

## Foraging behaviour and diet of an ectothermic herbivore: *Testudo horsfieldi*

Frédéric Lagarde, Xavier Bonnet, Johanna Corbin, Brian Henen, Ken Nagy, Baktjior Mardonov and Guy Naulleau

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Herbivorous vertebrates of arid regions are frequently faced with inadequate food quality, quantity or both. The time and energy devoted to foraging is vital to balancing their energy budgets. For desert ectotherms, a low metabolism should be advantageous, reducing their total energy requirement, but extreme ambient temperatures can strongly constrain these animals' activity periods. We provide the first data on the activity budgets, foraging behaviour and diet of a highly abundant, desert-dwelling, herbivorous ectotherm, the steppe tortoise *Testudo horsfieldi*. Extreme climatic conditions of Central Asia limit steppe tortoise's activity to only three months per year. They remain inactive most of their "active season" (90%), and spend very little time foraging (< 15 min per day). This suggests that steppe tortoises can satisfy their energy requirements with modest feeding efforts. Interestingly, steppe tortoises avoid feeding on grass species and feed mostly on plant species that are usually highly toxic to mammals. This result suggests that steppe tortoises and ungulates do not compete for food.

F. Lagarde ([lagarde@cebc.cnrs.fr](mailto:lagarde@cebc.cnrs.fr)), X. Bonnet, J. Corbin and G. Naulleau, Centre d'Etudes Biologiques de Chizé-CNRS, F-79360 Villiers en Bois, France. – B. Henen, Dept of Zoology, Biodiversity and Conservation Biology, Univ. of Western Cape, Belville 7535, South Africa. – K. Nagy, Dept of Organismic Biology, Ecology and Evolution, 621 Young South Drive, Univ. of California, Los Angeles, CA 90095-1606, USA. – B. Mardonov, Samarkand Div. of the Academy of Sciences, 40 Djisakskaya St., Samarkand, 703032, Uzbekistan.

An appreciation of the feeding ecology of a wide diversity of species is central to understanding the general processes of resource acquisition and allocation. Biologists debate the degree of influence of ectothermic and endothermic physiology upon the marked divergence seen in their feeding ecologies. Compared to endotherms, ectotherms are characterised by low metabolic rates, low energy requirements, and low food intakes (Pough 1980, Nagy 1983, Karasov et al. 1986, Zimmerman and Tracy 1989). These traits may represent pre-adaptations (or exaptations, Bradshaw 1997) in ecosystems (e.g., deserts) where food shortages occur frequently and may confer ecological ad-

vantages to ectotherms. These features enable ectotherms to have high densities (i.e., individuals per area), high biomasses and production values (Nagy 1983, Bradshaw 1986), relative to comparable-sized endotherms. Conversely, ectotherm sensitivity to environmental conditions, particularly ambient temperature, strongly constrains the periods when ectotherms can be active (Hutchison 1979, Peterson et al. 1993). Typically, the periods favourable for activity are greatly reduced in desert-dwelling animals that are subject to extremely harsh climatic conditions. Strict time-activity budgets can help organisms to satisfy the demands of growth, reproduction and maintenance

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under conditions of low energy availability. Yet, optimising or maximising foraging efficiency is further complicated when the food resource presents a poor nutrient value (e.g., energy content) per unit biomass as often occurs with many plants consumed by herbivores such as the steppe tortoise *Testudo horsfieldi*. Due to the extreme climate of central Asia, this reptile can be active no more than 3 months each year (early March to late May for males and mid March to mid June for females, Ataev 1997, Lagarde et al. 1999) which corresponds roughly to the period when their only food source, annual plants, are growing and available. The ambient temperatures and food quality or quantity before (cold temperatures and no germinated annual plants) and after (hot temperatures, dry habitat and dead, dry annual plants) this period offer essentially no opportunity for tortoises to be active or consume high quality food. *Testudo horsfieldi* thus bury deep into the sandy soil to aestivate and/or hibernate continuously for nine months. Very rarely are individuals seen aboveground in autumn or late winter (Bogdanov 1960, 1962, Yakovleva 1964, Ataev 1997, Lagarde et al. 2002). Foraging must support maintenance, growth, reproductive expenditures (for males and females), and nutrient storage for the long aestivation-hibernation period, so the favourable season's brevity may constrain foraging or these other functions and generate conflicts (e.g., trade-offs between growth and reproduction or storage).

Although this medium-sized tortoise is probably the most widespread and abundant species of tortoise world wide (Ernst and Barbour 1989, Iverson 1992), its feeding ecology is poorly documented. The range of plants consumed by *Testudo horsfieldi* has been reported (Bogdanov 1960, 1962, Yakovleva 1964, Mambetzhumayev 1972, Said-Aliev 1979), but we lack quantitative information on the relative contribution of each plant species to the diet, the seasonal variation in diet (or plant availability), or the time budget with regard to foraging. However, precise data on the feeding ecology of steppe tortoises are essential because the steppe tortoise is threatened by habitat destruction and over harvesting for the pet trade (Ataev 1997), and we may gain new insights by studying foraging strategies under *Testudo horsfieldi*'s extreme environmental conditions and life history. Incongruously, some propose removing more tortoises from natural and human habitats because tortoises allegedly compete with domestic herbivores (goats, sheep, cattle and camels) and gazelles (Mambetzhumayev 1972, Solomatin 1973, unpubl.) for grass. Our quantitative and qualitative data on the diet and foraging activity of wild *Testudo horsfieldi* are firsts for the species, and should help resolve the competition controversy. These data have been collected at a natural reserve that also contains domestic animals and wild ungulates (goats, horses, donkeys and gazelles).

## Material and methods

### Study area

Fieldwork was completed at the Djeiron Ecocenter of Bukhara, Republic of Uzbekistan (40°N, 65°E) from 2 March 1999 to 28 April 1999. This arid region neighbours the Kyzyl Kum Desert. Mean annual rainfall is < 175 mm, with considerable inter-annual variation (78–271 mm, Pereladova et al. 1998). The site has been described by Pereladova et al. (1998) and Bahloul (2000).

### Behavioural observations

Using continuous focal observations (Altmann 1974, Martin and Bateson 1993), 10 × binoculars, and a non-disturbing observation distance (ca 10 m), steppe tortoise behaviour was observed during the mating season, (= M: 27 March–14 April 1999) and during the post-mating season (= PM: 15 April–18 May 1999). We randomly selected and monitored 12 adult males and 12 adult females (6 males and 6 females during the mating and 6 different males along with 6 different females during the post mating periods), from the time they emerged from their overnight burial sites in loose sand (shortly after the sun rise) until late evening, when tortoises reburied themselves for the night (Bonnet et al. 2001). Males and females were considered as adult when exhibiting a carapace length > 118 mm and 148 mm, the mean size at maturity for males and females respectively (Lagarde et al. 2001). We accurately recorded each tortoise's behaviour and the plant species consumed during feeding. The steppe tortoises often ignored us when we hid behind bushes, moved slowly, or observed from horizontal positions. Behaviours (or attitudes) were classified into four main categories: buried = animal inactive in its burial site or "burrow", feeding = animal biting and/or swallowing a food item, inactive = animal aboveground and not moving nor engaged in any other active behaviour (i.e. burrowing), and, other = walking, mating, fighting or any other behaviour. Active time was considered as "out of burrow" time minus inactive time. Three males and 2 females remained completely inactive during focal observation. These tortoises were included in the estimation of mean active time or mean feeding time in the tortoise population. Otherwise, restricting the analysis to the active tortoises only would strongly bias the results by artificially enhancing activity levels.

In the present paper, we focussed on steppe tortoise feeding behaviour and feeding ecology analysis. The seasonal variations in other activities (i.e. movements, sexual behaviours) have been recently presented elsewhere (Lagarde et al. 2002).

## Diet

To evaluate relative plant species abundance and tortoise food preferences, we counted the number of plants, of each species, in 27 quadrats (1 m<sup>2</sup>) randomly distributed along five 200 m transects. To estimate plant species biomass (g fresh matter m<sup>-2</sup>), we multiplied plant number (per species per quadrat) by the mean aboveground mass of 100 individual plant samples of respective species, we weighed these immediately in the field ( $\pm 0.01$  g, miniature electronic balance) to avoid desiccation errors. We sampled plants during two periods (17 quadrats from mid-March to mid-April, and 10 quadrats from mid-April to mid-May), corresponding roughly to the mating (M) and post mating (PM) periods (Lagarde et al. 1999), to account for the quick composition changes that typically occur in desert plants.

Of the 24 tortoises we observed, 18 were observed foraging and we were able to note precisely the diet composition with 7 individuals during the mating season, prior to 15 April, (4 males and 3 females) and on 7 individuals during the post-mating period, after 15 April (3 males and 4 females). It was impossible to observe accurately the diet composition of the 4 remaining tortoises because when the tortoise were feeding, the observer was too far away to precisely identify each item consumed. We recorded 635 feeding observations during which we identified all the plants species consumed ( $45.4 \pm 20$  feeding observation per observed tortoise). We also recorded which part of the plant (leaf, stem, fruit, or flower) was consumed and the number of leaves stems, fruits, or flowers ingested. We measured the mean mass of plant parts (e.g., 100 leaves, 100 stems, 100 flowers and 100 fruits) from species consumed by the tortoises and we could then estimate the approximated individual feeding rate (fresh plant mass consumed per minute of foraging) and the overall diet composition (estimated mass of fresh plant observed consumed by tortoise for each plant species).

## Statistics

The proportion ( $p_i$ ) of a given plant species “i” in tortoise’s diet was calculated as the percentage of estimated fresh matter consumed for each plant species (g) relative to the total estimated fresh matter consumed for each tortoise we observed ( $n = 7$  in M and  $n = 7$  in PM). Then, we calculated the mean  $p_i$  in tortoise’s diet for each period. Similarly, taxonomic availability ( $q_i$ ) was calculated as the fresh mass percentage (g) of each plant species relative to the total plant fresh matter in each quadrat. Then, we calculated the mean  $q_i$  for the 17 quadrats we collected during the mating period and for the 10 quadrats during the post mating period. We used Hunter’s index ( $H_i = p_i/q_i$ , Hunter 1962) to distin-

guish preferred ( $H_i > 1$ ) from avoided ( $H_i < 1$ ) plant species. Preference or avoidance was considered as statistically significant if the 95% confidence limits of mean  $p_i$  did not overlap the confidence limits of mean  $q_i$ . This statistical procedure was preferred to a simple contingency table with  $\chi^2$  tests because it takes into account the spatial heterogeneity of the vegetation and inter individual diet heterogeneity. A Proportional Similarity Index ( $PSI = 1 - 0.5 \sum_i |p_i - q_i|$ , Feinsinger et al. 1981) was used to estimate to what extent the steppe tortoises consume a specialised or generalised diet. PSI can range from 1 when animals consume any plant at their disposal to “ $q_i$ ” when they narrowly select their food (Feinsinger et al. 1981).

Mean values were given with their standard deviation, except when specifically mentioned. All statistical tests were performed using Statistica 5.1.

## Results

### Patterns of feeding behaviour

Of 24 tortoises observed continuously from early morning to late evening, 5 (2 females and 3 males) remained inactive, 1 female was active but did not forage, and 18 were observed foraging. Considering all the 24 tortoises observed, males ( $1.80 \pm 2.11$  h [mean  $\pm$  SD],  $n = 12$ ) and females ( $1.17 \pm 0.88$  h,  $n = 12$ ) spent little time being active each day, and activity time did not differ between sexes (Kruskal Wallis Anova,  $H = 0.24$ ,  $p = 0.62$ ). The time spent feeding per day was also very short in males ( $0.13 \pm 0.18$  h,  $N = 12$ ) and in females ( $0.24 \pm 0.26$  h,  $N = 12$ ), without a significant difference between sexes (Kruskal Wallis Anova:  $H = 0.82$ ,  $p = 0.36$ ).

Females, but not males, apparently increased their feeding time by being more active during a given day (Fig. 1). Feeding rate was  $0.88 \pm 0.32$  g of fresh plant  $\text{min}^{-1}$  for females and  $1.86 \pm 2.17$  g for males, without significant difference between the sexes (Kruskal Wallis Anova  $H = 0.036$ ,  $p = 0.84$ ,  $n = 14$ ). Daily food consumption, the composite of feeding time and rate, was correlated with daily feeding time in females, but not in males (Fig. 2).

### Seasonal variations in plant community

Mean plant availability per quadrat (g m<sup>-2</sup>) differed between the mating and post-mating periods (ANOVA with species and time periods as factors: species effect:  $F_{23, 600} = 13.89$ ,  $p < 0.001$ , time period effect:  $F_{1, 600} = 0.94$ ,  $p = 0.33$ , interaction:  $F_{23, 600} = 6.03$ ,  $p < 0.001$ ), such that different plant species dominated the community between the two periods (Tables 1 and 2). The mating period was dominated by *Ceratocephalus falca-*

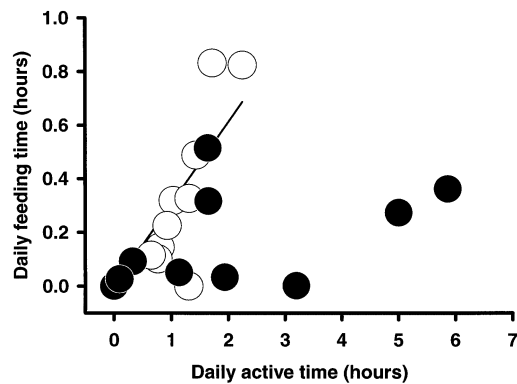


Fig. 1. Relation between time spent active per day and foraging time in male (black circles) and female (open circles) *Testudo horsfieldi*. The regression equations ( $F_{1,10} = 24.42$ ,  $r^2 = 0.70$ ,  $P < 0.001$ ) for females and no significant correlation was found for males ( $F_{1,10} = 4.03$ ,  $r^2 = 0.28$ ,  $p = 0.07$ ).

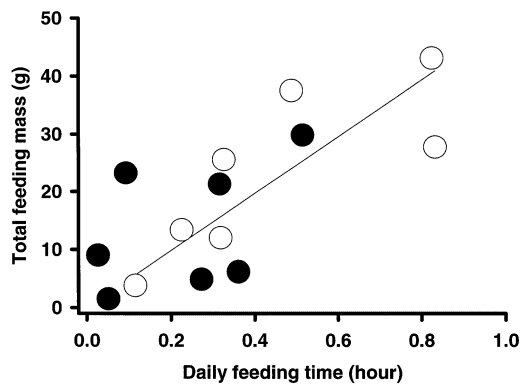


Fig. 2. Relation between daily feeding time and food consumed for male (black circle, Spearman's correlation  $r^2 = 0.42$ ,  $p = 0.33$ ,  $N = 7$ ) and female (open circle, Spearman's correlation  $r^2 = 0.85$ ,  $p = 0.013$ ,  $N = 7$ ) *Testudo horsfieldi*.

*tus* (43% of total biomass), Poaceae sp. (20.44%) and *Epilasia mirabilis* (14.43%) while Papaveraceae and Alyssum were rare and lacked flowers or fruits. In the post-mating period, almost all the *C. falcatus* were dry and represented a small proportion of the fresh plant matter available (2% of the annual plant biomass) while Papaveraceae (*Roemeria* sp. and *Papaver pavoninum*) and Brassicaceae spp. were flowering and/or fruiting, providing a relatively abundant source of food to the tortoises (respectively 28 and 20% of the total biomass available). Poaceae represented a major component of the steppe flora (13% of total biomass) during both periods.

### Seasonal variation in diet and food selectivity

Steppe tortoise did not show any preferences for the plant species present during the mating and the post-mating period. However, they avoided the Poaceae in

both periods, the Papaveraceae in the mating period, and *Alyssum desertorum* in the post-mating period (Tables 1 and 2). The switch between periods observed in Papaveraceae from avoided to consumed corresponds to the fact that this plant blossomed only in the post-mating period. The tortoises ate the Papaveraceae flowers and avoided the leaves (252 flowers eaten vs 6 leaves and 4 plants, flowers eaten vs other parts of the plant:  $\chi^2 = 142.1$ ,  $p < 0.001$ ). The Proportional Similarity Index (PSI) was 0.55 and 0.54 during the mating and post-mating periods, respectively, indicating that *Testudo horsfieldi* is intermediate between a selective and a generalist herbivore.

## Discussion

### Foraging when time is limited

The extreme continental climate of central Asia (hot and dry summer followed by a very cold winter) limits steppe tortoise activity to the spring only, three months a year on average (Lagarde et al. 1999 and references therein). During such a limited time period, the tortoises must meet the energetic requirements of maintenance, reproduction and growth, and they must store sufficient body reserves to fast through the long aestivation-hibernation period. Because activity is strongly limited by thermal conditions, one may expect tortoises to undertake important activities, notably foraging, every favourable day (no wind, no rain,  $> 15^\circ\text{C}$  and  $< 35^\circ\text{C}$ , Ataev 1997, unpubl.). Surprisingly, steppe tortoises were active  $< 2$  h per favourable day, and foraged  $< 0.25$  h per active day. We roughly estimated that there is  $< 65$  favourable days per active season (Lagarde et al. 2002), and then that steppe tortoises spent  $< 20$  h foraging per year. Another desert tortoise, *Gopherus agassizii*, also allocates very little time to foraging per day (0.57 h per day, Nagy and Medica 1986) but unlike *Testudo horsfieldi*, *G. agassizii* is active through spring, summer and autumn. Whatever the case, this suggests that tortoises gather enough resources by browsing during very short periods of time. The low metabolic requirements of ectotherms (Pough 1980) probably explain these seemingly low feeding times. Such highly flexible (and accommodating) nutrient requirements of tortoises, and other reptiles, enables these ectotherms to endure the extreme seasonal and annual fluctuations that occur in Uzbekistan (e.g., droughts, cold periods) and to grow and reproduce with a moderate foraging effort.

Sexual divergences in reproductive roles (Lagarde et al. 2002), and strong climatic constraints (e.g., sun and drought), are likely the main factors that shape the behaviour and the foraging activity of the steppe tortoises in the centre of their distribution range. Such strong climatic constraints that can inhibit foraging or

Table 1. Mean (and 95% CI) annual plant availability (% of total herb biomass available) and percentage of species in the diet of 7 *Testudo horsfieldi* during the mating period. 95% confidence intervals are indicated in brackets. Hunter's index indicates preferences ( $H > 1$ ) or avoidances ( $H < 1$ ). Bold faces indicate significant differences. Data are based on 17 quadrates analysed for plant availability and continuous focal observations on 7 wild foraging tortoises.

Plant taxonomy	Availability (% of herb biomass)	Dietary portion (% of fresh mass consumed)	H (Hunter's index)
<i>Centaurea</i>	0.00	19.87 (−11.51–51.26)	–
<i>Amberboa</i>	0.02 (−0.01–0.04)	0.00	0.00
Asteraceae	0.08 (0.02–0.14)	0.43 (−0.63–1.51)	5.37
<i>Allium</i>	0.09 (−0.04–0.21)	0.00	0.00
Brassicaceae sp.1.	0.09 (0.04–0.15)	0.00	0.00
<i>Koelipinia</i>	0.10 (0.02–0.18)	4.75 (−5.56–15.07)	47.5
<i>Hypocoum</i>	0.36 (0.02–0.70)	0.07 (−0.10–0.26)	0.19
<i>Matricaria</i>	0.97 (−0.52–2.47)	0.00	0.00
<i>Halosteum</i>	1.22 (0.67–1.75)	0.00	0.00
<i>Alyssum</i>	1.25 (0.45–2.04)	0.03 (0.09–0.20)	0.02
Papaveraceae	<b>2.39 (1.37–3.39)</b>	<b>0.23 (−0.33–0.79)</b>	<b>0.09</b>
<i>Veronica</i>	5.53 (0.54–10.52)	0.32 (−0.20–0.84)	0.05
Brassicaceae sp.2.	6.75 (3.32–10.17)	4.56 (−4.09–13.21)	0.67
<i>Epilasia</i>	14.43 (7.98–20.87)	4.86 (−7.04–16.78)	0.33
Poaceae	<b>20.44 (13.77–27.10)</b>	<b>0.00</b>	<b>0.00</b>
<i>Ceratocephalus</i>	43.64 (36.40–50.87)	64.84 (25.32–104.35)	1.48

Table 2. Same legend as Table 1. Post-mating period. Data are based on 10 quadrates analysed for plant availability and continuous focal observations of on 7 wild foraging tortoises.

Plant taxonomy	Availability (% of herb biomass)	Dietary portion (% of fresh mass consumed)	H (Hunter's index)
<i>Merendera</i>	0.01 (−0.01–0.04)	0	0
<i>Delphinium</i>	0.03 (−0.04–0.12)	0	0
<i>Arnebia</i>	0.04 (−0.03–0.12)	0	0
<i>Scabiosa</i>	0.07 (−0.08–0.23)	0	0
<i>Hypocoum</i>	0.08 (−0.1–0.26)	0.36 (−0.53–1.27)	4.5
Asteraceae sp.	0.12 (−0.07–0.32)	5.53 (−0.61–11.68)	46.08
Genus?	0.24 (0.005–0.48)	0	0
Brassicaceae sp.1.	0.32 (−0.07–0.72)	0	0
<i>Halosteum</i>	0.40 (−0.28–1.09)	0	0
Brassicaceae sp.2.	1.14 (−0.67–2.97)	0	0
<i>Veronica</i>	1.55 (−0.93–4.05)	0.26 (−0.38–0.92)	0.1
<i>Matricaria</i>	2.13 (−0.76–5.04)	0	0
<i>Ceratocephalus</i>	2.17 (0.35–3.99)	3.34 (−0.34–6.34)	1.53
Brassicaceae sp.3.	2.36 (−2.99–7.72)	0	0
<i>Koelipinia</i>	3.26 (−2.74–9.27)	25.59 (1.92–49.27)	7.84
<i>Centaurea</i>	3.29 (−0.14–6.73)	1.17 (−1.69–4.03)	0.35
<i>Epilasia</i>	3.94 (−0.59–8.48)	4.73 (−0.86–10.33)	1.20
<i>Roemeria</i>	6.48 (2.13–10.83)	1.72 (−0.78–4.22)	0.26
Poaceae sp.	<b>13.07 (8.13–18.01)</b>	<b>0</b>	<b>0</b>
<i>Alyssum</i>	<b>17.05 (6.69–27.41)</b>	<b>0</b>	<b>0</b>
Brassicaceae sp.4.	20.14 (−1.45–41.74)	20.73 (1.54–39.92)	1.02
<i>Papaver</i>	21.98 (4.57–39.4)	36.51 (22.54–50.48)	1.66

activity probably are not unknown in reptiles. For example, in western Australia, desert-dwelling lizards *Ctenophorus nuchalis*, are also limited in their foraging behaviour by high environment temperatures in late summer, and both field metabolic rate and dry matter intake decline precipitously in autumn, with all adults dying (Bradshaw 1986, Nagy and Bradshaw 1995).

### Do steppe tortoises select their food?

Our data indicate clearly that steppe tortoises are strictly herbivorous. Field observations were collected

over the activity period from 1996 to 2000 on > 1000 individuals (and many repeated observations per individuals), and we never observed tortoise feeding on any animal (except perhaps tiny insects present on the plant consumed). In steppe tortoises, as in other terrestrial chelonians, the diet shifts over time, and is closely associated with seasonal changes in food availability (McDonald and Mushinsky 1988, Moskovits and Bjornndal 1990, Mason et al. 1999). Soon after the winter emergence, from late March to mid-April, *Testudo horsfieldi* fed almost exclusively on *Ceratocephalus falcatus*, the most abundant and accessible plant species available at that time. Later, from mid-April to mid-

May, Papaveraceae, *Koelpinia* and Brassicaceae tend to dominate the annual plant community, and *T. horsfieldi*'s diet shifted towards those plants. However, steppe tortoises avoided some potential resources, particularly grass, abundant in the steppe plant community (second and fourth taxa in biomass in the mating and post mating periods respectively, Tables 1 and 2). Perhaps the relatively low water content of grasses (Barboza 1995) may make these plants less desirable for tortoises. Free water was very rarely available, even during the rain because the sandy substrate does not pool water, and we saw only one tortoise drinking over 5 yr of fieldwork. However, we occasionally saw tortoises gently lick the lower leaves of trees immediately after spring thunderstorms. In addition, consuming dry grasses can cause negative water and nitrogen balances in desert tortoises (*G. agassizii*, Henen 1997, Nagy et al. 1998), so grasses may pose other nutrient problems if consumed by *T. horsfieldi*. The steppe tortoise is midway between a specialist and a generalist herbivore like many other terrestrial chelonians (*Gopherus polyphemus*: McDonald and Mushinsky 1988, *Geochelone pardalis*: Mason et al. 1999, *G. denticularia*, or *G. carbonaria*: Bjorndal 1989, Moskovits and Bjorndal 1990). However, the marked avoidance of Poaceae by *T. horsfieldi* remains puzzling, and has not been reported in other tortoises.

### Drugs: foraging in haste?

Surprisingly, most of the plants consumed by *T. horsfieldi* have high contents of substances that are notorious for their toxicity to herbivorous mammals. *Papaver pavoninum* contains alkaloids that can be poisonous to many mammals, and cases of intoxication have been documented in ungulates that consumed closely-related species (i.e. *Papaver somniferum*, *Papaver rhoeas*, *Papaver nudicaule*, Kingsbury 1964, Frohne and Pfander 1983, Cooper and Johnson 1984). Similarly, *Koelpinia linearis* contains several terpenoids, Koelpinin-A, B and C, all of which are potentially toxic for mammalian herbivores (Koul et al. 2000). *Ceratocephalus*, like other species of the closely related *Ranunculus* genus, produces and accumulates significant amounts of ranunculin, a potent poison, at least for mammals. Crushing the plant releases an enzyme that changes ranunculin, a glycoside, into protoanemonin, a highly irritant, yellow, volatile oil. This latter chemical is unstable and is transformed into the non-toxic anemonin or is volatilised upon drying. The average LD-50 is 10.9 g of fresh plant  $\text{kg}^{-1}$  for sheep that consume aboveground plant parts in the flower to early-seed stage. Sheep fed 7 g  $\text{kg}^{-1}$  of body weight may develop transient anorexic effects. An intake of 13.9 g  $\text{kg}^{-1}$  would usually be lethal (Nachman and Olsen 1983, Olsen et al. 1983). In Utah, 150 of 800

sheep that ingested ranunculin-containing buttercup died (Olsen et al. 1983, Cusick 1989).

Such a diet that includes potentially toxic items has been documented in other chelonian species including *Testudo hermanni* and *Eretmochelys imbricata* (Meylan 1988, Longepierre and Grenot 1999). Such a diet has been interpreted in terms of anti-helminthic strategy (Satorhelyi and Sreter 1993, Longepierre and Grenot 1999). Female *T. hermannii* treated with vermifuge shift from a diet based on Ranunculaceae (with a high content of ranunculin) toward a diet based on Asteraceae (Longepierre and Grenot 1999), which lacks such compounds. Although steppe tortoises sometimes have a very high intestinal parasite loads (unpubl.), we can only speculate about the antiworm benefits of the plants consumed by the steppe tortoises.

### Conclusions

Our study provides the first accurate data on the feeding ecology of the steppe tortoise and suggest that a limited foraging activity enables steppe tortoises to gather enough energy to fuel maintenance, growth, reproduction and metabolism in the long aestivation-hibernation period. This strongly contrasts with what is observed in ungulates (Gordon and Lascano 1993) that need to forage over prolonged time periods to meet the very high energy requirements imposed by their very high metabolism (when compared to ectotherms). Such fundamental ectothermic/endothemic divergence should be considered in optimal foraging models. Interestingly, steppe tortoises avoid feeding on grass and feed mostly on plant species that are usually highly toxic to mammals, suggesting a limited (if any) competition for food between tortoises and wild or domestic ungulates. Although preliminary, our study is encouraging in providing a thorough baseline to set up experimental protocols and directions to better understand the feeding ecology of herbivorous ectotherms living in extreme climatic conditions. Such information is vital for fundamental and conservation purposes.

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