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GENERAL NOTES

TIME-TABLES IN HOME RANGE USAGE BY GRAY SQUIRRELS
(*SCIURUS CAROLINENSIS*)

For some time, naturalists have reported seeing their study animals in the same places at the same times of the day (Hediger, 1950). The classic studies of a "time sense" in bees provide the most objective evidence for such a phenomenon (von Frisch, 1967; Michener, 1974). In these cases, it was possible to induce individual bees to visit specific food sources at certain times of the day. Similar experiments have been performed successfully with birds (Stein, 1951). Most other evidence of such nonrandom orientation in time and space from the field has been essentially anecdotal (Enright, 1975). For example, Hediger (1950) cited accounts of a blue fox that was the first to arrive outside a hut at 1400 h, and of an individually recognizable tree porcupine that would appear between 1900 and 2000 h on its trail near the shore of a lake. Although these accounts provide indirect evidence for animals in nature following time-tables, they cannot be considered conclusive (Enright, 1975). Such data would be provided only by continuously monitoring an animal's position in time and space over a number of consecutive days. Leyhausen (1965) attempted to do this with free-ranging domestic cats. He reported that it proved impossible to follow a single cat day and night around the clock and keep a complete record of its movements. As a result, Leyhausen failed to produce any positive evidence that domestic cats follow a definite time-table, although he stated that his failure to observe this did not mean it could not occur.

In addition to the evidence from the field, there is also evidence from the laboratory that animals orient nonrandomly in time and space. Kavanau and coworkers (Kavanau and Peters, 1974; Kavanau and Rischer, 1968) studied running-wheel patterns of oldfield mice (*Peromyscus polionotus*) and a variety of other mammals maintained in enclosures and showed that in many instances complex patterns of time, direction, and speed of running were duplicated almost exactly from night to night. They related their findings to the accounts cited by Hediger (1950), and suggested "internal physiological clocks can serve as sequence programmers [for behavior], giving animals a series of accurately timed signals at preset intervals" (Kavanau and Rischer, 1968:1258).

I can now report that free-ranging gray squirrels (*Sciurus carolinensis*) follow time-tables in usage of their home ranges. The study was possible because of telemetry techniques that allow the collection of data from continuously radio-tracked individuals and with the developement of appropriate quantitative procedures.

Four male and two female transmitter-equipped gray squirrels were monitored at the University of Minnesota Cedar Creek Natural History Area tracking facility, Anoka County, over the period 20 August 1977 to 16 December 1977 (Cochran et al., 1965). Two towers spaced 0.8 km apart supported antennas that are continuously rotated at 1.33 rpm. Signals from the transmitters were fed to a receiving and recording system located in the Bioelectronics Laboratory between the two towers. Time, date, degree bearings, and activity data were recorded continuously on 16-mm film. Bearings and activity state were read from the film at 10-min intervals by an operator using a microfilm reader. Data were transferred to computer punch cards and locations were determined by triangulation. The squirrels were located within error polygons approximately 15 m on a side.

Home-range maps were computer generated for each squirrel at 10-day intervals by sorting the fixes into quadrats 40.2 by 36.7 m. These quadrats are much larger than the error polygons, and thus are well within the accuracy of the system. By employing this quadrat size the home-range maps could be laid directly over an existing vegetation map. A 10-day interval was chosen because the time-table patterns changed gradually with time and longer intervals would therefore have resulted in a damping effect. A shorter interval was not employed to insure that the time-table quantification was as conservative as possible. Due to tuning demands and changes in the squirrels' locations relative to the towers, missing data frequently occurred. Therefore, for a 10-day period to be included in the time-table analysis, it was arbitrarily decided that at least 50% of the potential fixes for the active hours of a given squirrel had to be present. The active hours of a squirrel were determined by noting the first and last hours of the day that contained fixes out of the nest-site quadrats.

TABLE 1.—*Time-table for squirrel 3220 for 30 August 1977 to 8 September 1977. The squirrel's tendency to occupy different parts of its home range at different times of the day is illustrated by the positive deviations (underlined). The index (I) for this time-table is 0.61.*

Clock-hour interval	Deviations from expected by quadrat						
	1	2	3	4	5	6	7
6–800	0.7	−7.1	−0.7	0.7	−0.4	<u>5.1</u>	1.7
8–1000	<u>13.4</u>	<u>7.7</u>	−3.2	−12.8	−4.8	−5.7	<u>5.4</u>
10–1200	−0.5	<u>15.0</u>	−3.3	−5.4	1.3	−5.7	−1.5
12–1400	−2.9	−2.6	<u>7.9</u>	−4.0	<u>3.9</u>	−3.4	1.0
14–1600	−5.3	−10.4	<u>3.7</u>	0.3	<u>5.6</u>	<u>7.4</u>	−1.3
16–1800	−5.4	−2.6	−4.4	<u>21.1</u>	−5.6	2.3	−5.4

Because hundreds of fixes were generated by the telemetry system, quadrats that were rarely occupied often contained a small number of fixes. Therefore, to be included in the analysis, it was arbitrarily decided that a quadrat had to contain at least 5% of the total fixes generated during the active hours of a given 10-day period. Part of the home range of 3208 and 3222 was an exception to the 5% requirement. Both squirrels visited on a regular basis a section of an oak lot in which a feeder was located; this oak lot was separated by unfavorable habitat (alder swamp) from the oak lot in which they nested and spent most of their time. Because these areas were isolated from the rest of their home ranges, quadrats in the separated oak lots often did not contain at least 5% of the total fixes, but it was readily apparent that they were not sporadically occupied. Therefore, quadrats in these sections were combined to meet the 5% requirement.

Two home-range estimates were obtained for the 10-day periods of each squirrel that met the requirement for time-table analysis: 1) the "total" home range, which consisted of quadrats that contained one or more fixes and unoccupied quadrats that were located immediately between occupied quadrats; 2) the "core" home range, which consisted of quadrats that contained at least 5% of the total number of fixes. Quadrats containing less than 5% of the fixes, but which were not immediately adjacent to at least one other quadrat containing a fix or fixes, were not included in the total home range. Core home-range quadrats were numbered and the fixes during the active hours tabulated at 2-h intervals.

"Expected" values for the core home-range quadrats were computed for each 2-h interval by the formula

$$P(Q) \times P(T) \times \text{total number of fixes}$$

where $P(Q)$ is the overall probability of finding a squirrel in a given quadrat and $P(T)$ is the overall probability of a given 2-h interval. The expected values reflect differences in habitat preference and variations in the number of fixes produced by the telemetry system throughout the day because $P(Q)$ and $P(T)$ vary directly with the number of fixes in a quadrat or time interval.

Deviations from expected values were obtained by subtracting the expected values from the observed values. A positive deviation indicates greater than expected occupancy of a quadrat by a squirrel over a 2-h time interval. Tables of deviations may therefore be viewed as time-tables by underlining the large positive deviations. Because a deviation is meaningful only in relation to the expected value, the positive deviations were squared and divided by the expected value, as is done in chi-square analysis. In order to be underlined, a positive deviation that was weighted in this fashion had to be equal to or greater than the χ^2/d.f. (.95) value for the appropriate degrees of freedom [(number of quadrats − 1) (number of time intervals − 1)] (see Dixon and Massey, 1969, Table A-6b). Finally, an index (I) was computed for each time-table by the formula

$$I = \frac{\text{number of positive deviations underlined}}{\text{total number of deviations} \geq 0}.$$

The index can range from 0 to 1, where I = 0 indicates no time-table usage and I = 1 indicates total time-table usage of the core home range.
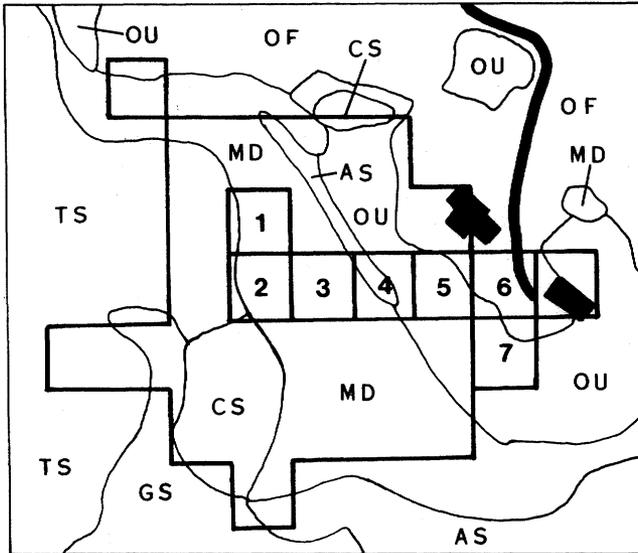
FIG. 1.—Total home range and core home range of squirrel 3220 for 30 August 1977 to 8 September 1977. OU = oak upland, MD = mixed deciduous lowland, AS = alder swamp, CS = cedar swamp, TS = tamarack swamp, GS = grass-sedge marsh, and OF = open field. Heavy black symbols denote buildings and a road.

The time-table obtained for 3220 for the period 30 August 1977 to 8 September 1977 is presented in Table 1 and corresponds to the usage of the core home range illustrated in Fig. 1. The time-table index for this period is 0.61. This squirrel was most frequently in quadrat 1 in mid-morning, quadrat 2 in mid- and late morning, quadrat 3 in early and mid-afternoon, quadrat 4 in late afternoon, quadrat 5 in early and mid-afternoon, quadrat 6 in early morning and mid-afternoon, and in quadrat 7 in mid-morning.

Table 2 reports the indexes obtained for all the time-table analyses; 18 of the 30 time-tables resulted in indexes greater than 0.33. Note that at various times during the mid-autumn data periods the index fell for all squirrels and then rose again (with the exception of 3207) in the last period. This may have been the result of feeder manipulation experiments that were carried out from 28 October 1977 to 6 December 1977. During different segments of this time span, covers were placed on two of the feeders so that the squirrels could obtain food only at certain times of the day. It is also possible that the low index values resulted from seasonal changes in that temperatures dropped dramatically and the first snow falls occurred during the mid-autumn data periods.

My findings, then, provide support for the view long held by some that animals do not move about randomly in nature. These results are also relevant for recent attempts to simulate animal movement patterns and to develop an optimal foraging theory which describes and explains

TABLE 2.—*Time-table indexes for each squirrel. ND indicates no data and RN indicates that the requirement for data selection was not met (see text).*

		Data period								
Squirrel	Sex	20–29 Aug	30 Aug–8 Sept	9–18 Sept	8–17 Oct	18–27 Oct	28 Oct–6 Nov	7–16 Nov	17–26 Nov	27 Nov–6 Dec	7–16 Dec
3220	♂	0.45	0.61	RN	ND	ND	RN	0.50	0.25	RN	0.40
3212	♂	RN	RN	0.60	ND	0.45	0.23	0.30	0.00	0.00	0.38
3218	♀	RN	RN	0.28	ND	ND	ND	ND	ND	ND	ND
3208	♀	ND	ND	ND	0.71	0.50	0.50	0.73	0.25	0.33	0.50
3207	♂	ND	ND	ND	RN	RN	RN	0.75	0.22	0.17	0.20
3222	♂	ND	ND	ND	0.50	0.64	RN	0.54	0.38	0.22	1.00

these patterns (e.g., Siniff and Jessen, 1969; Pyke et al., 1977). To date, simulation models have provided poor approximations to animal movements (Pyke, 1978). Better approximations might be provided by models that include factors that simulate time-table movement, at least with respect to the gray squirrel.

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GEOGRAPHIC VARIATION IN THE ENERGY CONTENT OF COTTON RATS

Variation in stored lipid levels in mammals relates to their ability to withstand various environmental conditions. This has been well studied for hibernation and migration, but not for less dramatic responses to stresses (Hsia-Wu-ping and Sun-Chung-lu, 1963; Fehrenbacher and Fleharty, 1976; O'Shea, 1976). The precise functional relationships for deposition and use of lipids are largely speculative; however, Fleharty et al. (1973) suggested that cotton rats (*Sigmodon hispidus*) at the northern limits of their range (Kansas) expended considerable metabolic energy for thermoregulation during winter when food was scarce and that fat deposition during the growing season provided a reserve source of energy. In contrast, accumulation and depletion of lipids was not noted in the prairie vole (*Microtus ochrogaster*) even though its food requirements were similar to those of the cotton rat (Fleharty and Olson, 1969). In the present study, we analyzed annual fat deposition by *S. hispidus* from several geographic localities (Kansas, Oklahoma, Texas).