



COMMENTARY

Slowness and acceleration: a new method to quantify the activity budget of chelonians

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Animals are constantly submitted to internal and external constraints. The processes that regulate the acquisition and allocation of resources among the competing demands of growth, survival and reproduction occupy a central place in evolutionary ecology (Candolin 1998; Ghalambor & Martin 2001; Ihara 2002). Many theoretical, empirical and experimental studies suggest that most behavioural decisions are the expression of such adaptive trade-offs (Houston & McNamara 1999; Kemp et al. 2006). For example, an individual cannot undertake simultaneously antagonistic activities such as foraging and ritual combats during reproduction. Therefore, collecting information on activity budgets of wild animals, especially the temporal organization of contrasted behaviours, is of prime importance to understand the processes of acquisition and allocation of resources in relation to physiological status and environmental conditions.

In natural conditions, recording accurately activity budgets is often a particularly difficult and time-consuming task. Behavioural observations of wild animals are generally limited to individuals met in the field, strongly enhancing the estimation of their activity, simply because visible individuals are almost always active whilst inactive animals are often hidden (Hailey & Coulson 1999). To limit such biases, it is possible to perform long time observations, on individuals monitored regardless of their activity (Hailey & Coulson 1999; Lagarde et al. 2003a). However,

these long time focal observations (e.g. daylong), despite their accuracy, are restricted to small sample size. Furthermore, whatever the efforts devoted in the field, the activity of hidden animals, possibly of major importance for most species, will remain inaccessible.

Over the last decades, major technical improvements for quantifying behaviours have been achieved. Notably, various miniaturized automatic data loggers record routinely physiological and behavioural information both with a high frequency and over long time periods (Handrich et al. 1997; Yoda et al. 1999; Franklin et al. 2003; Naito et al. 2004; Block 2005; Myers et al. 2006). Unfortunately, for logistical, traditional, and economic reasons, strong taxonomic biases limit the span of these technological progresses. First, the individuals fitted with automatic data loggers must exceed a certain body size to carry the equipment. Second, these technologies are often very expensive and consequently have been developed for species of economic value (i.e. many fishes; Lagardère et al. 1998) and/or used on taxa that traditionally attract considerable attention and funding, notably birds and mammals (Bonnet et al. 2002; Clark & May 2002). Third, it is easier, more spectacular to observe species that exploit contrasted habitats (e.g. deep diving behaviours during foraging are easily identified using data loggers; Hooker & Baird 1999; Hays et al. 2000; Lidgard et al. 2003; Tremblay & Cherel 2003; Tremblay et al. 2003; Guillemette et al. 2004; Hays et al. 2004) compared to slow moving and often inactive species that live in an apparently homogeneous habitat. In this latter case, records might be homogeneous themselves precluding the discrimination of different behaviours. As a result, most of the studies based on the use of automatic data loggers to

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measure activity budgets focused on relatively large endothermic vertebrates (mostly marine birds and mammals) plus few fish species, thereby ignoring the far most diverse array of ectothermic animals (Clark & May 2002).

The analysis of the activity patterns of ectotherms may cast new light on major adaptive trade-offs. For example, it is widely admitted that the weak energy content of plants forces endothermic herbivores to allocate a huge amount of time into foraging activity (Arnold 1984; Castro et al. 1989; Karasov 1990; Wirtz & Oldekop 1991; Spallinger & Hobbs 1992; Bairlein 1999). In stark contrast ectothermic herbivores spend only a very small proportion of their activity to forage (Iverson 1982; Lagarde et al. 2002, 2003a).

The main constraints (animal size and limited funds) sometimes lead to the use of small low cost devices, not directly designed for behavioural studies (e.g. human altimeters used in bird studies; see Weimerskirch et al. 2004) and sometimes indirectly related to the characteristics of the behaviour under focus (e.g. light decrease under the body as a proxy for bird landing; see Tremblay et al. 2003). Analytical procedures are necessary to extract the behaviours from the data series. A model that performs such a task automatically is necessary to process large data sets (see Methods).

During this study, we attempted to develop a method based on the use of a single automatic activity data logger (i.e. ActiTrac, IM Systems, Inc., Baltimore, MD, U.S.A.) fitted on a typically seldom-active, slow moving organism that lives in a relatively homogeneous habitat and that exploit a restricted home range: the Greek tortoise (*Testudo graeca graeca* Linnaeus 1758). This chelonian is an ectothermic herbivore for which the activity budget is still unknown. In chelonians, the use of activity acceleration data loggers was initiated on *Emys orbicularis* (Dall'Antonia et al. 2001), but only to analyse the variations in the time spent active without any characterization of the behaviours, and therefore no attempt to estimate the activity budget was undertaken. Indeed, the use of the raw acceleration data solely provides limited information. Notably, as no behaviour was identified there was no information on the time spent in different competitive activities such as sexual, feeding or walking behaviours. We emphasize that our main goal was not to simply record the activity level of the individuals (e.g. moving versus motionless), but to use the acceleration patterns to characterize and to monitor automatically long time behavioural sequences of free-ranging individuals. In other words, we attempted to set up a method to discriminate and records automatically the main types of behaviours: resting, digging, foraging, displacements and sexual activities. Finally, if successful, we aimed to use this technique to record and compare the activity budget of males and females under natural conditions during the spring.

Methods

Species

Testudo graeca is a terrestrial herbivorous tortoise widely distributed around the Mediterranean Sea (Iverson 1992). This chelonian is a diurnal medium-sized species (Ernst & Barbour 1989), for which several ecological information

are available; notably population dynamics (Andreu 1987; Bayley & Highfield 1996; El Mouden et al. 2001; Slimani et al. 2001), general ecology (Lambert 1969, 1981, 1983; Bayley & Highfield 1996), geographic variations (Highfield 1990a, b; Carretero et al. 2005) and feeding ecology (Bayley & Highfield 1996; Andreu et al. 2000; El Mouden et al. 2005). Many populations regressed markedly because of harvesting for pet trade (Lambert 1981, 1982) and anthropogenic environmental changes (agriculture, overgrazing and deforestation; Highfield 1994; Bayley & Highfield 1996; Slimani et al. 2001).

Study site

The study was conducted from March to April 2003. The area is located in the central Jbilet mountains 25 km north of Marrakech, Morocco (31°37'N, 8°02'W, 580 m above the sea level on average). The region is arid with mean annual rainfall of 240 mm occurring essentially between September and February (El Mouden et al. 1999; Znari et al. 2002). Average air temperature in the hottest month (July) can reach 39°C and the minimal annual temperature is normally above 0°C (Le Houérou 1989). The shrub stratum of the vegetation consists mainly of Jujube bushes, *Ziziphus lotus*, some scattered acacia, *Acacia gummifera*, along with Retams, *Retama monosperma*. Most of habitat is open, hard bare ground with stony soils on the flats and low hillsides that surround small sandy, pebbly or the stony riverbed of wadis. Seasonal overgrazing by domestic livestock (sheep and goats) strongly affects the vegetation structure. The herbaceous plants, the main trophic resources for *T. graeca*, are essentially concentrated under the spiny bushes of Acacia and Jujube, constituting a shelter for plants and tortoises. In the study site, the tortoises spend most of their time hidden under the bushes, often partly buried and immobile. However, they can be observed directly still under cover as many bushes are not very thick; the tortoises also move from bush to bush and hence become easily visible. Notably, when the observer remains completely immobile, the tortoises apparently ignore their presence and openly undertake foraging or sexual activities for example.

Data loggers

The activity of free-ranging individuals was assessed with automatic acceleration recorders (20g, dimensions: 5.52 × 23.52 × 21.2 cm; ActiTrac 1998 IM Systems, Inc.) routinely used to monitor sleep disorders in humans (Takahashi et al. 2003; Carney et al. 2004). Each electronic device records movements (i.e. slight accelerations) in two perpendicular directions with a piezoelectric cell. Considering the relatively weak activity of chelonians (Lagarde et al. 2002, 2003a), we chose to use the maximal sensitivity level available (0.312 mG; in our study site, 1 mG corresponds broadly to an acceleration of 9.8⁻³ m/s⁻²). With this sensitivity, the highest acceleration we could record is 78 mG. Although the data loggers we used were not designed to monitor free-ranging animals (and thus not used for such purposes before), they were easily fitted on the subjects. We removed the wristband and the devices were simply glued horizontally on the

top of the shell with synthetic resin. The acceleration was recorded 40 times/s, we set up the device to calculate and store a mean acceleration value every 2 s (storage capacity: 44 960 acceleration values). This information is automatically converted to a reference scale of data counts (0–250). An interface allowed downloading in the field directly the data on a laptop regularly. The acceleration data loggers were fixed on tortoises 1 day before the focal observation and the data recording, providing enough time for the tortoises to calm down after manipulation. Each tortoise was simultaneously fitted with a radio transmitter (5g and 20g depending upon tortoise's body mass; AVM Instrument Company, Ltd, Colfax, CA, U.S.A.; or Telonics, Mesa, AZ, U.S.A.) and located on a daily basis with a 4-element Yagi antenna connected to an LA12Q-AVM receptor. On average, the total mass of the equipment represented 8% of the animal body mass (range 5–10%). Such load did not exceed the weight represented by the stomach content and/or the faeces. Indeed, free-ranging tortoises can ingest more than 8% of their body mass during a single meal (Lagarde et al. 2003a, b); and can drop more than 8% of their body mass after defecation. At the end of the monitoring episode, we gently pushed the blade of a knife between the shell and the synthetic resin, and exerted a progressive torsion movement to remove the equipment. The whole assembly of electronic device plus resin took off very easily, leaving a clean shell surface. It was easy to take off the total equipment without damaging the shell. Importantly, each individual was fitted with the devices for short periods of time (see below and Results), thereby minimizing any disturbance that may have affected the welfare of the tortoises. We did not observe any adverse effects on the behaviours of the tortoises: all the individuals released with the full equipment moved freely under the spiny shrubs, foraged efficiently, and mated without any mechanical problem. None of the tortoise was observed attempting to get rid of the devices, for example, by rubbing their shell on branches or rocks. In a similar study carried out 1 year later (2004) on the same population and using the same methodology, we examined such issue. We monitored the body condition index of experimental (fitted) and control (non-fitted) individuals during a 2-month experimental study. The body condition index was calculated as the residual values of the regression between the logarithms of body mass (g) against the logarithms of carapace length (mm). We found no significant difference in the mean body condition index variations of 24 experimental males compared to 24 randomly sampled males in the study site between the beginning and the end of the 2-month experimental period (repeated measures ANOVA with body condition index as the dependent variable and the experimental status, involved into the experiment or not, as the factor, $F_{1,46} = 1.14$, $P = 0.28$). On the 24 fitted individuals, we found no significant effect of the load associated with the data loggers on the displacements showed by the animals (Friedman ANOVA for repeated measures over time with the distance travelled by each radio-tracked tortoise as the dependent variable and the presence of the acceleration data logger as a factor: chi-square test: $\chi^2_2 = 2.43$, $P = 0.297$). Overall, the

experiment per se, and the load owing to the electronic equipment had no significant impact on the body condition and on the distance travelled by the tortoises, suggesting that the tortoises tolerated well the procedure and the electronic devices plus the resin.

We monitored only individuals large enough to tolerate the equipment; hence our study was limited to adult tortoises (i.e. median carapace length exceeding 100 mm and evidence for a marked decrease of the width of the last scutes that characterize sexual maturity; Lagarde et al. 2001; Slimani et al. 2001). We monitored roughly the same number of females and males (see below). The sex was determined using the classic criteria for chelonians, notably the length of the tail and the shape of the plastron (Andreu et al. 2000; Bonnet et al. 2001; El Mouden et al. 2001).

Discrimination of the main behaviours

Five different behaviours were defined: immobility (animal without any displacement), feeding behaviours (animal seizing a plant or ingesting it), digging (=burying), walking and sexual behaviours (mating, copulating and fighting). Immobility should be associated with an absence of accelerations and should be easily distinguished. By contrast the acceleration patterns generated during walking or foraging activity are less intuitively separated on an acceleration pattern basis. Consequently, we adopted a step-by-step procedure.

Visual calibration. We visually monitored the behaviours of individuals fitted with both an acceleration data logger and a transmitter from March to April 2003. The individuals were observed either directly as free-ranging individuals in the field, or in an enclosure. Nineteen tortoises (10 females, nine males) were captured in the study site and rapidly fitted with the electronic devices (<20 min). The 19 tortoises were split into two groups: either monitored as free-ranging animals, or placed in an area limited by a chicken wire positioned around a Jujube bush within the study site. Ten focal observations were carried out outside the enclosure on 10 individuals (five females + five males), directly in the field, to observe feeding, walking and digging behaviours that were easy to record under natural conditions. By contrast, it is very difficult to observe the sexual behaviours of this species in the field. Therefore, we placed together females and males in the enclosure; the promiscuity of the animals elicited sexual activity and enabled careful observations of sexual behaviours. A maximum of five individuals were simultaneously present in the enclosure. Nine focal observations were performed on nine individuals (four females + five males) to record reproductive behaviours. The enclosure was circular (diameter 10 m); it included several potential shelters for the tortoises (shaded areas). The substratum was an alternation of schistose and sandy zones, and resumes the study area substratum heterogeneity. The tortoises observed in the enclosure were kept captive for a maximum of 5 days. They were fed daily with fresh flowers of *Arisarum*, one of their food items in the study population (El Mouden et al. 2006). Water was not

provided because drinking behaviour is very rarely observed in such an arid area, and we preferred not to interfere with natural conditions. Routinely, free-ranging tortoises do not drink over periods lasting months. All individuals we captured were released at the exact place of capture. The behaviours were sampled by focal observations (Altmann 1974; Martin & Bateson 1993) during the activity period (during the day) and were recorded continuously with a tape recorder. Focal observations were made from 20 m, with 10×52 binoculars. Every minute, the exact timing was recorded using a digital watch to detect potential temporal deviation between the tape recorder and the acceleration logger chronometers. The aim of this first step was to gather data allowing a direct comparison between acceleration profiles and the current behaviours expressed by the tortoises. Most of the behaviours (resting, walking, foraging, digging) were observed on free-ranging individuals. However, sexual behaviours (ritual male to male combats, mounting...) were essentially recorded in the small enclosure where the artificially high density of the tortoises somehow enhanced sexual activity and the probability to observe these sporadic behaviours.

Building the model. To link acceleration values with behaviour, we built a model using simultaneous visual observations and acceleration data as training data set. The model aimed to operate using solely the acceleration profile, to use an automatic discrimination process later on free-ranging animals not visually monitored. For each of the 19 above individual data sets, we compared the acceleration pattern and the behaviours observed synchronously. Fig. 1 provides an example of the acceleration patterns observed for each of the five main behaviours. For convenience, we used the scaling implemented on the devices (i.e. $1 \text{ RU} = 0.312 \text{ mG}$).

As expected, a single acceleration value did not permit to identify the associated behaviour. It was necessary to encompass a sequence of movement and the corresponding acceleration values (Fig. 1). The correspondence between the five behaviours and the specific characteristics of the acceleration sequences was successfully performed.

- Walking: the shell oscillates alternately from left of right, according to the walking rhythm. The mean accelerations values were of $77.9 \pm 37.8 \text{ RU}$.

- Immobility: acceleration values remained very close to zero.

- Feeding: vertical oscillations animated the shell, upwards or downwards, in association with the movements of the head and forelimbs allowing the catching of the coveted plant. The acceleration values were low ($9.2 \pm 9.2 \text{ RU}$ on average) and frequently interrupted by walking periods between each food patch.

- Digging: the tortoise was relatively stable with the legs rejecting the soil: the shell was animated with small oscillations. These sporadic movements were typically interrupted with immobility phases. The mean acceleration values were slightly greater compared to the feeding behaviour ($11.1 \pm 5.7 \text{ RU}$), but frequently interrupted by immobility periods superior or equal to

120 s. Importantly, even if the acceleration profiles of these two different behaviours entailed very similar mean acceleration values, the discrimination was none the less possible including successive behavioural sequences: a tortoise must walk between each food patch whereas a tortoise remains at the same place during burrowing activity.

- Sexual behaviours (mating, fighting): the movements were violent. The males walked rapidly around the sexual partner or the rival. Combats and mounting attempts generated rotation movements and repetitive shocks between the shells. These shocks induced maximal and frequent accelerations values in both sexes ($\geq 250 \text{ RU}$), and then a high mean acceleration value assorted with a large standard deviation ($192.3 \pm 78.5 \text{ RU}$).

From this training data set, a model was built to identify and extract behavioural sequences from the acceleration profiles. We used simple statistical operators (mean, median, maximum, standard deviation and mode) calculated on an 8-s temporal window to discriminate the behaviours. Such temporal window was determined to maximize both the accuracy and the power of the automatic procedure. In the absence of similar work, we adopted a conservative approach. We started from the minimal time window available (2 s), and progressively increased the time slot (4, 6, 8 s, etc.) to perform the analyses. This prudent incremental procedure led to an optimal window of 8 s (i.e. four acceleration values). Such time slot was the first enabling to discriminate accurately the behaviours (see Results); using a larger temporal window (e.g. 16 s) did not improve the performances of the system and automatically entailed a deterioration of the accuracy of the procedure. To tease apart feeding and digging behaviours: two behaviours distinguishable when a larger time context was considered (see above), a second temporal window of 120 s was used to explore the occurrence of walking behaviour downstream and upstream of the 8-s sequence. The value of 120 s was also determined after a progressive empirical exploration of the performances of the procedure. Table 1 synthesizes such procedures and provides further precisions. These decision rules were written in R program to allow an automatic classification of behaviours.

The performances of the model were tested statistically. Pearson's linear regressions were performed between the estimated and observed durations of the different behaviours (Table 2, Fig. 2). The regression line's equations allowed us to examine the distortion between the estimated and observed time budgets. The activity budget of animals monitored under natural conditions, determined using our model, could be corrected using these equations (see below).

Application of the method. Third, we applied this method to monitor free-ranging animals, without visual observation, to reconstitute and compare the activity budget of adult males and females during Spring 2003. Forty-eight separate daily activity budgets were obtained on 24 males and 24 females, from March to April 2003. Each animal was equipped only once. The tortoises were fitted with the electronic material more than 36 h before the beginning of the record to limit the possible influence of the

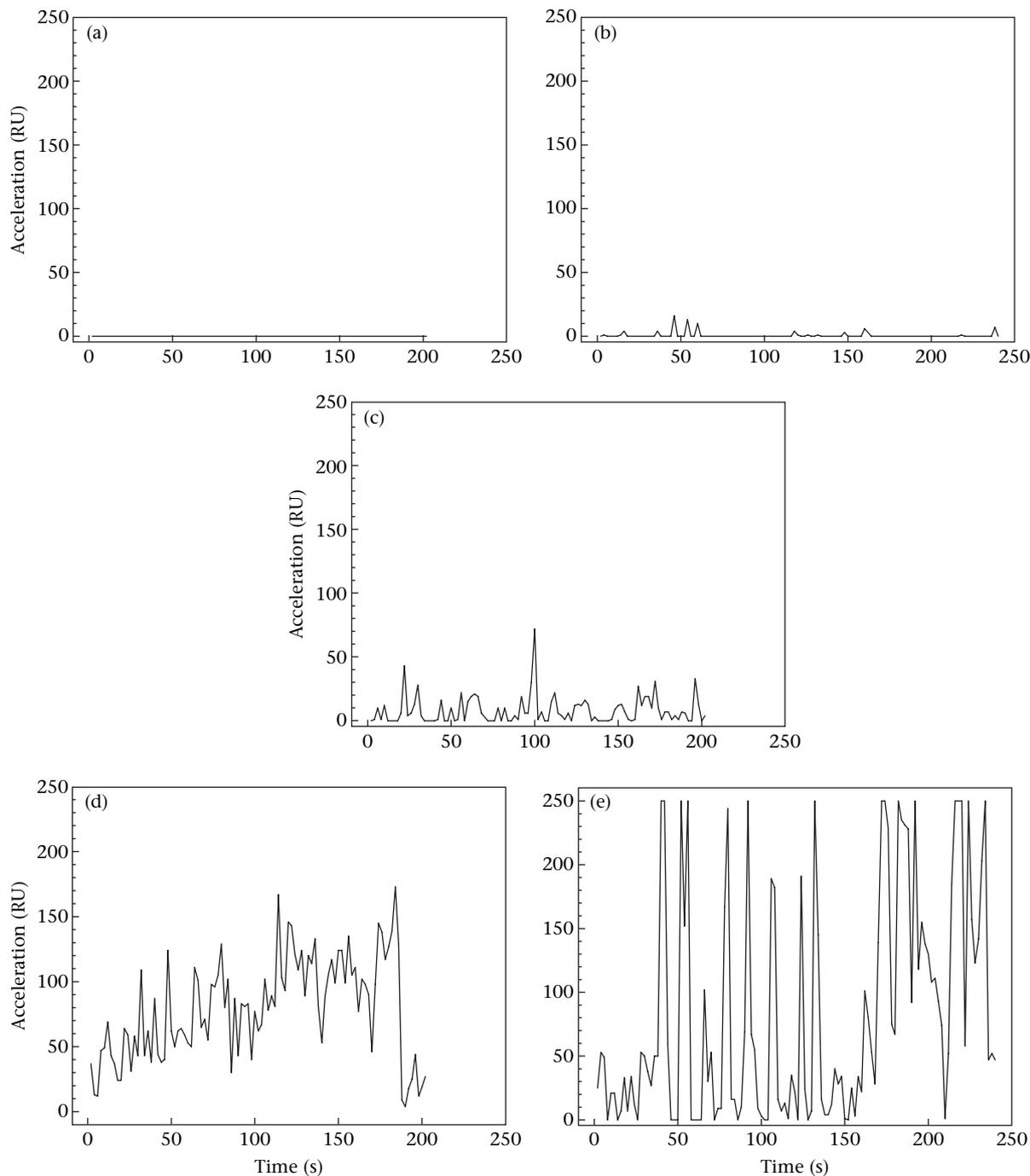


Figure 1. Examples of acceleration patterns for *Testudo graeca graeca* behaviours. Each acceleration pattern was obtained with an accelerometer (ActiTrac, IM System) glued on the shell of an observed tortoise. Left labels of the Y axis gives acceleration value in mG, right labels in reference unity (RU in the text). Each pattern corresponds to another behaviour (a: immobility; b: digging; c: feeding; d: walking; e: sexual activity).

manipulation. All individuals were localized at least once per day. As above, all the equipment was gently removed at the end of the monitoring episode, and the tortoise immediately released at the exact place of the last capture.

Statistical analysis

Data loggers generate rapidly considerable data sets. The automatic identification of the behaviours using the model, the extraction of the associated behavioural sequences and

the quantification of the activity budget for each studied animal were carried out using R statistical software that can handle very large data sets (R Development Core Team 2006). All the statistical tests were performed with Statistica 6.1 software (Statsoft, Tulsa, OK, U.S.A.).

The normality of the data was tested with a Shapiro–Wilk test before analyses (Lindman, 1974). The distribution of the activity periods (total time spent on feeding, walking and mating) did not significantly differed from

Table 1. Discriminate model we used to identify the *Testudo graeca* behaviours from the acceleration data

Behaviour	Formula to discriminate behaviours
Walking	[15<mean<75] AND [(max>15) OR (med>15)]
Immobility	max<2
Reproductive behaviour	[mode(200)>0] AND [med>19] AND [sd>74]
Feeding and digging	[(med<10) AND (sd<11) AND (mode(0)<3)] OR [max<30] OR [(med<mean) AND (med<41)]
Digging	Occurrence (walking)=0
Feeding	Occurrence (walking)>0

The statistical parameters were calculated on an 8-s temporal window and were given in reference unity (1 RU = 0.312 mG). mean = Mean acceleration value; sd = standard deviation of acceleration value; med = median acceleration value; max = maximal acceleration value; mode(x) = mode of the 'x' acceleration value on the 8-s window; occurrence(walking) = presence of the walking behaviour in a 120-s temporal window following behaviour identified in the eight previous seconds (used to discriminate digging and feeding behaviours). 'AND' and 'OR' are the basic Boolean operators.

a normal distribution (Shapiro–Wilk test: $\lambda = 0.93$, $P = 0.12$) and the differences between males and females were tested with a t test. The distribution of the total time associated with other behaviours failed to reach normality, even after logarithmic transformation. Then, the comparison of the activity budget of males and females was performed with nonparametric Mann–Whitney test.

Means were given as \pm SD.

Results

Testing the model

Graphically, the behavioural sequences (hence the total activity budgets) inferred from direct visual observations and automatically calculated with the models were very similar (Fig. 3). A close examination of the two profiles (observed and calculated activity patterns) revealed that the model rarely miss-associated acceleration patterns and actual behaviours (Fig. 2). Hence, using few typical short sequences to calibrate the models led to an operational automatic method to extract long-term behavioural sequences from the acceleration patterns. The correlations between the calculated and the actual duration of each type of behaviours were not perfect; however, the R^2 remained high (on average $R^2 > 0.79$, $P < 0.017$, $N = 19$;

Table 2. R^2 value, standard error and equation of the linear regression between observed (t obs.) and estimated (t est.) durations of the different *Testudo graeca graeca* behaviours

Behaviour	R^2	Standard error	Equation of linear regression line
Reproductive	0.96	2.96	$0.7245 \times t \text{ est.} - 9.2838$
Walking	0.90	53.56	$0.7550 \times t \text{ est.} + 128.6425$
Digging	0.96	18.93	$1.0356 \times t \text{ est.} - 32.0407$
Immobility	0.98	54.21	$1.1237 \times t \text{ est.} - 56.232$
Feeding	0.79	68.59	$1.2846 \times t \text{ est.} - 10.92$

Table 2, Fig. 3) suggesting that the model provided reasonably accurate estimates. We used the respective equations of the regressions linking observed and calculated behaviours to estimate more accurately the duration of the main behaviour (Table 2). These equations allowed us to correct a posteriori the activity budgets measured in free-ranging animals (see below).

Reconstitution of the activity budget of the free-ranging *Testudo graeca graeca*

The acceleration patterns show that the 48 individuals (24 males and 24 females monitored during 24 consecutive hours) remained inactive at night: the acceleration was virtually equal to zero (Fig. 4). On average, the daily activity time was 76 ± 50 min. Six individuals remained mostly inactive during the survey; their total activity was less than 5 min/day. Four of these six motionless individuals were monitored under unfavourable climatic conditions: strong wind combined with an ambient temperature lower than 15°C . Excluding the six 'inactive' tortoises, the duration of the total activity time was on average less than 2 h/day.

The mean daily active time (including the inactive animals) was significantly longer in females compared to males (94 ± 55 min versus 60 ± 39 min, respectively, t test with sex as factor and mean activity time as the dependent variable; $t_{46} = 2.40$, $P = 0.02$). During activity, the tortoises devoted most of the time to walking and foraging behaviours (40% and 36% of the total activity time, respectively; Table 3). Sexual and fighting behaviours were very sporadic and presented less than 2% of the total activity time, both in males and females. Burrowing behaviour lasted broadly 20 min/day without difference between the sexes. Similarly, the duration of the time spent walking per day was not sexually divergent (Table 3). Males spent significantly more time immobile compared to females; foraging activity was more often recorded in this latter sex relative to males (Table 3).

Discussion

Our results show for the first time that, using a single data logger, it is possible to discriminate the main behaviours and consequently to reconstitute and quantify the activity budget of a slow moving free-ranging ectothermic vertebrate that lives in a relatively homogeneous habitat. We emphasize that our goal was not to simply record activity patterns over time (i.e. intensity of activity), but to determine any time the actual behaviour of each monitored animal, a far more complex task. Terrestrial tortoises, as many ectothermic animals, move slowly. Although not initially designed for our purposes, the sensitive data loggers we used provided simple data sets (acceleration profiles solely) that, after the analyses, enabled to distinguish the main behaviours showed by the tortoises.

The strong point of our approach was to calibrate the model with direct visual observations (long time focal samplings). We succeeded to discriminate the five main types of behaviours showed by *T. g. graeca* in Morocco: walking, feeding, immobility, burrowing, and sexual

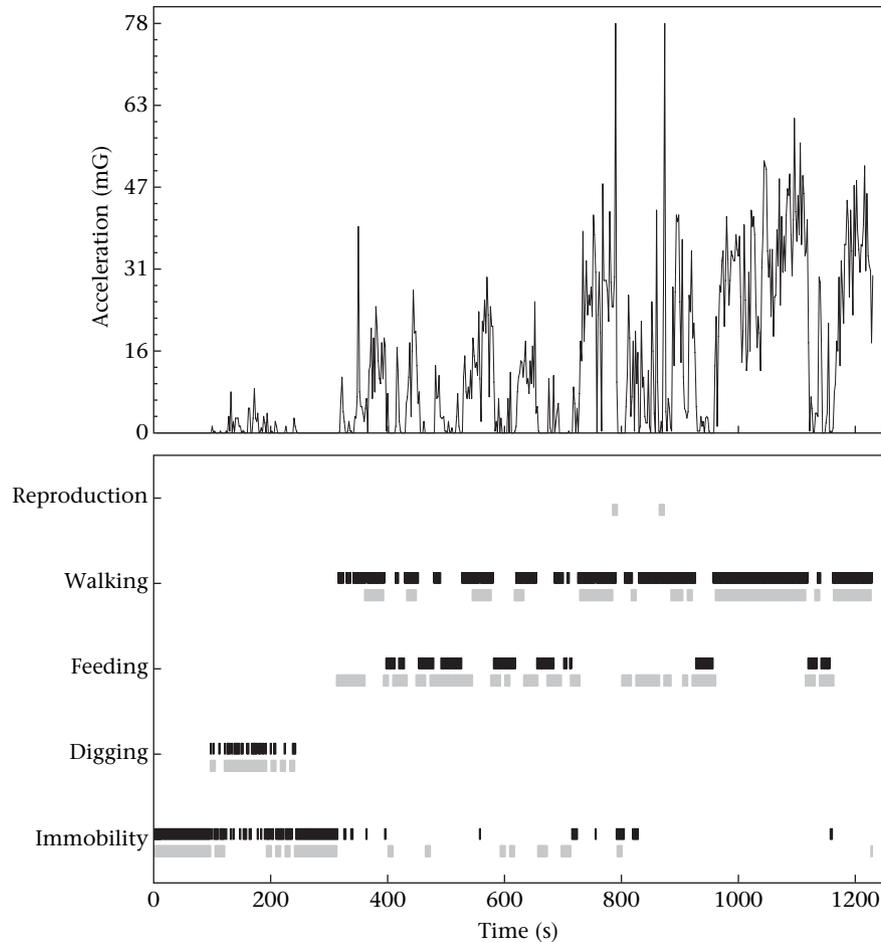


Figure 2. Comparison between a *Testudo graeca graeca* acceleration profile and the observed (black bars) and reconstituted (grey bars) behaviours. See text for the procedure.

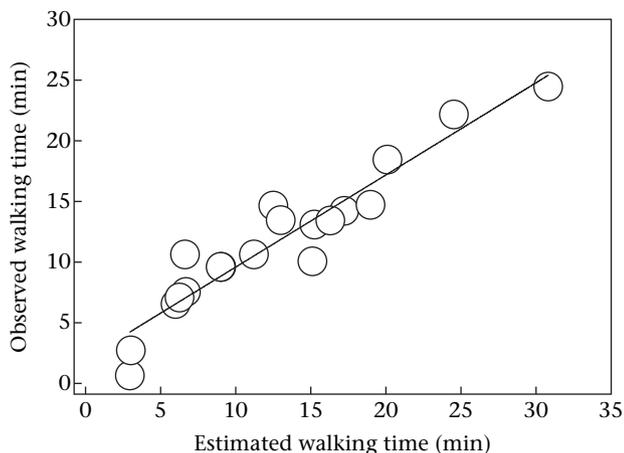


Figure 3. Example of relation between observed and estimate durations of a behaviour (walking behaviour here) in *Testudo graeca graeca*. Each point corresponds to the values we obtained on different tortoises ($N = 19$). Each animal was observed continuously for an accurate behaviour duration measure, and was equipped with an accelerometer for activity budget estimates.

behaviours (mating and fighting). Burrowing and feeding, two very different behaviours otherwise undistinguishable using the acceleration patterns solely, were correctly identified by the models. Our main methodological advance was to use the temporal and behavioural context of behavioural sequences within data profiles to extract and sort different behaviours. This simple approach is probably applicable in many instances to gather automatically complete long-term sequences of behaviours of free-ranging animals and to reconstruct the activity budgets.

Our method was not immune from methodological problems, however. Several behaviours tended to be slightly but chronically underestimated (food, immobility, burying), and as expected others were slightly overestimated (walking, reproduction behaviours; Table 2). These biases were inherent to our discrimination method. The crucial parameters were calculated on eight or 120 s temporal windows. Such time spans were longer than the minimal duration of several behaviours. Therefore, when a peculiar behaviour was expressed sporadically, it was inevitably included in the surrounding behaviours and consequently underestimated. This was typically the case for feeding behaviour: very short feeding movements (e.g. a tortoise seizing a single flower) were absorbed by

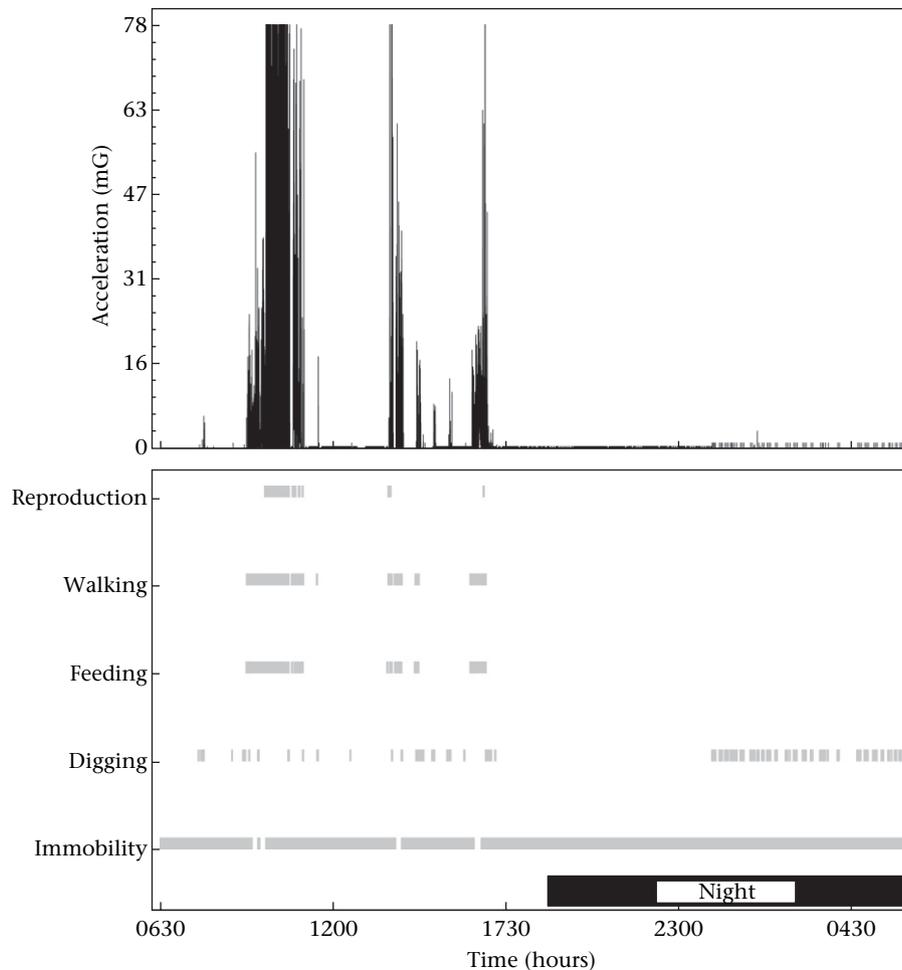


Figure 4. Example of a 24-h acceleration profile obtained on a wild *Testudo graeca graeca*. The behavioural temporal organization we reconstituted with our model was presented in grey bars.

a walking sequence. On the other hand, walking duration was overestimated. Using the regressions between observed and calculated behaviour durations enabled, at least partially, to take into account this bias. More problematic, immobility always led to long sequences of null values. However, motionless animals are not necessarily performing similar behaviours: resting, hiding from predators and digestion are very different in terms of physiology and/or thermal requirements, but

none the less led identical immobility patterns (Hutchison 1979; Iverson 1982; Zimmermann & Tracy 1989, Van Marken Lichtenbelt 1992; Lagarde et al. 2003a). In the future, improvements in the behavioural identification procedure are feasible by taking into account biological variables (sex, size, body mass), and several environmental variables (ambient temperature, distribution of the resources); all parameters susceptible to affect the global level of activity and to drag an important variance in

Table 3. Activity budget of males and females wild *Testudo graeca graeca* in the spring, in the Central Jbilet, Morocco

Behaviour	Males (N=24)		Females (N=24)		Comparisons between the sexes (Mann–Whitney)	
	Duration (min)	%	Duration (min)	%	<i>U</i>	<i>P</i>
Immobility	1360.1±49.3	94.8	1322.0±60.7	92.4	183	0.03
Walking	33.2±24.6	2.3	45.8±29.8	3.2	216	0.14
Feeding	26.2±18.4	1.5	46.3±30.5	2.6	169	0.01
Digging	19.5±14.7	1.4	24.1±16.8	1.7	245	0.38
Reproductive	1.0±1.5	0.1	1.8±4.0	0.1	287	0.99

Activity budget was estimated on wild animals (24 males and 24 females) equipped with acceleration loggers, for behaviour recording (see text for method) during 24 consecutive hours. Activity budget of males and females was compared with a Mann–Whitney *U* test.

the acceleration patterns associated with different behaviours.

Testing the method: activity budget of *Testudo graeca graeca*

The activity budget has been successfully studied for very few terrestrial chelonian species (e.g. *Geochelone pardalis*, *Testudo horsfieldi*) using direct visual focal sampling (Kabigumila 2001; Lagarde et al. 2002, 2003a). It is important to note that in both cases, the tortoises were observed in a very open habitat where the individuals remained visible for long time periods; a peculiar situation not necessarily representative, notably many species live under cover (grass, bushes, forests) and remain hidden most of the time. Dall'Antonia et al. (2001) used acceleration data loggers on the European pond turtle (*Emys orbicularis*) but only to analyse the variations in the activity level. Consequently, our study reports the first automatically recorded analyses of the activity budget based on continuous behavioural sequences of a reptile species.

Arid climatic conditions shape the activity cycle of *T. g. graeca* in the Central Jbilet. The maximal activity was observed in spring, before the summery torpor phase (Ernst & Barbour 1989). However, our results showed that, even during such a vernal favourable period, the total daily activity remained for 2 h. The time spent feeding was lower than 1 h/day (<5% of the total daily active time, and <8% of the diurnal potential activity window). The rare studies carried out on herbivorous reptiles using different methods suggest a low activity rate in herbivorous reptiles (Moberly 1968; Iverson 1982; Nagy and Medica 1986; Hailey & Coulson 1999; Lagarde et al. 2003a); reinforcing the notion that there is a fundamental contrast between ectothermic and endothermic herbivores (Bonnet et al. 1998; Lagarde et al. 1999; Pough et al. 1999).

Our results also enabled to precisely quantify a difference between the sexes (Fig. 5). Females were more often active relative to males, notably they showed a more intensive feeding activity. Such a sexual difference in the foraging behaviour observed in *T. horsfieldi* (Lagarde et al. 2002) is likely associated with the necessity for females to acquire resources during vitellogenesis (Lagarde et al. 2002; Henen 1997). By contrast, and surprisingly, no sex difference was observed for walking: apparently male Greek tortoises do not patrol intensively to locate their mates.

Conclusions and Perspectives

Despite the very sporadic and poorly contrasted activity of terrestrial tortoises, we succeeded to set up a method to monitor automatically whole sequences of behaviours in free-ranging individuals. The main advantages of this method are linked with its safety for the animals, simplicity, and to the relatively low costs of the procedure (with little risks to lose the equipment). This method could be easily extended to other zoological taxa, and may be helpful to better understand the impact of environmental changes on various organisms.

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