or on the nest, either quiescent or occasionally tinkering with the rim. This reallocation of

TABLE 6. Mean percentage of daytime spent in three activities and mean daily energy expenditure by female Willow Flycatchers during the nestling phase.

Days <sup>a</sup>	Activity (%)			<i>N</i> <sup>b</sup>	<i>T</i> <sub>a</sub> <sup>c</sup>	kJ/day	
	Perching	Flying	At nest			<i>DEE</i> <sub>tot</sub>	<i>DEE</i> <sub>act</sub>
0-1	39.9	1.7	58.4	2	20.0	49.6	29.6
2-3	77.5	1.9	20.6	3	15.0	56.3	30.2
4-5	59.8	2.4	37.8	4	17.2	53.8	31.1
6-7	71.3	2.7	26.0	3	20.2	51.5	31.7
8-9	82.2	3.2	14.6	4	17.3	55.6	32.6
10-12	85.8	3.6	10.6	2	24.4	48.4	33.1

<sup>a</sup> Day 0 = day the first egg hatched.

<sup>b</sup> Number of budgets.

<sup>c</sup> Mean daytime temperature, °C.

power consumption from perching and flying to mainly resting offsets the cost of egg production, and *DEE*<sub>tot</sub> therefore shows no conspicuous peak coinciding with ovulation, unlike Black's (1975) model for *Dendroica caerulescens* and, less conspicuously, Kendeigh's (1972) model for *Passer domesticus*. Total power consumption in daytime activity after day -1 or day 0, however, is essentially stable, and so there is no compensatory reduction in this component of the energy budget (during egg laying *per se*) to offset the cost of production (Table 5).

The male's *DEE*<sub>tot</sub> is at a seasonal maximum during the nest-site selection and construction phase, mainly because of increased flight time (Table 2) and longer flights (Table 4), as he frequently accompanies the female during her nest-building activities.

*Incubation phase.*—Neither the mean *DDE*<sub>tot</sub> ( $50.1 \pm 1.6$ ,  $n = 7$ , vs.  $51.7 \pm 0.8$ ,  $n = 12$ ) nor mean *DEE*<sub>act</sub> ( $28.8 \pm 0.7$  vs.  $28.8 \pm 0.3$ ) for females differed significantly between 1977 and 1978, and so the data were pooled. Because of the potential for variation between years, particularly in *DEE*<sub>act</sub>, the concordance of the data was unexpected and was therefore double-checked. The female's attentiveness at the nest during the daytime was quite variable through the incubation phase, ranging from 54.3 to 86.7% and averaging  $74.4 \pm 2.3\%$  ( $n = 19$ ), which is essentially the same as the average of about 75% for other flycatchers (Davis 1959, Davis et al. 1963, Mumford 1964) and passerines constructing open nests (for review, see Kendeigh 1952, Weeden 1966). Percent attentiveness was not correlated significantly with mean daytime air temperature ( $r = 0.028$ ) or with the day of incubation ( $r = -0.019$ ), and so we have pooled the data without regard to the stage of incubation (Table 3).

There was a significant reduction of *DEE*<sub>tot</sub> ( $P < 0.001$ ) and of *DEE*<sub>act</sub> ( $P < 0.05$ ) in female Willow Flycatchers between nest construction and incubation, partly as a result of increasing air temperature (*DEE*<sub>tot</sub>) but also as a result of the two-fold reduction of flying time during incubation (Table 3) caused by briefer flights at a lesser rate than in the previous phase (Table 4). This supports the contention (Walsberg and King 1978) that the incubation phase is a period of reduced power consumption by females of this species and by others with similar nesting habits and reinforces our realization that the disagreement about the alleged energy-stress of incubation derives mainly from disparate definitions of incubation as either simply a thermal exchange between parent and eggs (Kendeigh 1973) or as a more complex ecological process involving adjustments of the entire energy budget (King 1974).

The male Willow Flycatcher takes no part in incubation and was not observed



feeding the female at the nest. Such feeding is known in *Empidonax* spp. but is apparently uncommon (Davis 1959, Davis et al. 1963, Mumford 1964). The male's  $DEE_{tot}$ , like the female's, reached a seasonal minimum during the incubation phase (Table 2), but sample sizes are too small to support statistical tests of significance between phases. The male's  $DEE_{act}$  likewise decreased from its level during nest construction (Table 2), mainly because of a more than two-fold reduction of flying time and secondarily because of a reduction in the frequency of singing. The reduction of flying time is correlated with a waning of courtship and of territorial disputes with neighbors. Territorial advertisement by singing continued to diminish through the incubation period, compared with preceding phases, presumably because territorial boundaries had stabilized and could be maintained with diminished effort, although this is speculation.

*Nestling phase.*—Mean  $DEE_{tot}$  in females differed significantly during the nestling phase between 1977 and 1978 ( $51.0 \pm 1.1$ ,  $n = 12$ , vs.  $57.4 \pm 1.1$ ,  $n = 7$ ,  $P < 0.01$ ), entirely because 1978 was colder during this phase. The average of the 2 yr is reported in Table 3. Mean  $DEE_{act}$  did not differ significantly between years ( $31.7 \pm 0.4$  vs.  $30.9 \pm 0.5$ ,  $P > 0.2$ ), as was the case also during the incubation phase.

Our small sample sizes preclude a statistical examination of intraphasic variation in activity and  $DEE$ , but ordination of the budgets in the sequence of days since hatching nevertheless reveals some clear-cut trends (Table 6). The female initially broods the nestlings for long periods in the daytime as well as feeding them, and so her time at the nest is maximal during days 0–1. Brooding continues sporadically for brief periods until about days 7–8, when the nestlings are well feathered (King 1955) and presumably homeothermic. The daytime duration of nest attendance (mainly feeding trips) decreases sharply on days 8–12 as growth rate also decreases. Young Willow Flycatchers begin to lose weight a day or two before fledging (King 1955), and our results suggest that this is because of diminished attendance by the parents rather than an inability to feed them enough. Time spent in flight by the female steadily increases by more than two-fold during the course of nestling growth, and time spent in alert perching (loafing and/or hunting?) reaches a maximum in the last third of the phase, as do also her total number of flights per day and the number of flights per minute of perching (Table 4, footnote c).

The most intriguing aspect of our data for the nestling phase is the intraphasic stability of  $DEE_{act}$  in spite of large variations in the activity budget itself (Table 6). The portion of  $DEE_{tot}$  allocated to activity steadily increases by about 12% between the beginning and the end of the phase, and the difference between days 0–5 and 6–12, although small, is statistically significant ( $30.4 \pm 0.3$ ,  $n = 9$ , vs.  $32.4 \pm 0.2$ ,  $n = 9$ ,  $P < 0.001$ ). Nevertheless, the stability or small range of variation is unexpected, as in the case of the incubation period, and merits further discussion later.

Our information for males is much less detailed than for females during the nestling phase (Tables 2, 4). The male assists the female in feeding the nestlings, visiting the nest on the average about 0.75 times as often as the female (152 flights per day compared with 203 at the midpoint of the phase, for an average of 1 flight each 3rd min for the two parents). We assume that this accounts for the small increase of the male's flying time compared with that in the incubation phase (2.7 vs. 2.3% of the day, Table 2) and for the increase of flights per minute of perching time (Table 4). The time spent in singing decreases to essentially zero at about the time of fledging or soon after.

TABLE 7. Energy expenditure in activities above the basal and thermostatic requirements ( $DEE_{act}$ ) during the breeding season.

Phase of cycle	Days	kJ/day		kJ/phase	
		Male	Female	Male	Female
Territorial establishment	7	31.0	—	217	—
Prenesting	2	—	35.0	—	70
Nest construction	7	35.4	—	247	—
Nest construction and ovulation	7	—	30.9	—	216
Incubation	12	32.2	28.8	386	340
Nestlings	13	33.0	31.4	429	408
Total, kJ				1,279	1,034
Mean kJ/day				32.8	30.4

#### INTERPHASIC VARIATION OF $DEE$

The interphasic variation of  $DEE_{act}$  in Willow Flycatchers is  $\pm 6.4\%$  of the median for males and  $\pm 10.2\%$  for females, averaging  $\pm 8\%$  (Table 7). This accounts roughly for the residual variation ( $\pm 5\text{--}8\%$ ) of  $DEE_{tot}$  not attributable to variation in thermostatic demand. Females exhibit much larger interphasic shifts than males in energy (and time) allocation to various categories, mainly in perching. Perching females are either foraging or loafing, while males are foraging, loafing, singing, and probably engaged in visual advertisement of territorial boundaries. By "loafing," we mean activities that are not obviously directed toward self-maintenance or reproduction. We cannot directly quantify time or energy allocation to these categories during perching, but we can suggest some indirect, first-order estimates. We note first that incubating females spend an average of only about 4.4 h/day in perching, and we assume that loafing time is then near minimal and foraging time is near maximal. The female's  $DEE_{tot}$  (51.7 kJ/day) is at a seasonal minimum during incubation, which may ameliorate the pressure on her available foraging time. If the female requires about 4.4 h/day in foraging for self-maintenance, however, then it is obvious that the 9.3 h/day spent perching during the nest-construction phase ( $DEE_{tot} = 58.0$  kJ/day) must consist about half of loafing time. The fraction of loafing time, based on this same argument, will be even greater in the prenesting phase (Fig. 1). The relatively small differences of  $DEE_{tot}$  do not explain the relatively large differences in perching/foraging time, and we do not believe that variations of food supply or of foraging efficiency (which are unlikely to be large through the span of a few days in the riparian habitat of our study plot) explain it either.

The increase of the female's perching time during the nestling phase is undoubtedly due in part to increased foraging to support the nestlings but still may include some spare time in spite of the pace of her activity. By the methods of Ricklefs (1974) we can estimate that the maintenance and growth of three nestlings during the period of maximum weight gain total about 50 kJ/day, or slightly less than the female's own  $DEE_{tot}$  (53 kJ/day). If the efficiency of assimilation is about 0.8, then food equivalent to  $50/0.8 = 63$  kJ/day must be delivered to the nestlings, roughly half of which is supplied by the male. The female must therefore acquire in 12.7 h/day of perching/foraging time about  $31 + (53/0.8) = 97$  kJ/day for self-maintenance and food for nestlings. The ratio of perching times between the nestling and incubation phases is  $12.7/4.4 = 2.9$ , while the ratio of estimated food requirements is  $97/66 = 1.5$ , strongly suggesting that there will be spare time left over from foraging even during the nestling phase if food supply and foraging efficiency have remained reasonably stable.

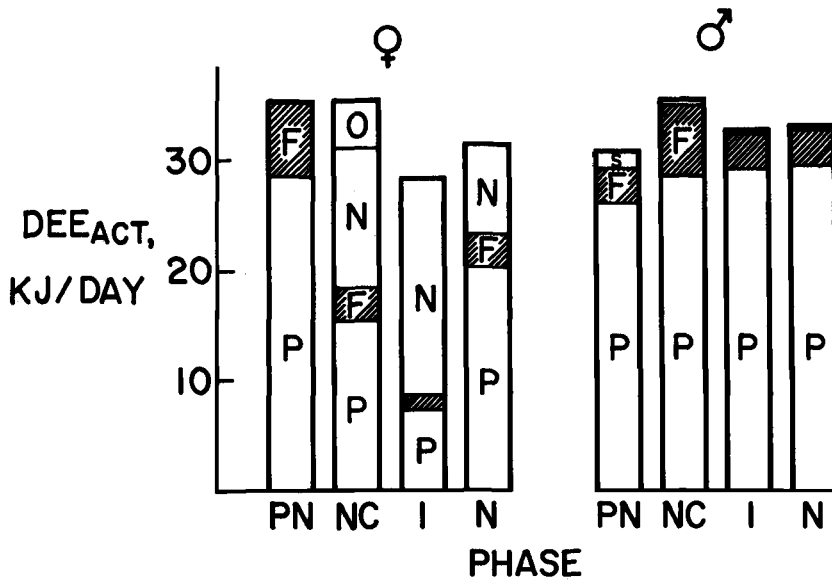


Fig. 1. Allocation of power consumption by Willow Flycatchers to activity (P = perching, F = flying, S = singing, N = female at or on the nest) and to ovulation (= O) during four phases of the reproductive cycle (PN = prenesting, NC = nest construction, I = incubation, N = nesting).

Analysis of the allocation of perching time to subcategories by the male is confounded by his utilization of perching for singing and perhaps visual advertising in addition to foraging and potential loafing. If a 12.7-g female can maintain herself on 4–5 h/day of foraging time at most, however, then so can a 12.6-g male, and the 17.1–17.5 h/day that he spends in perching (including singing time) very probably includes a large fraction of loafing time in which he is not engaged either directly or indirectly in territorial defense.

If a “loafing” component in an animal’s time budget is to be generated and maintained by selection, it must contribute to fitness. We believe that Wilson’s (1975) hypothetical “principle of stringency” provides a rationale for this and that our data illustrate its operation. Wilson suggests that time and energy budgets have evolved to accommodate episodes of extra energy or time demand such as increased expenditure in foraging when seasonal food supplies are poor, when young are being fed, or when unpredictable events such as cold weather, rain, or snow cover reduce the food supply. Aerial insectivores are especially susceptible to vagaries of weather and so should be among the species most likely to conform clearly with the stringency principle. Periods of apparent loafing provide a buffer against episodes of stringency that threaten either adult survival or reproduction. Unpredictable events affecting the food supply would be of major selective significance especially if coincident with episodic stringencies such as the nestling phase or incubation phase when loafing time for the female is minimal.

It follows from the foregoing arguments that selection has acted primarily on the time budget, but with secondary effects on the energy budget, because power consumption continues even while an animal is loafing. We suggest that this accounts for the relative stability of  $DEE_{act}$  in the Willow Flycatcher through the phases of

the reproductive cycle, a stability that otherwise seems inexplicable or supportable only through hypotheses about limitations imposed by food supply or about maximizing energy "throughput" to improve fitness (Hamilton 1973, Schoener 1969) that are associated with  $r$ -selected species, which the Willow Flycatcher is not. The least energy-demanding activities predominate in all phases of the reproductive cycle, which tends to smooth out interphasic variations of power consumption.

Comparative data on avian time-and-energy budgets that are inconsistent with the foregoing arguments are sparse and ambiguous. Data consistent with our arguments are abundant but resist straightforward quantitative synthesis because of differences in definitions and methods. Nevertheless, nearly all reveal (1) a substantial component of "resting" or undefined activity in diverse species (e.g., among many others, Greenlaw 1969, Scharz and Zimmerman 1971, Wolf and Hainsworth 1971, Custer and Pitelka 1972, Verbeek 1972, Dwyer 1975, Black 1975, Murdock 1975, Hubbard 1978), and (2) relatively small variations of  $DEE_{act}$  and/or  $DEE_{tot}$  within the breeding season (Utter 1971, Black 1975, Hubbard 1978), through the annual cycle (Mahoney 1976, Mugaas 1976, Walsberg 1977), or among diverse breeding habitats (Mahoney 1976, Walsberg 1977). In short, the interphasic uniformity of power consumption is much more obvious than its variability, which we suggest results from Wilson's principle of stringency as translated from time budgets to energy budgets.

In sum, the Willow Flycatcher fits the category of "time minimizers" (Schoener 1971) that can engage more or less simultaneously in foraging, protection of food supply and mates from intruders, and in vigilance against predators. This overlap minimizes the time that would be required by these activities if they were performed sequentially and also minimizes the time required by foraging if the energy supply is protected and exclusive. Wilson (1975, see also Schoener 1969) suggests that this pattern of time and energy allocation is characteristic of  $K$ -strategists, which is consistent with the life-style of the Willow Flycatcher. This bird cannot improve its reproductive output by increasing the food supply to the usual number of nestlings, because the growth rate of nestling passerines has evidently been maximized (Maher 1964, Ricklefs 1973). We believe that more than the usual (3–4) number of young could be nourished by their parents in a typical season by a reduction of loafing time and an increase of foraging time, which (if true) means that the clutch size has been fixed by other selection pressures, such as unpredictable trophic crises in "nontypical" seasons. Wiens (1977) emphasizes in the context of competition theory that environmental stringency is unpredictable and that selection is therefore episodic, which is consistent with the viewpoint that we present here.

#### INTERSPECIFIC COMPARISONS

The mean  $DEE_{tot}$  ( $\pm$ SE) during the breeding season in male Willow Flycatchers is  $58.1 \pm 1.14$  kJ/day ( $n = 12$ ) and in females is  $53.6 \pm 0.76$  ( $n = 46$ ). The grand weighted mean of these is  $54.5 \pm 0.64$  kJ/day ( $n = 58$ ). For a 12.6-g bird such as a Willow Flycatcher, this is 1.6% less than the value (55.4 kJ/day) predicted by Walsberg's (in press) equation for birds in general and falls between his prediction for birds that feed on the wing (73.2 kJ/day, hummingbirds and swallows) and those that do not feed on the wing (46.9 kJ/day). The  $DEE_{tot}$  of the Willow Flycatcher differs significantly from that of hummingbirds and swallows ( $P < 0.05$ ) but not

from that of other types of foragers. We had assumed a priori that the  $DEE_{tot}$  of flycatchers as a group would be closer to that of other aerial foragers than to that of ground foragers, browsers, and foliage gleaners, but a comparative examination of time and energy budgets reveals why this is not so. Except in the truly aerial foragers, time spent in flight is only a small fraction of the time budget but exerts a disproportionate effect on the energy budget because of the intensity of power consumption by flight. In spite of its mode of foraging, the Willow Flycatcher devotes less time (and hence less energy) to flight than do many ground foragers and foliage gleaners, as shown by data summarized by King (1974) (which adequately reflect the range of values that have been reported subsequently for additional species). Although a Willow Flycatcher may engage in more than a thousand foraging sorties or longer flights per day throughout its breeding season, these flights are brief on the average and sum to less than the daily flying time of many species that rely on other modes of foraging. This re-emphasizes the economies of sit-and-wait predation, which telescopes foraging time with other vital processes and transfers at least part of the hunting time to the movements of the hunted.

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