TIME BUDGET OF THE MALE LONG-BILLED MARSH WREN DURING THE BREEDING SEASON

By Jared Verner

In order to survive and reproduce, a bird must effectively perform a variety of activities, each requiring an expenditure of time. By recording how much time is spent in each activity one can construct a time budget. In a very vague, unquantitative way, the concept of the time budget has appeared in avian literature for years. Only recently, however, have serious attempts been made to express time budgeting more precisely (see Lees, 1948; Kluijver, 1950; Gibb, 1954, 1956, and 1960; Orians, 1961; and Verbeek, 1964).

It has been argued (Orians, 1961) that even very subtle differences in time budgeting can affect an individual's reproductive success and thus have evolutionary implications. In this sense, natural selection might be compared to an efficiency expert. It follows, then, that there is a hypothetical "best" time budget for any given set of circumstances and that selection will favor those individuals whose budgets most closely approach this. Clearly, the best budget will be different for each individual, since no two exist in precisely the same environment. Consequently, selection should also favor an adaptable time budget, one that is strongly influenced by environmental factors. It is the purpose of this paper to present diurnal variations in time budgeting of male Long-billed Marsh Wrens (*Telmatodytes palustris*) throughout one breeding cycle and to suggest how the general pattern is selectively advantageous.

STUDY AREA

Field work was conducted in marshes adjacent to Lake Washington, in the University of Washington Arboretum, Seattle, Washington. These consisted of extensive patches of cattail (*Typha latifolia*) with scattered stands of bulrush (*Scirpus acutus*). More detailed descriptions of these marshes have been given elsewhere (Verner, MS; 1965).

The wren population (*T. p. paludicola*) at Seattle is resident. Males were polygamous and began constructing courting nests as early as late February one year but not until early to mid-March in two other years. The earliest recorded laying date was March 23, 1961, and the latest was July 23, 1962. Ideally a pair of wrens could rear three broods per season at Seattle, although none did so because of predator interference. The breeding season coincided almost perfectly with the period during which the marshes had standing water (March through late July to early August), and roughly the first half of the breeding season occurred in the rainy season while the second half occurred in the dry season.

METHODS

Symbols were used to represent each of the various activities of males, and all activities of a given bird were recorded in sequence during a standard observation period of 30 minutes. Time was recorded each minute on signal from an automatic timer. Most observations were made from 10-foot high towers placed so two territorial males could be effectively observed. Normally observations were maintained for several hours, alternating 30-minute periods between two males to give a reasonable sample of the activities of each for the entire period. In 1961, 68 hours of records were obtained from 11 males, but these were not systematically taken and

were useful principally in familiarizing me with the birds' activities and with an efficient system for recording them. In 1962 about 240 hours of records, distributed throughout the day and season, were obtained from five males.

From inspection of the record for each minute, I estimated, to the nearest quarter of a minute, the time spent in each activity. This method probably rarely resulted in errors of greater than five seconds, and with a large sample, errors should cancel out. In handling the data it has been necessary to make some simplifications in the categories of male activities, in diurnal periods, and in phases of the breeding cycle. These are described below.

ACTIVITIES OF MALES

1. Foraging.—This includes those activities associated with food getting, chiefly moving in search of food. Marsh wrens normally forage on or near the marsh floor and so were usually out of sight when they foraged. The only major assumption made about time expenditure was that a male was regarded as foraging whenever he was out of sight. All other activities were performed in exposed places or involved vocalizations or both, so attention was quickly drawn to them. Some time spent in resting and preening has inevitably been included in that allotted to foraging, and an estimate of the extent of this error can be obtained from the relative number of times birds were actually observed foraging when near the marsh floor as opposed to the times they were seen resting or preening. Of recorded observations of males in these locations, foraging was noted 357 of 385 times (92.7 per cent). Resting occurred between songs (see beyond) but was so rarely observed at other times that I always recorded it. Even in the heat of the day these birds appeared to be in a state of continuous activity.

2. Singing.—This includes the time the wren was resting and preening between songs as well as the time used in vocalization. Actual song time has been calculated from the total number of songs in a given period and from the mean duration of songs (1.38 seconds, based on 68 sonagrams).

3. Territorial defense.—This includes all activities, exclusive of song, that can be associated definitely with this function, that is, boundary disputes, aggressive displays in certain contexts, and special calls. Song also functions in this capacity, but it is apparently more important in this species in connection with mate attraction. Since it is impossible to evaluate the relative role of song in these two capacities, singing time has been treated separately.

4. Nest construction.—This includes the time spent gathering, carrying, and incorporating nest materials into a nest.

5. Courtship.—This includes all the time spent in sexual chases and displays. Since the multiple nests of males of this species function in courtship (Verner, MS; 1965), nest construction might properly be considered courtship time.

From March 13 to July 30, 1962, 240 hours of observations were obtained on five males (only four after April 3). Of this time, 61.2 per cent was devoted to foraging, 31.6 per cent was devoted to singing, 0.8 per cent was spent in territorial defense, 5.2 per cent in nest construction, and 1.2 per cent in courtship. It is also possible to estimate the percentage of time spent in nest building from knowledge of the mean time to build one nest (558 minutes or 9.3 hours). Since the males in this study completed an average of 13.7 nests, they spent a mean of about 127 hours apiece in nest construction. They were active for about 1893 hours during the nest-building season, so they spent about 6.7 per cent of that time in nest construc-

tion. The value of 5.2 per cent obtained from the direct observations is an under-estimate, since many observations were made prior to and after the season of nest building. Correcting for this gives a new estimate from direct observations of 5.6 per cent. The close correspondence of these two estimates strengthens the assumption that the observational data provide a fair estimate of male time budgeting during the 1962 breeding season.

PHASES OF THE REPRODUCTIVE CYCLE

1. Pre-building.—The period between the obvious onset of internally motivated singing and the beginning of nest construction is designated as the pre-building period. Data from this period were obtained between March 13 and 26, by which time most males had begun nest work.

2. Pairing.—This is the period from the onset of nest construction up to and in-cluding the fourth day prior to the day of first egg deposition. Pairing was known to take place as early as three or four days after nest building began, but the shortest duration between first pairing and the start of laying is unknown. It was not until about the third day preceding laying, however, that there was any striking change in the behavior of males.

3. Pre-laying.—This period includes the three days prior to laying of the first egg in a clutch, whether it involves the first clutch of the season or a later one. Males frequently began construction of new courting nests during this phase.

4. Laying.—This includes all days during which eggs were deposited by any female of a given male.

5. Incubation.—This is the period of incubation which starts after the last day of egg deposition (the female actually begins incubation earlier); it also includes the first three days during which there are any young in the nest. This division was made because males do not usually begin feeding nestlings until the oldest is about two days old. From the standpoint of the males' time budget, then, the first three days of the actual nestling period are similar to the incubation period.

6. Nestling period.—This includes the remaining days after the first three during which there are young in the nest.

7. Fledgling period.—This period includes the first 12 days after the young leave the breeding nest, even though fledglings may return to roost in the nest. A 12-day period is somewhat arbitrarily used for this phase, since males have been noted feeding young after the twelfth day. However, the resumption of nest build-ing may be as early as the fifth day of the fledgling period (rarely males continued to build throughout this phase), and since there is a fairly gradual renewal of mate-attracting behavior it is not possible to define the phase precisely.

8. Between cycles.—This period includes all days following successful or un-successful nestings up to the pre-laying period of a new cycle. If a nest is broken up at any stage, "between cycles" begins the following day. Although there was not always an obvious change in the males' behavior, especially with destruction of a nest during laying or incubation, loss of young was followed by a marked change from little song and nest building to much song and an immediate resumption of nest building.

DIURNAL INTERVALS

Days were divided into six approximately equal parts (fig. 1), using noon as the mid-point. Since noon was not always exactly the mid-point of the wrens' active day, the duration of the three morning periods, or diurnal intervals, was not always
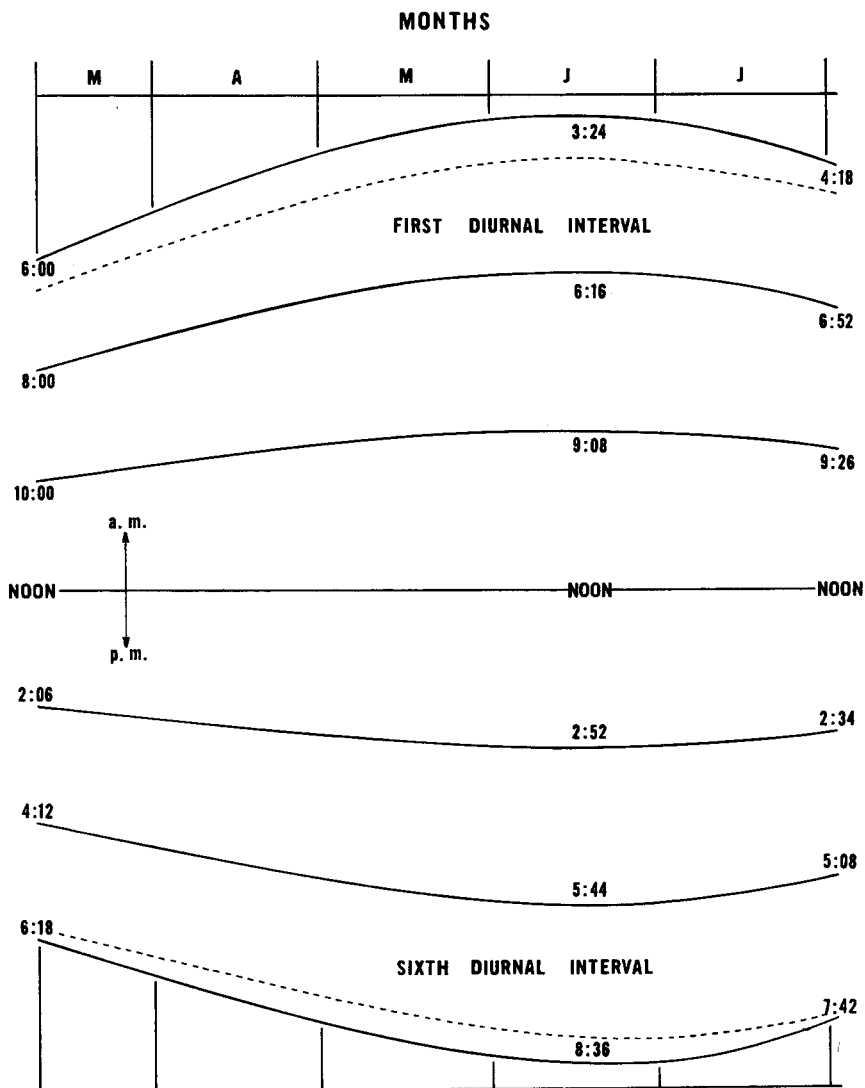
MONTHS

Fig. 1. Daily active period, divided into six equal intervals; sunrise and sunset are indicated
by dashed curves; times indicated are PST.

the same as that of the three afternoon intervals; however, the greatest difference
between them was only six minutes. The days have been divided in this manner
to show diurnal variations in time budgeting and to make observations at different
times during the breeding season more comparable. For example, 8:00 a.m. on
March 16 is nearer to sunrise than is 8:00 a.m. on June 16, so the hour-by-hour
times are not equivalent from the birds' standpoint.

The beginning and end of the male wrens' active day has been approximated
from times of first and last songs of the day. That these actually set the limits of
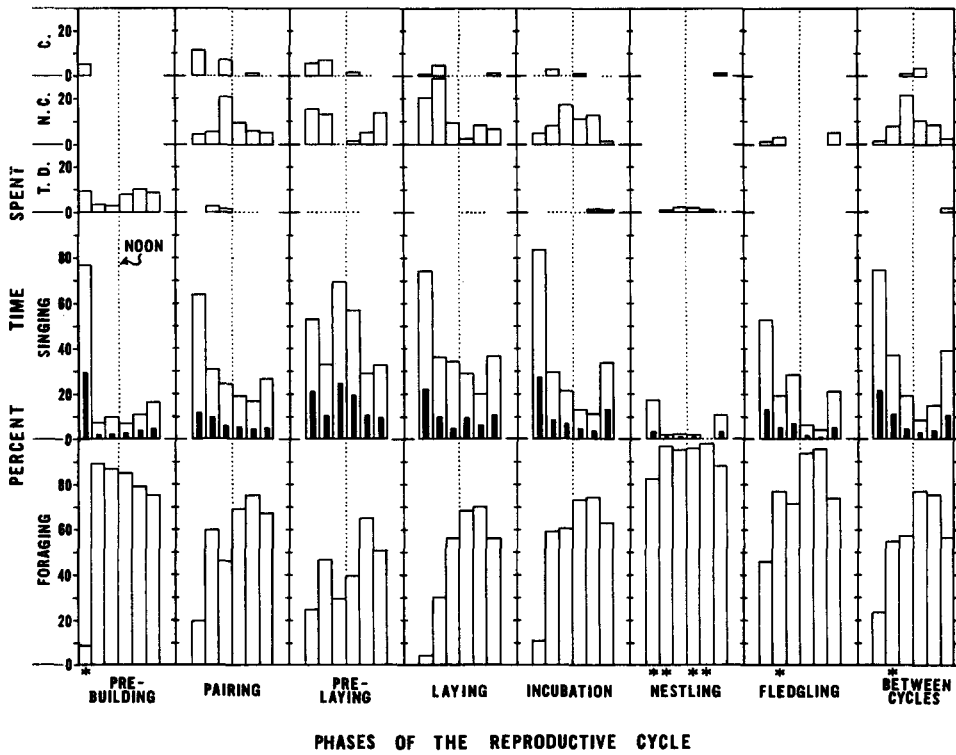the wakeful period cannot be proved, but that they probably do set the limits of

Fig. 2.   Diurnal variations in time budgets throughout one breeding cycle, each phase being
divided into the six daily time intervals. Black bars within singing histograms represent
time in actual vocalization, the remainder of the time being spent resting or preening
between songs. T.D. = territory defense, N.C. = nest construction, C. = courtship; dots
in place of columns indicate less than one per cent of the time spent in that activity.

the period of activity is attested by the fact that males were frequently heard to
deliver their first and last songs of the day from within nests in which they were
known to roost.

<div align="center">RESULTS</div>

Time budgets can be expressed either in terms of the total amount of time spent
in each of the various activities or as percentages of the total time available appor-
tioned to each activity. Each method has its special merits, and conceivably utiliza-
tion of the two together could yield results not possible from either method alone.
In the present analysis, expenditures are expressed as percentages of the total time
available, which tends to reduce bias resulting from differences in the length of the
active period. The data have also been expressed as total time in the various activ-
ities, but these results will not be presented here since they are only slightly different
from the percentages and lead to no different conclusions.

Since all males exhibited behavior conducive to multiple matings, it is not possible
to refer to monogamous or bigamous individuals. However, when a male became
polygamous his time budget was subject to influences not affecting those that were
not polygamous. It is therefore necessary to differentiate the functionally monogam-
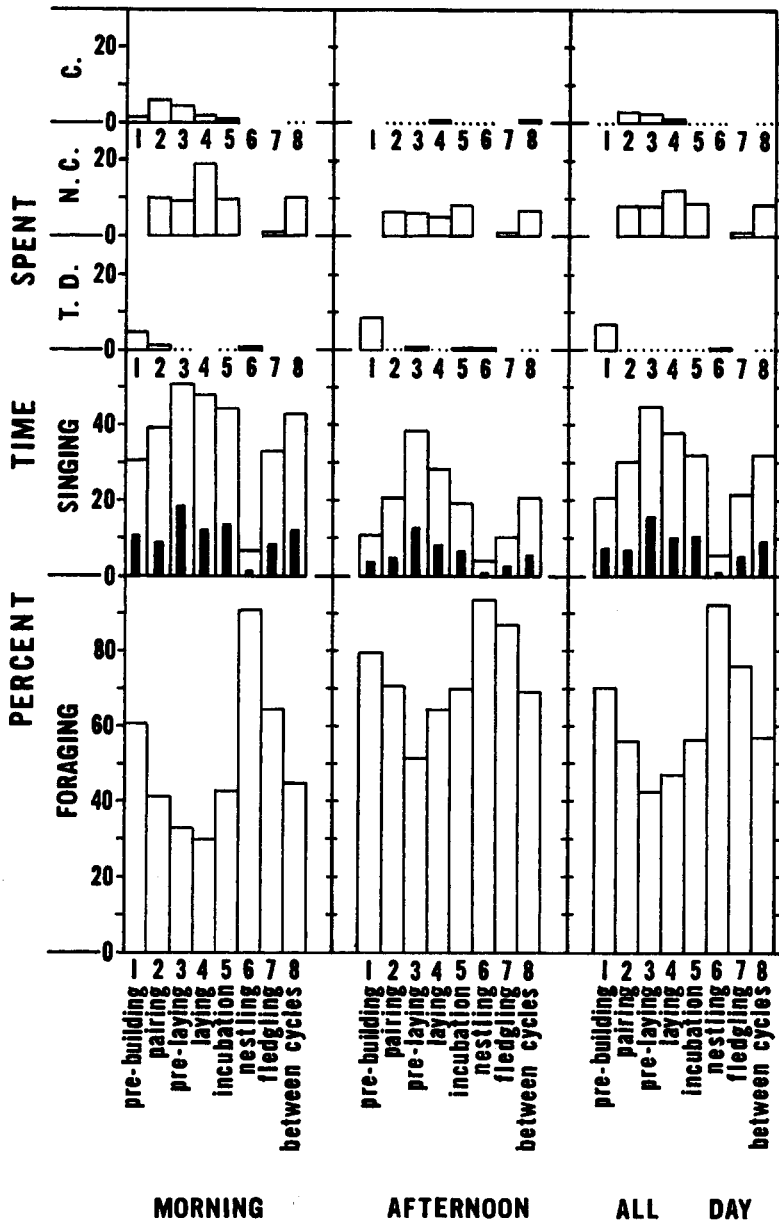
Fig. 3. Morning, afternoon, and daily variations in time budget throughout one breeding cycle. Format of this figure as in figure 2.

ous from the functionally polygamous birds. In the following pages, all references to time budgeting not otherwise designated refer to functionally monogamous or to unmated males. The data are inadequate to permit a very thorough analysis of time utilization by polygamous birds.

Figure 2 presents histograms of the average time budgets of four males, and that of a fifth male during pre-building and pairing, in 1962, based on the combined observations on all males. These are expressed as percentages of total observed time in each activity during each of the six diurnal intervals and during each of the reproductive phases. Only those data collected between March 13 and June 6 are included, a division made on the basis of major weather trends. Each column in the figure, consisting of separate blocks for each activity, totals 100 per cent vertically, and those for which less than 90 minutes of observation are available are so indicated by an asterisk at the bottom of the column. A total of 9304 minutes (155.7 hours) of observation are used for this part of the analysis.

No observations were obtained for the second and fourth intervals of the nestling phase, and only 30 minutes were obtained for the fifth interval. In the last case, the male under observation had only a single nestling, for which the female alone was able to provide. Consequently, the male was not spending as much time foraging as he would with more young. For these reasons, I have estimated the time budgets for those diurnal intervals. The estimates are based on considerable experience with males at those times, partly from observations in 1961 and partly from functionally bigamous males. Moreover, the general diurnal patterns of activity during other phases provide additional aid in estimating the three intervals during the nestling phase.

In figure 3 the same data have been used to graph time budgets for the morning and afternoon as well as for the full day. It should be stressed that whereas blocks in figure 2 show diurnal changes in budgeting during the different phases, those in figure 3 show changes in budgeting during a comparable portion of the day from one part of the breeding cycle to another. To calculate a.m. and p.m. percentages, the means during each of the three respective intervals were averaged, and estimates of day-long budgets were derived by averaging a.m. and p.m. percentages.

DISCUSSION

DIURNAL VARIATIONS

Figure 2 demonstrates basic similarities in diurnal variations in time budgeting throughout the breeding cycle, especially as reflected in foraging budgets. Foraging consumes the least proportion of time during early morning of every phase and usually the greatest proportion during early or midafternoon, followed by a reduction in late afternoon. Since I assumed males were foraging when they were out of sight and silent, it could be argued, that much of the midafternoon time was spent resting. According to Palmgren (1949:564) "a tendency towards a diphasic sleep is inherent in most birds, indicated by their afternoon period of inactivity, well known to field ornithologists." Earlier, however, Palmgren (1935) noted that singing in the Chaffinch (*Fringilla coelebs*) was inhibited by low relative humidity and that Chaffinches sang more during cool, moist afternoons, suggesting that an afternoon rest period may not be essential. Kuusisto (1941) found that the per cent of time spent in foraging by female Willow Warblers (*Phylloscopus trochilus*) reached a peak during warm afternoon hours, and Lees (1948) demonstrated midmorning and midafternoon peaks in the frequency of visits to traps, baited with food, by European Robins (*Erithacus rubecula*), Blue Tits (*Parus caeruleus*), and Blackbirds (*Turdus merula*) from October through March, although in the last species the second peak occurred in early afternoon.

Field evidence of afternoon rest periods stems chiefly from a reduction in song output, not from observation of resting birds. Observational data from the marsh wren support the view that even during midafternoon they were foraging nearly the entire time they were near the marsh floor and silent. Moreover, the marsh wren is a small species and Gibb (1960) has shown clearly that smaller species spend a longer time foraging than do larger ones. Larger bird species may, in fact, exhibit normal afternoon rest periods, but this is less likely to be true of small species.

Certainly the most important activity of any organism is the accumulation of sufficient energy to exist. Only when this occurs in less than the total available time can other activities, such as those associated with breeding, occur. If food can be more readily obtained at one time of the day than another, selection should favor those individuals that forage at the better time, since an equivalent amount of food could be acquired in less time, leaving more time for other activities. For an insectivorous species, such as the marsh wren, food species would be less active, hence less conspicuous, at lower temperatures. They would also be more easily seen in bright than in dull light. Consequently, the most efficient period for a marsh wren to forage is probably during the afternoon, when ambient temperature reaches a maximum. A bird must also store enough energy to pass the night, which should favor foraging as late in the evening as is efficient. Moreover, enough energy must be stored to meet unexpected exigencies during the night, such as sudden temperature drops or disturbance from a roost. A marsh wren probably stores more than just enough energy to survive the night since a great deal of singing and other nonforaging activity is performed early in the morning.

During the breeding season, male birds must establish a territory to attract a mate, and females must seek and find a mate. Selection should favor those individuals that perform these activities on the excess energy available early in the morning after it becomes light enough to move about but is still not light enough to forage with high efficiency. Evidence on these points is scanty, but figure 2 reveals that most courtship in the marsh wren occurred during early and midmorning (this was not true of territorial defense, which usually involved encounters with neighboring males already on territories). The few cases in which females were seen to enter more than one male's territory in apparent mate-seeking behavior were all in the morning. Lack (1946) reported that pair formation in the European Robin usually takes place in the morning, and G. H. Orians has told me that nonterritorial male Redwinged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) fly over the marshes in search of unoccupied territories most often in the morning. This being the case, selection should also favor high song outputs by territorial males at the same time—also at the expense of the energy remaining at the end of the night. It was clearly evident, for instance, that at dawn males sang longer without interruption following warm rather than following cold nights. Very early in the breeding season males rarely sang continuously for over 30 minutes after dawn. Later, however, when nights were shorter and warmer, males frequently sang for 60 or even 90 minutes at dawn with rare, short interruptions to forage.

At the end of the day, an increased song output is probably advantageous for at least two reasons. First, if unattached males were prevented from roosting in the territory they might be less likely to acquire an attachment to it. Second, if an unmated female were attracted to roost in a male's territory, the male would have a higher probability of being first to court her the following morning and probably
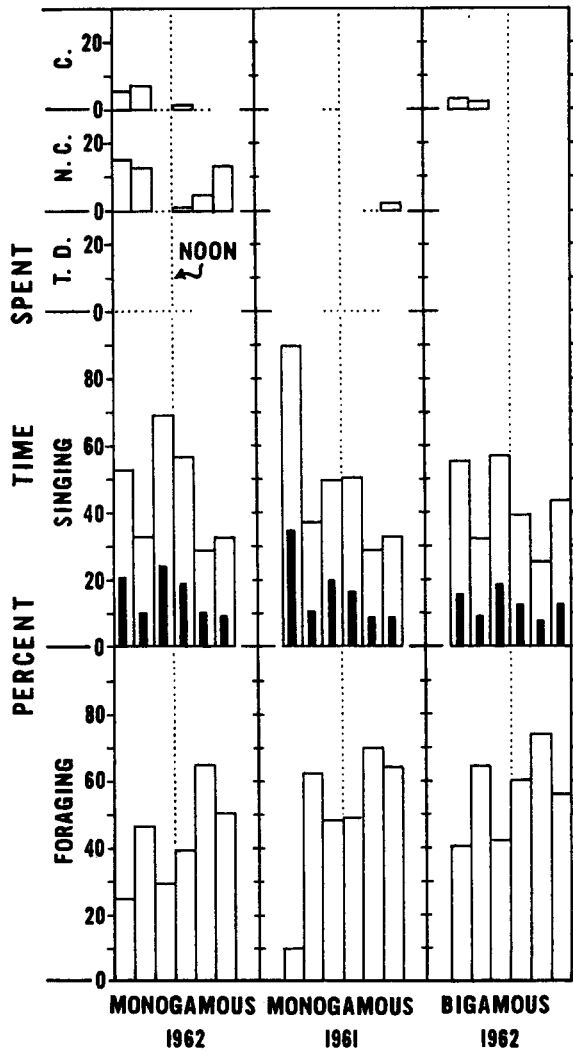
Fig. 4. Diurnal variations in time budget during the pre-laying phase as determined for monogamous males in 1961 and 1962 and for one bigamous male in 1962.

also of acquiring her as a mate. With selection for increased song output as well as for extensive foraging late in the afternoon, a compromise has probably been reached. In fact, foraging begins to decline before any appreciable decrease in light intensity or ambient temperature at the end of the day. At the same time, singing never consumes as much time in late afternoon as in early morning, foraging being interspersed among song bouts until roosting time.

Only during the pre-laying phase did the configuration of singing time deviate notably from the U-shape that seemed to characterize diurnal variation in singing time during other phases. During pre-laying· the configuration of singing time is better characterized as W-shaped. Further evidence suggesting that this is not the

result of sampling error comes from functionally monogamous males in 1961 and from a functionally bigamous male in 1962 (fig. 4). The bigamous male had a second female about to lay. In both of these cases, as with monogamous males in 1962, there was a marked increase in time spent in singing during midday that was not seen in any other phase of the cycle.

At the time the female is ready to lay it is essential that the pair achieve rapport not only in their reproductive physiology but in their social relations as well. Behavioral interactions could serve this end through mutual stimulation of the sexes and reduction of aggressive tendencies that might otherwise prevent copulation. In several species, for example, it has been shown that the male is normally dominant over the female but that the dominant-subordinate roles undergo an inversion shortly before laying (discussion in Marler, 1956). In the Reed Warbler (*Acrocephalus scirpaceus*) the male performs a curious wing-shivering display that begins after pair formation, reaches a peak a day or two prior to laying, and subsides about the third day of laying. This behavior recurs at later nestings and is reported to be "kept up for hours on end" (Brown and Davies, 1949). Visual displays of this sort, however, are incompatible with the polygamous mating system of the marsh wren. It seems likely that song, in addition to attracting prospective mates to the territory and repelling other males (especially important at this time, since copulation occurs), serves the added function during the pre-laying phase of increasing the female's receptivity to approach by the male, making it possible for copulation to occur. As a result, males spend more time singing during the pre-laying phase than at any other time. They already sing about as much during early morning and late evening as is compatible with their foraging requirements, and midmorning is probably a time to replenish exhausted energy stores while midafternoon is used to store most of the energy for the night. Consequently the increased song output during the pre-laying phase is manifested during midday.

Phasic Variations

It is seen in figure 3 that foraging consumed proportionally less time as the season progressed. Production of insects should increase with increasing temperature and photoperiod (see beyond), so as the season advanced wren food species probably became more abundant. With more food available, an equivalent amount could be obtained in less time so foraging time decreased. The sudden and spectacular increase in foraging time during the nestling-fledgling period needs no discussion. However, it is of interest that foraging before and after these two phases took more than 50 per cent of the males' time, and in eight full days of incubation females spent 49.2 per cent of their time out of the nest.

If it takes adult wrens nearly half their available time just to meet their own energetic demands, they must be seriously pressed to feed four or five young as well. One female was noted to have lost all her rectrices on June 29, 1962, while she had young in the nest. She successfully fledged and reared the young to independence and by late July had started a new nest. On August 21, 1962, the female was trapped and examined carefully; at that time the young in her new nest were nearly fledged. No trace of any replacement of tail feathers was in evidence—almost two months after the tail was lost. This incident strongly suggests that there is an internal mechanism whereby feather replacement can be delayed and that this female was pushed to the limit of her ability to accumulate enough energy just to maintain herself and her reproductive activities (cf. Miller, 1961).

Young birds were fed on larger and larger items as they grew older, whereas the adults continued to eat very small items, such as aphids and mites. Obviously large food items are more efficiently transported to the young since they contain more energy than small ones. Thus it is probably adaptive for adults to consume a different variety of foods than those carried to the older young, since it reduces competition for food between the adults and their offspring while permitting the adults to forage for themselves and their young simultaneously. By gleaning the smaller, more abundant invertebrates for themselves as they move along and taking all larger food items to the young when they are encountered, the adults can probably feed themselves and their young with little more time than it would take just to feed the young.

Data on territorial defense agree well with the general observations of numerous workers on many passerine species. Early in the season, considerable time was devoted to those activities directly associated with establishing and defending territorial limits. With the onset of nest construction, territorial defense was apparently effected mainly through song. The beginning of nest construction, therefore, probably provides a tangible clue to the fact that a male's territory is firmly established. In one case in a population studied at Turnbull National Wildlife Refuge in eastern Washington, a male entered the marsh after others were on their territories. He spent three weeks establishing his territory by starting first at the boundary between two others and usurping a portion of one of them. The two established males began nest construction on April 1 and 2, respectively, but the male that was delayed in establishing his territory did not begin nest construction until April 19.

ENVIRONMENTAL FACTORS

Various laboratory studies have demonstrated a linear increase in metabolic rates of birds with decreasing ambient temperature below the thermoneutral zone (Kendeigh, 1939, 1944; Wallgren, 1954; Steen, 1957, 1958; Dawson, 1958; Dawson and Tordoff, 1959; Misch, 1960; Hart, 1962; and others). Some have demonstrated a linear relationship between gross energy intake and changing temperature and photoperiod (Kendeigh, 1949; Seibert, 1949; Steen, 1957; and Cox, 1961). More recently Verbeek (1964) has shown that the amount of time spent foraging by Brewer Blackbirds (*Euphagus cyanocephalus*) in the field increased with decreasing ambient temperature during the winter.

If food were equally available over the whole range of temperatures studied, the rate of change in time spent foraging should be equal to the rate of change in energy requirements. If, however, food were more plentiful at high than at low temperatures, for example, the per cent of time spent foraging should decrease proportionally more rapidly than the amount of energy required with increasing temperature.

In the present study, enough observations were obtained to estimate the foraging time of males during the incubation period in spring and again in midsummer of 1962 (table 1). Since the same males were observed on approximately the same territories during equivalent stages of different breeding cycles in the same year, the principal variables were ambient temperature and mean daily active period.

Seibert (1949) has determined gross energy intake at different temperatures and photoperiods for the Slate-colored Junco (*Junco hyemalis*), White-throated Sparrow (*Zonotrichia albicollis*), and the House Sparrow (*Passer domesticus*) under laboratory conditions. By taking the means of his results for these three species, one can estimate energy requirements of a 22 gm. bird at various combinations of temperature

TABLE 1

FORAGING BUDGETS OF MALES DURING THE INCUBATION PERIODS OF DIFFERENT BREEDING CYCLES
IN THE SAME SEASON AT SEATTLE, WASHINGTON, 1962*

Diurnal intervals	Minutes observed	Minutes foraged	Per cent of time foraging	Mean daily active period (hrs.)	Mean ambient temperature (°C.)
			May		
1	270	29	10.7	16.1	9.3
2	210	125	59.5	16.2	10.1
3	300	182	60.7	16.0	11.1
4	150	111	74.0	15.9	12.2
5	330	224	74.0	15.8	12.5
6	289	182	62.9	15.7	12.3
Mean	258	146	56.9	16.0	11.3
			Late June to early July		
1	150	6	4.0	17.0	13.1
2	120	43	35.8	17.0	14.7
3	120	49	40.8	17.0	19.0
4	150	87	58.0	17.0	20.4
5	120	76	63.4	17.1	20.2
6	180	65	36.1	17.1	19.5
Mean	140	54	39.7	17.0	17.8

* Temperatures were recorded in the field at the time of observation.

and photoperiod. Then, using King and Farner's (1961) formula for basal metabolism of adult birds of different weights ($logM = log 74.3 + 0.744 logW \pm 0.074$) and 11 gm. as the mean weight of male marsh wrens (personal observation; Kale, MS), it is possible to calculate a wren's energy intake (Cal. per day) from that of the juncos and sparrows. Under comparable conditions of temperature and photoperiod for which data on foraging budgets are available (table 1), a wren consumed on the order of 14.1 Cal. per day in May but only about 13.5 Cal. per day in late June to early July. This is a difference of 0.6 Cal. per day or a drop of 4.3 per cent. The difference in per cent of time spent in foraging, on the other hand, was 17.2 or a drop of 30.2 per cent. Clearly food was more rapidly obtained in late June and early July than it was in May. In spite of the fact that the estimates of energy intake are crude, it is unlikely that refinement of the measures would significantly alter this conclusion. Doubling gross energy intake (since calculations are based on caged birds) does not change the per cent of drop in intake, and using Brody's (1945) formula for basal metabolism instead of King and Farner's gives a percentage drop of 4.6 instead of 4.3.

For two weeks prior to the periods of observation in late June to early July the mean ambient temperature was about 5°C. higher (based on U.S. Weather Bureau records taken at Sandpoint Naval Air Station, three miles from the study area and also adjacent to Lake Washington) and photoperiods about an hour longer than those prior to the observations in May. The longer the photoperiod, the more solar energy is put into the ecosystem; and the higher the temperature (within limits) the more rapid is the rate of production. Consequently, insects were probably more abundant during the later period of observation, accounting, at least in part, for the more efficient foraging at that time. An additional factor results from the fact that insects are more active at higher temperatures (see Dobzhansky and Wright, 1943; Andrewartha, 1961); so they would probably be more conspicuous to a foraging wren. Thus the same number of insects might be caught in less time at high

than at low temperatures with no change in the total number of insects in the environment. Finally, the possibility that the timing of emergence of various insect species on which the wren could specialize might have been important here must not be overlooked. This factor was probably not of great consequence, however, judging from the generalized diet and the very extended breeding season of the wrens. Moreover, May of 1962 was typified by abnormally adverse weather conditions and wren breeding activities suffered heavily (Verner, 1965), supporting the view that food was less plentiful in May than later in the season.

SUMMARY

Diurnal variations in time budgets of male Long-billed Marsh Wrens (*Telmatodytes palustris*) were determined for one breeding cycle, from March 13 through June 6, 1962, at Seattle, Washington, based on 156 hours of detailed records of five males supplemented by an additional 152 hours obtained later in 1962 and in 1961. Foraging was least time consuming early in the morning of each phase of the breeding cycle and most time consuming in early or midafternoon, while the reverse was true of singing. Prolonged singing at dawn was largely dependent upon stored energy not consumed during the night so it continued longer with almost no foraging following warm nights rather than cold nights. Large song outputs early in the morning are probably adaptive, since unmated females are more likely to be seeking mates then (which also consumes energy left at the end of the night) and nonterritorial males are more likely to be seeking territories.

During the two or three days prior to laying there is a marked increase in time devoted to singing. It is postulated that this functions importantly in increasing the female's receptivity to approach by the male, making it possible for copulation to take place. At the same time, additional females may be attracted, since males are polygamous, and other males may be repelled.

During nestling and fledgling periods the adults consume very small insects and carry larger items to their young. In this way they are probably able to feed themselves and their young in little more time than it would take just to feed the young.

It was shown that males spent less time foraging during the incubation period in late June to early July than would be predicted from that during incubation in May, considering the effect of ambient temperature and photoperiod on energy requirements. This probably resulted from the fact that the long-term mean temperature prior to observations in late June and early July was higher and the mean photoperiod longer than that prior to May observations. Consequently productivity was probably greater and insects more abundant in late June and early July so an equivalent amount of food could be obtained in less time than in May.

LITERATURE CITED

Andrewartha, H. G.
    1961. Introduction to the study of animal populations (Methuen, London).
Brody, S.
    1945. Bioenergetics and growth (Reinhold, New York).
Brown, P. E., and Davies, M. G.
    1949. Reed-warblers (Foy, East Molesey, Surrey).
Cox, G. W.
    1961. The relation of energy requirements of tropical finches to distribution and migration.
        Ecology, 42:253–266.
Dawson, W. R.
    1958. Relation of oxygen consumption and evaporative water loss to temperature in the
        cardinal. Physiol. Zool., 31:37–48.
Dawson, W. R., and Tordoff, H. B.
    1959. Relation of oxygen consumption to temperature in the evening grosbeak. Condor, 61:
        388–396.
Dobzhansky, T., and Wright, S.
    1943. Genetics of natural populations. X. Dispersion rates in *Drosophila pseudoobscura*.
        Genetics, 28:304–340.
Gibb, J.
    1954. Feeding ecology of tits, with notes on treecreeper and goldcrest. Ibis, 96:513–543.
    1956. Food, feeding habits and territory of the rock pipit *Anthus spinoletta*. Ibis, 98:506–530.
    1960. Populations of tits and goldcrests and their food supply in pine plantations. Ibis, 102:
        163–208.
Hart, J. S.
    1962. Seasonal acclimatization in four species of small wild birds. Physiol. Zool., 35:224–236.
Kendeigh, S. C.
    1939. The relation of metabolism to the development of temperature regulation in birds.
        Jour. Exper. Zool., 82:419–438.
    1944. Effect of air temperature on the rate of energy metabolism in the English sparrow.
        Jour. Exper. Zool., 96:1–16.
    1949. Effect of temperature and season on energy resources of the English sparrow. Auk,
        66:113–127.
King, J. R., and Farner, D. S.
    1961. Energy metabolism, thermoregulation and body temperature. *In* Biology and Com-
        parative Physiology of Birds. Vol. 2. Edited by A. J. Marshall (Academic Press, New
        York), pp. 215–288.
Kluijver, H. N.
    1950. Daily routines of the great tit, *Parus m. major* L. Ardea, 38:99–135.
Kuusisto, P.
    1941. Studien über die Ökologie und Tagesrhytmik von *Phylloscopus trochilus acredula* (L.)
        mit besonderer Berücksichtigung der Brutbiologie. Acta Zool. Fennica, 31:VIII + 1–120.
Lack, D.
    1946. The life of the robin (Witherby, London).
Lees, J.
    1948. Winter feeding hours of robins, blackbirds, and blue tits. Brit. Birds, 41:71–76.
Marler, P.
    1956. Behaviour of the chaffinch *Fringilla coelebs*. Behaviour Suppl. 5:VIII + 184.
Miller, A. H.
    1961. Molt cycles in equatorial Andean sparrows. Condor, 63:143–161.
Misch, M. S.
    1960. Heat regulation in the northern blue jay, *Cyanocitta cristata bromia* Oberholser. Physiol.
        Zool., 33:252–259.

Orians, G. H.
　　1961. The ecology of blackbird (*Agelaius*) social systems. Ecol. Monogr., 31:285–312.
Palmgren, P.
　　1935. Über den Tagesrhytmus der Vögel im arktischen Sommer. Ornis Fennica, 12:107–121.
　　1949. On the diurnal rhythm of activity and rest in birds. Ibis, 91:561–576.
Seibert, H. C.
　　1949. Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. Auk, 66:128–153.
Steen, J.
　　1957. Food intake and oxygen consumption in pigeons at low temperatures. Acta Physiol. Scandinavica, 39:22–26.
　　1958. Climatic adaptation in some small northern birds. Ecology, 39:626–629.
Verbeek, N. A. M.
　　1964. A time and energy budget study of the Brewer blackbird. Condor, 66:70–74.
Verner, J.
　　1965. Breeding biology of the long-billed marsh wren. Condor, 67:6–30.
Wallgren, H.
　　1954. Energy metabolism of two species of the genus *Emberiza* as correlated with distribution and migration. Acta Zool. Fennica, 84:1–110.

Department of Zoology, University of Washington, Seattle, Washington, June 2, 1964. (Present address: Department of Zoology, University of California, Berkeley, California.)