

MEASUREMENT OF TIME BUDGETS FROM CONTINUOUS OBSERVATION OF THREAD-TRAILED TORTOISES (*KINIXYS SPEKII*)

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Five thread-trailed hingeback tortoises (*Kinixys spekii*) were observed continuously for a total of 260 hr on four hot days (at intervals of 1-2 weeks) in the rainy season. Activity occurred in all hours from 06.00-19.00 hr; the population daily activity period was 13 hr. The daily duration of surface activity of individuals was on average 8.2 hr day⁻¹ between first and last daily movement. The daily time budget included 1.95 hr locomotion, 0.86 hr feeding, and 5.2 hr stationary above ground (including long periods in indistinct surface refuges). There were no significant differences in total activity between individual tortoises or study days. Combining the daily activity period of the population and data from single sightings would greatly overestimate the amount of time spent active; observations over complete days are necessary for a true time budget. Increasing the number of days of observation of each individual decreased the variability of the data only slightly.

Key words: *Kinixys*, tortoise, time budget, activity pattern

INTRODUCTION

Breder (1927) devised the technique of thread-trailing to obtain more data on the behaviour of terrestrial chelonians than available from chance sightings or the infrequent recapture of marked individuals. She listed several aspects which could be investigated by this method: movements, home range, homing; searching for nesting sites, water, sun and shade; correlations with sex, season, and weather. Thread-trailing has subsequently been used to describe the home range and homing ability (Stickel, 1950; Chelazzi & Francisci, 1979); seasonal and sexual variation of movements (Hailey, 1989; Diaz-Paniagua, Keller & Andreu, 1995); the intensity of use of the home range (Hailey & Coulson, 1996a), the relation between activity and weather (Hailey & Coulson, 1996b), and movements to nesting sites (Hailey & Coulson, 1997) and areas of mineral-rich soil (Marlow & Tollestrup, 1982; Hailey & Coulson, 1996a) in a variety of terrestrial chelonians. Thread-trailing provides more information than radio tracking for many of these questions, as it records the exact path followed by an animal (except in very open habitats).

An additional use of thread-trailing would be to track individuals during continuous observation, to give information on activity and time budgets. Studies of tortoise activity face the problem that individuals may be inactive and difficult to locate for much of the time. For example, the use of standard transect sampling techniques (which correct for the difficulty of

observing animals further away) in areas of known population density showed that only 10-25% of individual *Testudo hermanni* were active even during peak activity periods (Hailey, 1988). Inactive tortoises are very difficult to locate by undirected searching (rather than any form of tracking), so that a time budget based on single sightings would overestimate the level of activity of individuals. In this study, thread-trailed hingeback tortoises were observed continuously during the complete daily activity period to produce a time budget for one set of weather conditions. The bias likely to result from the use of single sighting data was then assessed.

METHODS

Tortoises were studied in the Sengwa Wildlife Research Area, Gokwe District, Zimbabwe, in open miombo woodland and bushed grassland (the habitat is described in more detail by Hailey & Coulson, 1995). Five adult *Kinixys spekii* (two females and three males) were each followed by thread-trailing from 5 January to 14 February 1993 (Hailey & Coulson, 1996b), and were observed continuously on four days at intervals of 1-2 weeks; 12 and 23 January and 6 and 12 February. The tortoises had thus been trailed for at least one week before the first day of intensive observations. The four days were all within the rainy season, and had similar, partly cloudy weather; the mean percentage of cloud cover was 48%, 50%, 55%, and 32%, respectively, and there was some cloud cover at most times on each day. Nevertheless, the days were all hot, with maximum shade air temperatures of 31° and 32°C (A study of the thermoregulation of *Kinixys spekii* defined hot days as those with maximum shade air temperature above

29°C, when activity is bimodal; Hailey & Coulson, 1996c).

Activity was recorded at 5 min intervals from 06.00 hr (shortly after dawn) to 19.00 hr (dusk), after the tortoises had been followed to a refuge the previous evening. A total of 12 observers, mostly game scouts who were skilled trackers (Cumming, 1975), were used in shifts up to 5 hr long. Tortoises were observed with binoculars from 10-20 m, the distance depending on the level of cover available to the observer. The trailed tortoises appeared to be unaware of the presence of the observers; they showed visible reactions to other causes of disturbance.

Studies of reptiles have used a wide range of meanings for activity, ranging from walking only, through inclusion of other types of behaviour (such as feeding), to all time when the animal is away from its overnight refuge. The need for precise definitions is particularly important in *Kinixys spekii* as animals were often stationary on the surface for long periods during the day, but not in distinct refuges; tortoises simply stopped in a patch of scrub or long grass, and remained alert for long periods, changing position if the sun moved on to them. Behaviour was recorded as one of the following: *Locomotion* - walking, without other behaviour; *Feeding* - ingesting food or pausing between bites at a single food item (a tortoise which paused during a period of foraging, in which it moved between different food items, was classed as stationary above ground); *Courtship* - any interaction between a male and a female; *Nesting* - digging a nest; *Stationary above ground* - not moving or engaged in any other behaviour, and not in a burrow. Basking was not seen in *Kinixys spekii* at Sengwa (Hailey & Coulson, 1996c). The term 'specialized activities' is used to indicate animals which were undoubtedly active, and includes locomotion, feeding, courtship and nesting. The daily activity period was used as a population measure - the times of day (or period of time) when specialized activities occurred in the population. A different term was used for measurements on individuals; the duration of daily activity was the period between the first and last specialized activity on one day, including time 'stationary above ground' but excluding time in a burrow. Statistical significance was accepted at $P < 0.05$.

RESULTS

ACTIVITY

Specialized activities were observed in *Kinixys spekii* all hours from 06.00 hr to 19.00 hr. Tortoises were already active when located at 06.00 hr on only two occasions, and these animals had apparently only recently become active: one had moved 1 m from its hole, the other had moved 5 m from the cover where it was left the evening before. Only one tortoise was active after 19.00 hr: a female which was still digging a nest as darkness fell at 19.10 hr (Hailey & Coulson, 1997). Activity outside the period 06.00-19.00 hr was thus infrequent, and probably restricted to just before or after this time, so that the daily activity period of the population was 13 hr. The behaviour of the five individuals was assumed to be representative of that of the population as a whole on hot days. There were no significant differences in the number of observations of different types of activity among individuals or days (Table 1), so that the data were not biased by inclusion of outliers. The non-parametric Kruskal-Wallis test gave similar P values to the analysis of variance shown in Table 1.

All five individuals used burrows during the continuous observations, but only 15 of the overnight refuges were burrows, the other 24 being in surface cover (the nesting female was not followed to an overnight refuge). The proportion of refuges which were burrows (38%) was significantly lower than the 66% found by Hailey & Coulson (1995) ($\chi^2 = 6.69$, $df = 1$, $P < 0.01$). That study did not follow animals until they became inactive, and could only identify obvious refuges from the trailed threads. The difference between the two studies is thus probably due to the indistinct nature of most surface refuges. Burrows were also only rarely used as temporary refuges during the day. Entry into a burrow and re-emergence on the same day was only observed four times (in three individuals), for durations of 5, 15, 20, and 70 min respectively.

TIME BUDGETS

A total of 3117 observations was recorded at 5 min intervals. Time budgets based on these observations are shown in Table 2; the small percentage of time

TABLE 1. Test of differences in activity among individuals and days. The mean number (\pm SD) of observations of each type of activity is shown for individuals, averaged across days. Values of F and P for ANOVAs are for individuals (averaged across days) and days (averaged across individuals), respectively.

	Individuals			Days	
	Number	$F_{4,15}$	P	$F_{3,16}$	P
Locomotion	25.7 \pm 9.0	1.3	0.31	0.7	0.55
Feeding	8.6 \pm 3.9	2.0	0.14	0.7	0.55
Reproduction	1.8 \pm 1.9	0.6	0.66	1.0	0.41
All specialized activities	36.0 \pm 12.7	1.6	0.23	1.0	0.41

TABLE 2. Time budgets for *Kinixys spekii*, based on: (1) the population daily activity period; (2) the duration of daily activity of individuals; (3) simulation of undirected searching. The upper section shows the mean time represented by the total number of observations, and that spent in different types of behaviour, each day. The lower section shows the percentage of the total time made up by each behaviour; values of hr d⁻¹ in the lower section of budget 3 are based on the population daily activity period of 13 hr.

Time budget	(1)	(2)	(3)
Total no. of 5 min observations	3117	1963	894
Mean total time (hr d ⁻¹)	13.0	8.2	3.7
Specialized activity (hr d ⁻¹)	3.0	3.0	3.0
Stationary above ground (hr d ⁻¹)	7.8	5.2	0.7
In burrow (hr d ⁻¹)	2.2	-	-
Locomotion (% , hr d ⁻¹)	15.0, 1.95	23.8, 1.95	52.2, 6.79
Feeding (% , hr d ⁻¹)	6.6, 0.86	10.4, 0.86	22.9, 2.98
Courtship (% , hr d ⁻¹)	1.0, 0.13	1.6, 0.13	3.6, 0.47
Stationary above ground (% , hr d ⁻¹)	60.1, 7.81	63.3, 5.18	19.5, 2.53
In burrow (% , hr d ⁻¹)	16.8, 2.18	-	-

unaccounted for in the table was due to nesting by one female (Hailey & Coulson, 1997). The first time budget is based on all observations made during the daily activity period of 13 hr, including time in burrows and before the start and after the end of individual tortoises' activity each day. This time budget shows a low proportion of the day spent active – for example, 15% locomotion and 6.6% feeding. Note that these are proportions of the potential activity time of the tortoises, when they could have been active – as some members of the population were at any given time within the daily activity period.

The second time budget is based on the daily duration of activity of individuals, between the first and last observation of specialized activity each day, excluding only time in burrows. The mean duration of daily activity was 8.2 hr. This time budget includes a greater

percentage of specialized activities, for example 23.8% locomotion. Nevertheless, although the percentage of specialised activities increased, this was out of a shorter total time; the actual duration of these activities was of course unchanged. There were 3.0 hr of specialised activity per day, of which 2.1 hr was spent in movement (locomotion and courtship) and 2.8 hr was potentially foraging (locomotion and feeding).

Tortoises remained stationary above ground for periods ranging up to several hours (Fig. 1). There was an inflection in the frequency distribution, which was used to separate short pauses during activity (1 or 2 consecutive observations) from inactivity in surface refuges (three or more consecutive observations). The third time budget (Table 2) simulates the results of undirected searching, by including the specialized activities and short pauses, but excluding inactivity in surface refuges. This budget shows a much greater percentage of specialized activities, but of a much shorter total time. A calculation based on the behaviour of tortoises found by undirected searching and the population daily activity period would grossly overestimate daily activity – for example, 6.79 hr of locomotion compared to the true 1.95 hr (Table 2). A time budget based on short periods of observation of focal individuals (for example, for 30 min; Ruby *et al.*, 1994) would also be biased if the animals were active when first located (not shown).

DISCUSSION

ADVANTAGES OF CONTINUOUS OBSERVATION

Undirected searching and focal studies clearly overestimate the level of activity of tortoises, as suggested by Moskovits & Kiester (1987), and give no information on the daily duration of activity of individuals. Combining data from undirected searching with the population daily activity period is particularly misleading, giving for example a three-fold overestimate of locomotion in *Kinixys spekii*. Undirected searching or

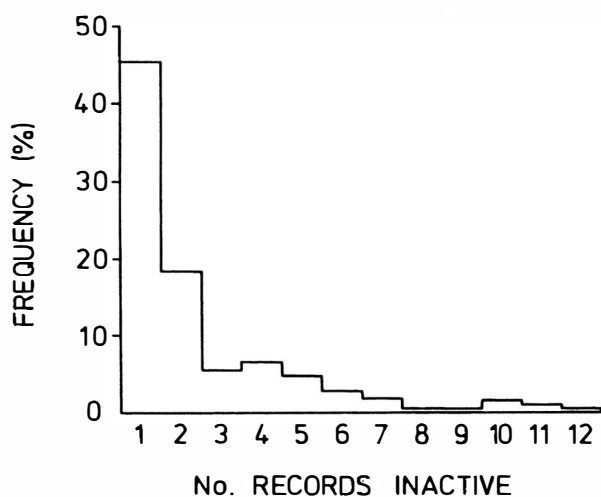


FIG. 1. The frequency distribution of the length of periods stationary above ground, shown as the number of consecutive observations at 5 min intervals, excluding time before the first and after the last specialized activity each day. In addition to those shown, 10.8% of periods stationary above ground were longer than 60 min, with a mean of 193 min.

focal observations may be used to compare the proportions of different types of behaviour – for example, between seasons (Meek, 1988). Comparisons of the level of activity or true time budgets require information on individuals observed through the complete daily activity period.

There were no significant differences between individuals or days, so that the data were not distorted by outliers and can be considered representative of the activity of the population in general during this type of weather. *Kinixys spekii* has a short annual activity period at Sengwa, limited to 4-5 months in the rainy season (Hailey & Coulson, 1996b), and pronounced seasonal variation within this period is therefore unlikely. There is, however, likely to be a strong effect of weather. The daily movement distance of *Kinixys spekii* increases on cool days (Hailey & Coulson, 1996b), so that an increase in locomotion, and possibly other types of behaviour, would be expected in cool weather. This hypothesis, and others such as differences between sexes or species, should be tested using individual tortoises as the basis of analysis (for example, the data in Table 1), rather than pooled time budgets. Repeated observations are useful in increasing the reliability of data for each individual, but do not increase the sample size as such.

The collection of behavioural data is time consuming, and the question is: are repeated observations worth the extra effort? As an example, the mean number of observations of specialized activities was 36 ± 17 on the first day of observation (\pm SD among individuals). The number was 32 ± 17 on days 1 and 2, 38 ± 11 on days 1-3, and 36 ± 13 on days 1-4 (Table 1). Repeated observations therefore had little effect in reducing the inter-individual variability of these data, and thus the confidence interval and usefulness for testing hypotheses. The best allocation of resources would therefore be to observe as many individuals as possible, each for one day in each situation of interest (type of weather, season).

The number of individuals observed in any set of conditions depends on the reliability required for the time budget. Using the example of the number of observations of specialized activities, the SE was 21% of the mean with five individuals each studied for one day. A sample size of $n=22$ would be needed to give a SE of 10% of the mean, and $n=89$ to give a SE of 5% of the mean. A very large number of individuals would thus only increase the reliability of the estimate by a moderate degree. The sample size needed also depends on the variability of behaviour between days. For example, activity of *Testudo hermanni* varied greatly in summer, with about 50% of individuals being completely inactive on any given day (Hailey, 1989). Study of time budgets by continuous observations would be impractical in these circumstances, as a very large sample size would be needed and much of the time would be wasted on inactive animals.

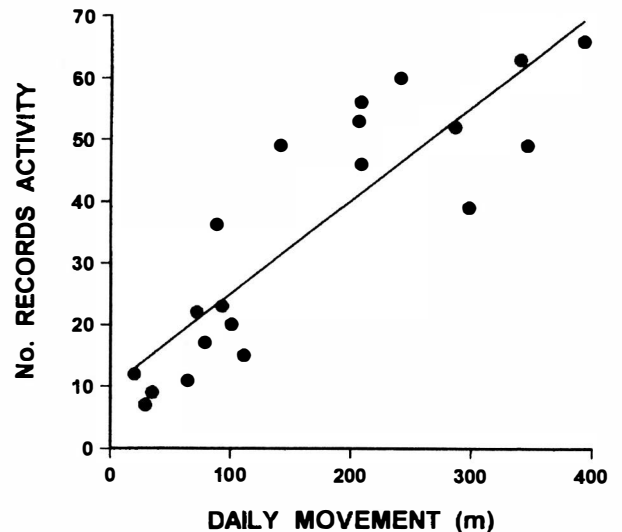


FIG. 2. Relationship between behavioural activity (the number of records of locomotion, feeding and courtship in one day) and the daily movement distance. Regression equation: $y=10.0+0.15x$ ($r^2=76.3\%$).

Time budgets in seasons of low or variable activity are best estimated by calibrating data from single sightings or focal individuals. It would be necessary to collect such data in seasons of both low and high activity, together with a detailed time budget in the season of high activity and a measure of total activity (such as the daily movement distance of thread-trailed animals) in both seasons. This method depends on a strong relationship between behavioural activity and daily movement distance (Fig. 2). Rarely observed types of behaviour present a similar problem, as their occurrence is likely to vary widely between individuals and days. For example, the SE of the number of observations of reproduction was nearly 50% of the mean, even after averaging across four days of observation (Table 1). The level of such rare types of behaviour is also best estimated from short-term observations, calibrated using the total level of activity from continuous observations.

Continuous observation would also be useful when assessing thermoregulation by animals in novel circumstances, for example to show the effects of climate (Hailey & Loveridge, 1998) or familiarity with the home range (Chelazzi & Calzolari, 1986). It is necessary to show that any differences in body temperature are responses to the thermal environment, rather than to disturbance. For example, Chelazzi & Calzolari (1986) found that translocated *Testudo hermanni* had daily mean body temperatures different to those of resident animals, but these were measured automatically by radiotelemetry throughout the daily activity period without reference to activity of individuals. Chelazzi & Francisci (1980) noted altered behaviour of translocated tortoises, including both an initial period of inactivity lasting up to 4 days, followed by hyperactivity with unusually linear movements. Both of these

types of behaviour suggest that thermoregulation was partially abandoned (within the constraint of avoiding critically high body temperatures) rather than made more difficult. Detailed behavioural observations of translocated and resident animals would resolve this question.

ACTIVITY AND TIME BUDGETS

Activity of *Kinixys spekii* on hot days can be compared to the scanty data for other species of tortoise, from long-term observations, thread-trailing, and radiotelemetry. The duration of daily activity of 8.2 hr was rather longer than the 3 hr reported for *Gopherus agassizii* (Nagy & Medica, 1986), the only other tortoise for which this has been measured. This difference is probably due to the severe thermal constraints on activity of the desert tortoise (Zimmerman *et al.*, 1994), which is supported by the difference in daily movement distance between these species. *Kinixys spekii* moved on average 172 m on hot days (Hailey & Coulson, 1996a), compared to about 35 m in *Gopherus agassizii* (Ruby *et al.*, 1994).

Kinixys spekii was moving for 2.1 hr out of the 8.2 hr duration of daily activity, thus spending 26% of time moving. This value is exactly the same as that found in *T. graeca* observed for long periods (Meek & Jayes, 1982). The population daily activity period (13 hr) is similar to the 12.5 hr reported for two other tropical tortoises, *Geochelone carbonaria* and *G. denticulata* (Moskovits & Kiester, 1987). It is possible to calculate that the latter two species spent about 1.7 hr moving each day, similar to the 2.1 hr in *Kinixys spekii*. Huot-Daubremont, Grenot & Bradshaw (1996) studied activity of *T. hermanni* in a large outdoor enclosure. Feeding made up about 4% of the daily activity period of 11 hr (periods 2 and 3 in that paper) during July and August, similar to the value of 6.6% for *Kinixys spekii*.

Results for activity of *Kinixys spekii* are thus generally similar to the little data available for other tortoises. More data are available for lizards: values for the time spent moving each day are of particular interest, in relation to the exercise physiology of lizards and tortoises. Reported values are: 0.4 hr in *Egernia cunninghami* (Wilson & Lee, 1974); 0.8 hr in *Varanus rosenbergi* (Christian & Weavers, 1994); 1.5 hr in *Cyclura nubila* (Christian *et al.*, 1986); 1.6 hr in *V. gouldi* (Christian *et al.*, 1995); 1.7 hr in *Conolophus pallidus* (Christian & Tracy, 1985). *Kinixys spekii* (and *Geochelone* spp.) thus spent more time moving than most lizards, even the particularly active Varanidae. The only exception was *V. panoptes* which moved for 3.5 hr day⁻¹ in the dry season, when making daily journeys to forage around water courses (Christian *et al.*, 1995). The comparison of lizards and tortoises therefore supports the conclusion that exercise physiology is related to the intensity of activity, not to the time spent moving each day (Christian & Conley, 1994).

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APPENDIX

Nesting by one of the trailed tortoises was described by Hailey & Coulson (1997). That note was not seen in proof and contains some errors. Page 13, last line should read: 17.16 hr digging under *Mundulea sericea* tree (nest 3); 18.32 hr digging under *Pseudolachnostylis maprouneifolia* tree (nest 4). Page 16, line 6: 100 mAs should read 10 mAs. Page 17, line 15: 80°S should read 8°S.

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