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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 (20*g*, 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