A short spring before a long jump: the ecological challenge to the steppe tortoise *(Testudo horsfieldi)*

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Abstract: The steppe tortoise *(Testudo horsfieldi)* is probably the most widespread and abundant of all living terrestrial tortoises, but paradoxically, this chelonian as been studied only superficially. Steppe tortoise populations are declining rapidly as a result of massive harvesting for the pet trade and extensive disruption of their habitat by intensive agriculture. Thus, it is urgent to acquire accurate information on major life-history traits. Our 5-year field study at the Djeiron Ecocenter in the Republic of Uzbekistan indicates that steppe tortoises usually remain buried in one place for over 9 months, which helps them cope with the extreme environmental conditions that occur in summer, fall, and winter. After emerging in late winter, steppe tortoises have less than 3 months in spring to forage to obtain the fuel needed for growth and reproduction, and replenish the body reserves necessary for the subsequent 9 months of total starvation. The mating period occurred between the end of March and mid-April and the egg-laying period from the end of April to mid-June. Using radio-tracking and focal sampling, we measured the time devoted to different activities by males and females. During the mating period, males allocated a large proportion of their daily activity to sexual behaviours, whereas females' sexual activity tended to be cryptic. However, males devoted less time to feeding and resting than did females. During the postmating period, both males and females spent much time foraging. The strong sexual divergences indicate that each sex copes differently with the extreme continental climate. The seasonal and interannual changes in body mass indicate complex interactions between climatic conditions, activity budget, and body reserves.

Résumé : La tortue des steppes *(Testudo horsfieldi)* est probablement l'une des tortues terrestres les plus répandues mais, paradoxalement, sa biologie reste méconnue. Cependant, la dégradation des milieux naturels et la récolte intensive des adultes pour le commerce d'animaux sauvages entraînent un déclin marqué de ses populations. Il est, par conséquent, urgent d'acquérir des informations précises sur les principales caractéristiques de son cycle biologique. Notre étude, étalée sur 5 années, d'une population ouzbèke de tortues des steppes indique que cette espèce peut rester inactive plus de 9 mois, enterrée dans le sable à la même place, ce qui lui permet de faire face aux conditions climatiques extrêmes de l'été, de l'automne et de l'hiver. A la fin de l'hiver, les tortues reprennent leur activité et disposent donc de moins de 3 mois, au printemps, pour acquérir l'énergie et la matière nécessaire à la croissance, à la reproduction, et à la reconstitution des réserves corporelles requises en vue des 9 mois de jeûne complet qui suivront. La période des accouplements s'étend de la fin de mars à la mi-avril et la période des pontes, de la fin d'avril à la mi-juin. L'observation continue d'animaux équipés d'émetteurs nous a permis de préciser le budget des activités chez les mâles et les femelles. Durant la période des accouplements, les mâles allouent une grande part de leur activité quotidienne aux comportements sexuels, alors que 1'activité sexuelle des femelles est beaucoup plus cryptique. Par conséquent, les mâles allouent moins de temps au repos et à 1'alimentation que les femelles. Après la période des accouplements, les mâles et les femelles passent plus de temps à s'alimenter. Les fortes divergences entre les budgets des activités des mâles et des femelles suggèrent que chaque sexe répond différemment aux contraintes sévères du climat continental. Les variations saisonnières et annuelles de la masse corporelle indiquent 1'existence d'interactions complexes entre les conditions climatiques, le budget des activités et la condition physique.

Introduction

One objective of conservation biology is to provide guidance in establishing plans for the sustainable management of wild populations. However, habitat destruction often con-founds plans with the multiple goals of sustainable agriculture, harvesting of wildlife, and conservation. Frequently, basic biological knowledge about endangered species, such

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as population size and population dynamics, is simply not available. The steppe tortoise *(Testudo horsfieldi)*, probably the most widespread of all terrestrial tortoises, is no exception. This species is found from the southeast of the former USSR to northeastern Iran, Afghanistan, northwestern Pakistan, and eastern China (Ernst and Barbour 1989; Iverson 1992). Population densities have declined markedly through-out the species' range (Stubbs 1989), owing to habitat destruction and extensive collecting for the pet trade (Brushko and Kubykin 1982; Kubykin 1995), as is unfortunately the case for many other species of terrestrial tortoises (Luiijf 1997). Consequently, *T. horsfieldi* is listed in Annex II of the Washington Convention and is considered "critically endangered", and recommendations to severely restrict harvesting have been proposed for over a decade (Stubbs 1989). Because of high mortality during transport and acclimation of commercial specimens, a ban on imports was recently imposed (September 1999, European Union (EU) wildlife trade regulation 338/97). This applies to all 15 member states of the EU. Nevertheless, huge numbers of steppe tortoises are still being removed from the wild in central Asia every year, mainly for American pet shops and the Asian market (Altherr and Freyer 2000). In addition, the natural habitat is still under-going profound changes.

Russian studies provide important information on several aspects of the biology of this species (reviewed in Ataev 1997), but accurate data on its ecology and demographics are unavailable despite the urgent need for appropriate conservation plans. In 1996 we initiated a long-term field study of the steppe tortoise in the Republic of Uzbekistan in central Asia that investigated their ecology, behaviour, physiology, and demography. Like other tortoises living in desert areas (Nagy and Medica 1986), steppe tortoises must cope with severe environmental conditions and numerous ecological challenges. Notably they must deal with extreme variations in ambient temperature and a prolonged shortage of food and water.

This study provides a baseline that describes important links between environmental conditions and the temporal organization of the natural history of the steppe tortoise. We characterize climatic conditions, describe the phenology and activity patterns of the tortoises during their active season, estimate the time budgets of males and females separately, and finally analyse seasonal and annual variations in body condition as an indicator of fluctuations of the nutritional status of individuals.

Materials and methods

Study site
The study population of *T. horsfieldi* was situated at the Djeiron Ecocenter in Bukhara, Republic of Uzbekistan (40°N, 65°E). This arid region is near the Kyzyl Kum Desert and receives less than 250 mm of rain annually (Pereladova et al. 1998). The sandy soil supports xerophytic vegetation such as the shrubs *Halloxylon aphyllum* and *Astragalus* sp. and a thin cover of annual plants (e.g., *Bromus tectorum, Hypecoum parviflorum, Papaver parvoninum, Ceratocephalus falcatus, Alyssum desertorum)* in spring. From 1996 to 2000, five consecuti-ve field sessions were conducted during the annual above-ground activity period of the steppe tortoise (Table 1).

Table 1. Dates of the field session to study the steppe tortoise, *Testudo horsfieldi,* at the Djeiron Ecocenter, Republic of Uzbekistan.

Year	Beginning of the field session	End of the field session
1996	13 March	17 May
1997	28 March	7 July
1998	23 March	22 June
1999	7 March	5 May
2000	1 April	24 April

Climatic conditions
Rainfall data for the Bukhara region from 1994 to 2000 were obtained from the Global Precipitation Climatology Centre (http://www.dwd.de/datas.research/gpcc), which provides grid analyses (resolution 1° by 1°) of quality-controlled data measured by rain gauges and includes correction factors for systematic measurement of errors (Rudolf et al. 1994). Regional temperatures for 1994-1998 were obtained from the Bukhara weather station.

Microclimatic temperatures in the study area were gathered using an automatic temperature-acquisition system (Gemini dataloggers, Tinytag, temperature range -40 to +85°C, accuracy 0.4°C). Air temperature was recorded every 11 min continuously from 8 March to 24 April 1999. One automatic station recorded field air temperature directly 10 cm above the substrate, whilst another recorded air temperature 15 cm underground in a tortoise burrow.

Animals
During the 5 study years, 863 tortoises were individually marked using permanent and temporary systems. Each animal observed in the field was identified with a code using shell notches and a number painted on the shell for use during behavioural observations. On average, females and males reached sexual maturity at 10 and 13 years of age, respectively (Lagarde et al. 2001), after which it was easy to sex them using the length of the tail (Ernst and Barbour 1989; Bonnet et al. 2001*b*). Body size (length, width, and height of the shell; ±1.0 mm) and body mass (±0.1 g) were recorded at first capture. Each time we had visual contact with an animal, we recorded its behaviour and the date and time of observation. Behaviours were categorized as follows (Hailey and Coulson 1999): *walking; feeding; sexual activity* (any inter-action between males and females such as male-male com-bat, courtship, or copulation); *stationary* (immobile and not in a burrow); *burrowed* (in a burrow, presumably inactive); and *other* (other behaviours). Our database contains 2069 observations gathered during capture-recaptures, allowing us to precisely determine the steppe tortoises' mating period (period with observations of sexual activity) and activity period (period with observations of active tortoises).

To describe seasonal variations in the daily activity pattern, we counted all tortoises seen active in 1997 and 1998 and categorized them according to the hour of day and the date.

To test for between-year differences in the intensity of males' sexual behaviours, we calculated a sexual activity index, which is the percentage of males in our study

population seen engaging in sexual behaviours (male-male combat, courtship, and mating) during the mating season each year. Fourteen females and 13 males were fitted with AVM transmitters (AVM Instrument Company, Colfax, California) soon after winter emergence (i.e., shell still covered with a crust of dry sandy mud) in 1998. Each transmitter weighed 25 g, less than 10% of the total body mass. Thereafter, each individual was relocated daily. Approximately 3 months later, at the apparent end of the active season, when an animal had spent at least 4 consecutive days buried at the same place, we declared that the tortoise had started to aestivate. Its transmitter was removed and the tortoise reburied. The location of the putative "aestivation/hibernation" site was then marked with plastic flagging and the exact underground position of the tortoise was marked with a small metal spike placed near the tortoise in the sand and tied with a string to the aboveground plastic flagging to allow easy relocation of the tortoise the following year. In addition, toothpicks were aligned in a row over the place the tortoise entered the soil. The toothpicks were monitored daily until the end of the 1998 field session to determine whether the tortoise moved after our manipulation. Seven males and five females moved immediately after disturbance, but six other males and nine females remained buried until the end of the field session. At the beginning of March 1999, each of these 15 burrows was checked again for the presence of tortoises.
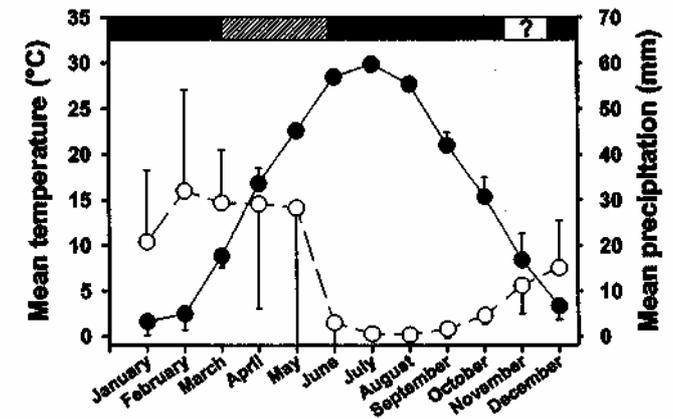
Time budget

Time budgets were estimated for 22 active males and 22 active females in April and May 1998 using opportunistic focal-animal observations (Altmann 1974). Because time bud-gets may vary according to the hour of the day, 22 observations were conducted in the morning and 22 in the afternoon to minimize such bias and allow analysis of sexual and temporal variations in time budgets. We followed individuals as long as possible, remaining appro-ximately 20-50 m away from them to reduce disturbance, and we used 10x binoculars or a 20x telescope. The duration of observation periods ranged from 20 min to 2 h, during which time we continuously recorded behaviours. We calculated the percentage of time allocated to each behaviour during each observation period. However, sometimes individuals remained invisible (0.93 ± 3.36% (mean ± SD) of each observation period) and this time was systematically removed from the analyses (Mar-tin and Bateson 1993). Because the duration of observation pe-riods varied among individuals, we randomly selected a se-quence of only 20 min per observation period for analysis.

To estimate the total time tortoises spent above ground during a day, we scan-sampled (Altmann 1974) eight males and eight females with a radiotelemeter between mid-April and mid-May 1998. These scan-samplings were done under good climatic conditions (no rain, cloud, or strong wind). Observations were made from 07:30, before tortoises emerged, to sunset, when tortoises burrowed underground. One observation was made approximately every half hour (28 ±15 min), yielding an average of 25 observations per individual.

Seasonal and interannual changes in body mass

To analyse seasonal changes in body mass, the 27 tor-toises equipped with a radiotelemeter (14 females and 13 males) were recaptured and weighed four times during the

Fig. 1. Climatic conditions and steppe tortoise, *Testudo horsfieldi,* phenology at the Djeiron Ecocenter, Republic of Uzbekistan. The monthly shaded air temperature (mean ± SD) (•) and precipitation (O) were calculated over the period 1994-1998. The annual activity cycle of the steppe tortoise is shown at the top: time spent inactive in the burrow (solid), active above ground during daylight (hatchhed), and possible sporadic activity ("?") (see the text).

year (electronic balance; ±0.1 g): at initial capture in March, then 1 month later at the end of the mating season in late April, again just after the animals began to aestivate in the burrow in late June, and finally just before emergence from hibernation the following (1999) spring.

Between-year variation in body condition was evaluated for two periods: the beginning of aboveground activity in late March - early April and the end of the mating period in late April - early May. All tortoises captured and weighed each year during both these periods were used for this analysis. To account for differences in body size between years for tortoises sampled and in shape between the sexes (Bonnet et al. 2001*b*), we used a body-condition index (BCI; body mass adjusted to size). BCIs were calculated as the residual values of the regression between the logarithm of body mass (g) against the logarithm of carapace length (mm).

Statistical procedure

We used analysis of variance (ANOVA) to evaluate differences in time budgets and mean BCIs, and Kruskal-Wallis ANOVA when the sample size was small or the assumption of normality was violated. To analyse changes in body mass in the same individuals over time, we compared individuals' trajectories. The dependence among data violated the assumption of sphericity (in all of our repeated-measures tests, Mauchley's sphericity tests, $p < 0.01$). Thus, we used repeated-measures ANOVA (MANOVA; O'Brien and Kaiser 1985). All statistical tests were performed with Statistica 5.1.
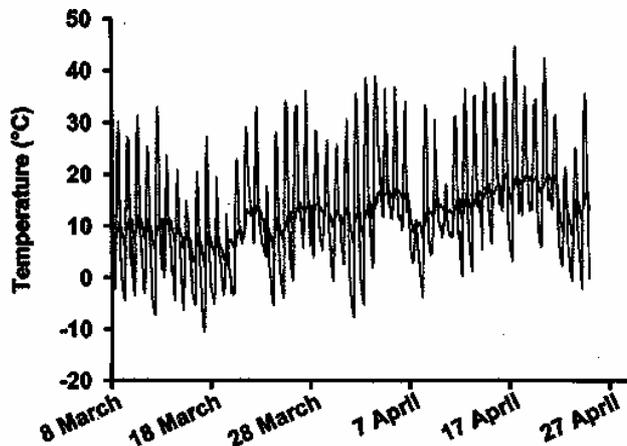
Results

Climatic conditions

Regional climate

During the years of our study, the climate in the Bukhara area was typical of continental regions (Fig. 1). From 1994 to 1998, the shaded air temperature in January was only 1.6 ± 1.5°C (mean ± SD) and in July it was 29.8

Fig. 2. Daily air-temperature profiles in a *T. horsfieldi* burrow 15 cm below ground (solid line) and 10 cm above the surface of sandy soil (shaded line). These profiles were compiled from one temperature record obtained every 11 min from 8 March 1999 to 24 April 1999.

Fig. 3. Total numbers of *T. horsfieldi* seen active in the field (shaded line) or engaged in sexual activity (solid line) during the study period (1996-2000).

Table 2. Precipitation in the Bukhara area, Republic of Uzbekistan.

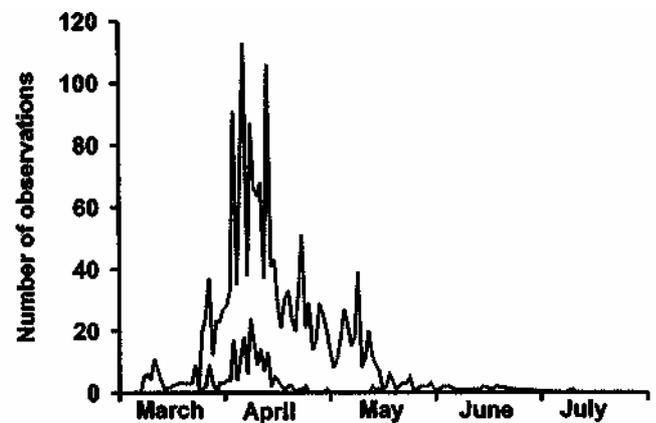| Year	precipitation (mm)	precipitation (mm)
1995	123	150
1996	93	78
1997	271	238
1998	249	247
1999	124	111
2000	93	85

Note: Annual precipitation was calculated using the 12 months of the calendar year. Wet-season precipitation corresponds to cumulative precipitation from November to May of the following year.

± 0.6°C. Mean annual rainfall was 175 mm a year, almost all (96%) falling between November and May. From June to October, steppe tortoises experience a long drought period. There was considerable variation in annual rainfall (from 96 to 271 mm during our study; see Table 2), so steppe tortoises may experience relatively dry years as well as dry summers.

Daily microclimatic conditions

The daily air temperatures we recorded between 8 March 1999 and 24 April 1999 on sandy soil were 28.9 ± 7.7°C (mean ± SD), ranging from 10.2°C (7 April 1999) to 43.8°C (2 April 1999). By comparison, daily temperature ranges in the burrows were significantly attenuated, ranging from 1.4°C (27 March 1999) to 7.2°C (2 April 1999) (4.2 ± 1.6°C (mean ± SD); ANOVA, $F_{[1.94]} = 472$, $p < 0.001$; Fig. 2). Burrows did not freeze regardless of the external temperature during the study period. On 17 March 1999, for example, we recorded a minimum air temperature of -11°C at 06:56 and a maxi-mum air temperature of 27.4°C at 14:38. At the same time, the air temperature in the burrow ranged from 2.3 to only 7.3°C.

Seasonal variation in activity patterns

Seasonal activity

Based on the 2069 contacts made with 863 different tortoises during the 5 study years, the first active animals were observed at the beginning of March and active animals were last seen at the beginning of July (Table 3). Fall and winter activity is apparently rare. Only one tortoise was observed above ground between July and March in 1997, a year during which we continuously observed the study area.

In 1998, we precisely located the aestivation burrow of nine females and six males (see Materials and methods). At the beginning of March 1999, five of nine females were found in exactly the same place where they had buried them-selves the preceding summer, but none of the six males were found where they had buried themselves. Males tended to become active 3 weeks earlier (and to aestivate 3 weeks earlier) than females (Table 3), so it is likely that we arrived too late in 1999 to witness the emergence of the males. Indeed, all males were active when we arrived. In 1998, males began aestivating significantly earlier (27 May ± 6 days; $N = 13$ tortoises with transmitters) than females (14 June ± 4 days, $N = 14$; ANOVA, $F_{[1,25]} = 79$, $p < 0.001$).

During the 5 years of study, 95% of sexual behaviours and mating occurred between 27 March and 17 April (Fig. 3). However, the occurrence of sexual behaviours in early May has been noted anecdotally. For simplicity, we suggest that the mating season occurs from late March to mid-April and that the postmating period corresponds broadly to the period from mid-April to late June. The intensity of sexual behaviours varied greatly from year to year (Fig. 7; $\chi^2 = 27.73$, $p < 0.001$).
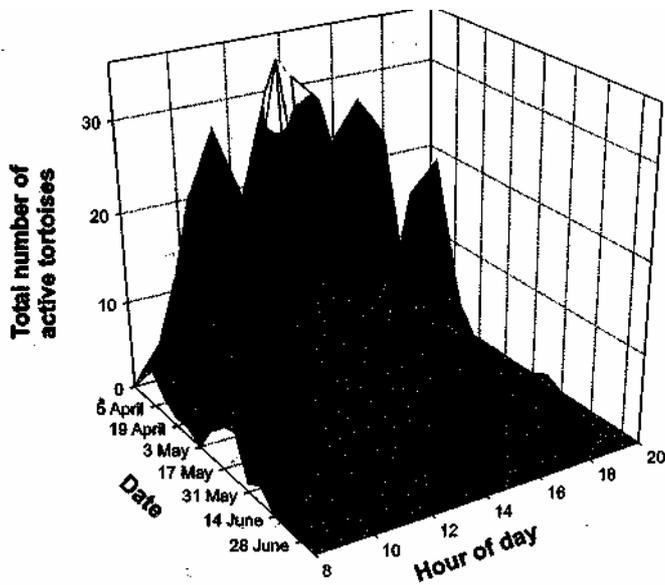
Daily activity pattern

During the active season, the daily distribution of tortoises active above ground shifted from a unimodal to a bimodal pattern (Fig. 4). Early in the active season (before mid-April), numerous active individuals were seen between 10:00 and 17:00. Later in the season, two peaks of activity were observed, the first from 09:00 to 12:00 and the second from 16:00 to 18:00. Observations of

Table 3. Extreme dates of observed active or mating *T. horsfieldi* in the Republic of Uzbekistan.

	Active period				Mating period	
	First observation		Last observation			
	Males	Females	Males	Females	First observation	Last observation
1996	(13 March)	25 March	—	—	2 April	—
1997	(28 March)	(28 March)	5 June	(7 July)	30 March	13 May
1998	(23 March)	27 March	24 May	(22 June)	27 March	14 May
1999	8 March	22 March	—	—	24 March	—

Note: Dates in parentheses coincide closely with the beginning or end of field observations in that year (dates may be in error).

Fig. 4. Total numbers of active *T. horsfieldi* in 1997 and 1998. Daily activity shifts from a unimodal to a bimodal pattern between winter emergence and aestivation. The *y* axis represents the total numbers of animal observed active per week and per hour in 1997 and 1998.

Fig. 5. Mean time budgets of male *(n = 22)* (a) and female *(n = 22)* *(b) T. horsfieldi* during the mating period (solid columns) and postmating period (open columns); vertical lines show the standard deviation (see Table 4 for statistics).
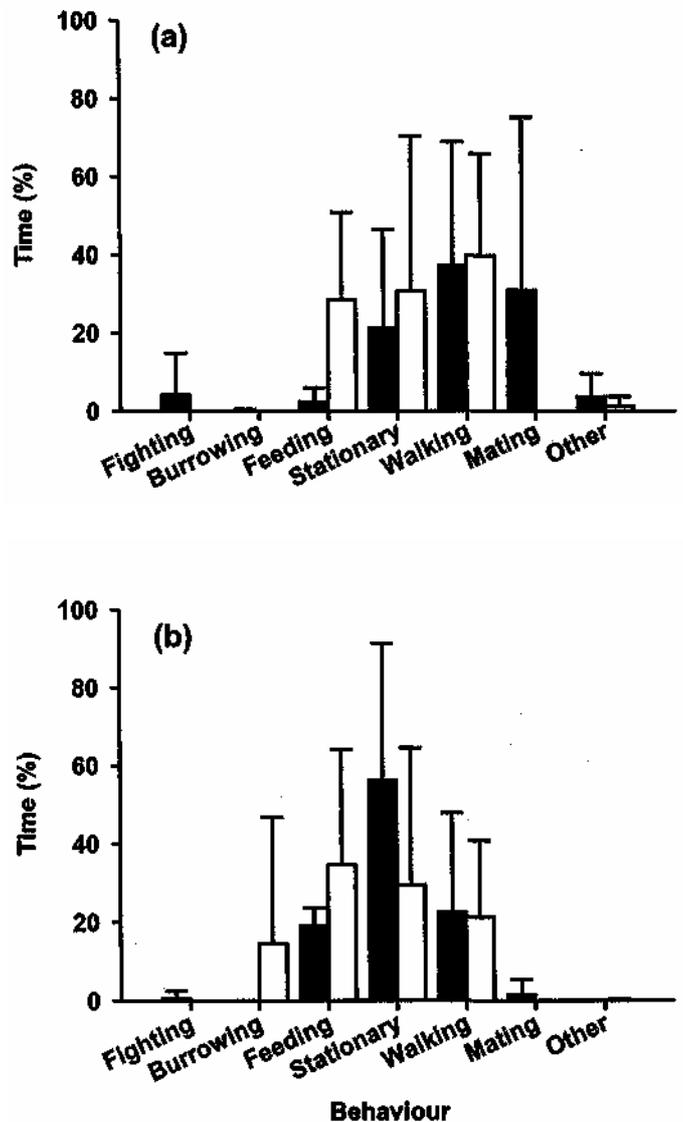

active tortoises became rare after 10 May. Periodic nighttime checks of telemetered tortoises during the active season indicated no nocturnal activity.

Time budget

Scan-sampling of 16 radio-tagged tortoises indicated that daily times spent above ground were very similar among males (5.2 ± 2.8 h/day (mean ± SD), $N = 8$) and females (4.8 ± 2.6 h/day, $N = 8$; Kruskal-Wallis ANOVA, $\chi^2 = 0.0$, $p = 1.0$). The analysis of the focal samples of 22 males and 22 females showed mat during the mating season, males spent more than 30% of their time above ground in sexual behaviours (Fig. 5), which is significantly more than females (2% of the time; Table 4). During the mating period, females spent more time feeding (20% of time spent above ground) than did males (2.5%). Both males and females spent more time feeding after the mating period ended. Males spent nearly twice as much time walking than females, both during and after the mating period. Males spent significantly less time stationary during the mating period than females (21 and 56%, respectively).

Fig. 7. Annual variation in rainfall (•) and sexual-activity index (O) *(a)* and body condition *(b)* for *T. horsfieldi* (sexes combined). Mean BCI values at the beginning of the active season (•) and the end of the mating period (O) are shown; vertical lines' show the standard deviation. Wet years are indicated by an arrow with + and dry years with an arrow with -.
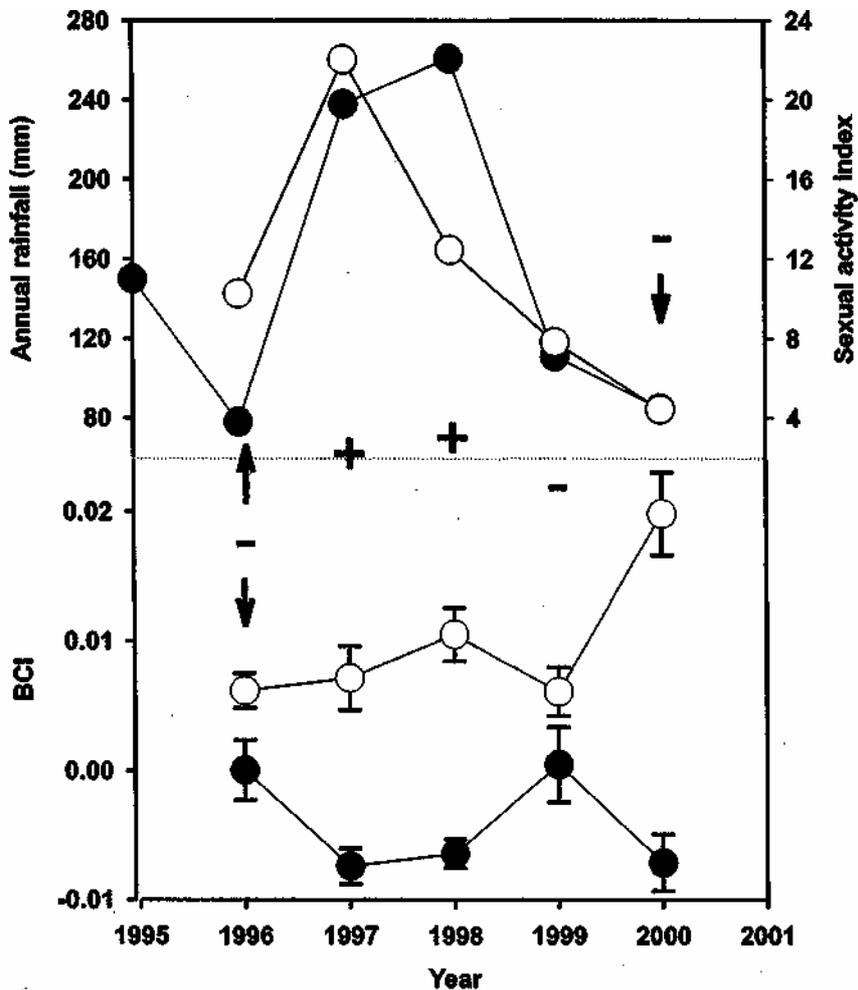
strong wind were often recorded, sometimes for as long as a week. Such weather conditions inhibit steppe tortoise activity and favourable meteorological conditions for steppe tortoises occur on approximately 65 days/year. Assuming that tortoises are out of the burrow for 5 h/day (Fig. 4, Table 3), we estimate the annual time spent above ground by an individual steppe tortoise to be about 325 h/year. This is only 3.4% of the 8760 h in a year. In summer, fall, and winter, environmental conditions are very hot, very dry, and very cold, respectively. Only one tortoise was seen active during those seasons over a year of continuous observation.

Our data on time of emergence from hibernation for males are less accurate than those for females. All nine males that we monitored from June 1998 to the beginning of the 1999 field season had left their aestivation/ hibernation sites before we arrived. Males, like those of many other reptiles, are more likely to emerge from hibernation as soon as climatic conditions are favourable (Naulleau et al. 1987), probably in anticipation of the mating period (Bonnet et al. 2001*a*). In contrast, more than half of the females that we monitored remained in the same place from mid-June 1998 to late March 1999. On the other hand, males began aestivation significantly earlier than females.

Table 5. ANOVA of sex, season, and year effects on variations in body-condition index (BCI) of *T. horsfieldi* in the Republic of Uzbekistan.

Factor	df	*F*	*p*
Sex	1.505	2.34	0.12
Period	1.505	74.32	**<0.001**
Year	4.505	0.61	0.65
Sex x period	1.505	0.17	0.67
Period x year	4.505	1.10	0.35
Sex x year	4.505	4.90	**<0.001**
Sex x year x period	4.505	0.28	0.88

Note: Values in boldface type show significant effect.

Overall, nearly all of the marked steppe tortoises remained underground, buried in the sandy soil, for 9 consecutive months. Although our observations may not apply to all populations of steppe tortoises, we believe that they represent a typical situation. Our study site is situated in the middle of the geographic distribution of this species, and in the typical habitat. Sporadic activity by a few individuals may occur in fall or winter, as has been documented for other populations of *T. horsfieldi* (Ataev

1975, 1997) and is often the case with other Mediterranean and desert tortoises (Morafka et al. 1981; Stubbs and Swingland 1985; Nagy and Medica 1986). Certainly more studies are needed to evaluate the likely influences of environmental conditions such as altitude, winter temperature, or plant production, which vary greatly over the broad geographical range of the steppe tortoise (Dubinin 1954; Chernov 1959; Bogdanov 1960, 1962; Yakovleva 1964; Ataev 1979, 1997).

Because tortoises are ectotherms and require environmental heat in order to be active, the onset of activity in spring depends on climatic conditions that allow individuals to warm up their body by basking in the sun. The minimum air temperature we recorded for active animals in the field was 17°C (F. Lagarde, X. Bonnet, J. Corbin, B.T. Henen, and K.A. Nagy, in preparation). The sexual size dimorphism in this species may explain the difference in the timing of the onset of activity between males and females. Males are smaller than females (Chernov 1959; Yakovleva 1964; Ataev 1975; Brushko 1978; Bonnet et al. 2001*b*; Lagarde et al. 2001), therefore they can warm up their body more rapidly than the females when basking. For example, the American desert tortoise, *Gopherus agassizii,* exhibits the opposite sexual size dimorphism, with males larger than females. This species presents the opposite pattern of winter emergence, with females becoming active sooner than males (Bailey et al. 1995). We do not know how such mechanisms may interact with the fact that males emerge from burrows before females in order to optimize their access to females (Bonnet et al. 1999). However, the clear result is that we observed a strong sexual dimorphism, with males emerging and aestivating sooner than conspecific females.

Broadly speaking, the onset of the activity period corresponds to the annual onset of plant growth. The steppe tortoise is strictly herbivorous and feeds mainly upon annual vegetation (Ataev 1997). This trophic resource is available for only 3 months, from the beginning of March to the end of May. In summer, the scarcity of precipitation combined with the increase in ambient temperatures creates very dry conditions. This hot, dry, foodless period is immediately followed by the rapid decrease in temperatures in fall and winter. The combination of the short period of food availability and unfavourable ambient temperatures poses difficult environmental conditions for steppe tortoises during most of the year.

Even when tortoises were active in spring, changes in ambient temperature had a strong effect on the daily activity pattern. During the mating period, nighttime temperatures were low, often below freezing (Fig. 2). Consequently, tortoises required relatively long periods of time to warm up and attain a functional body temperature, and they could be active only during the hottest part of the day. From mid-April to the end of May, when the midday temperature be-came excessive, tortoises remained sheltered underground and concentrated their activities in the morning and evening. As temperatures rose in late spring, activity became more occasional, and tortoises spent more time underground. Similar shifts in daily activity patterns have been recorded in other steppe tortoise populations (Ataev 1997) and in other chelonian populations (Lambert 1981; Luckenbach 1982; Hailey et

al. 1984; Willemsen 1991; Panagiota and Valakos 1 992). In steppe regions, the thin vegetative cover may not provide suitable shelter against the extreme nighttime and daytime temperatures (which range from -10 to +45°C during the activity season) above ground. Tortoises must bury themselves in the sandy soil, where temperatures are strongly attenuated (Fig. 2). The morphology of the steppe tortoise, notably the round shell and powerful legs, which allow freedom of movement when buried, could be interpreted as an adaptation to the intense burrowing activity of this species (Mlynarski 1966).

During the short period when environmental conditions are favourable, steppe tortoises invest their limited time in foraging and reproduction and their limited energy intake in growth, reproduction, and energy storage for hibernation. The mating season starts immediately after females emerge and lasts only 3 weeks. We observed a female that emerged from hibernation to be immediately courted by a male; thus, her first activity after 9 months of inactivity was copulation. Mating immediately following prolonged hibernation (8-9 months) has also been observed in snakes living in cold climates, such as adders *(Vipera berus)* living in the cool regions of Europe and in Canadian garter snakes *(Thamnophis sirtalis parietalis)* (Gregory 1977; Luiselli 1995).

Focal sampling of active animals during 20-min periods overestimates the activity level of individuals (Hailey and Coulson 1999). Because such a bias applies equally to both sexes, and because we did not detect any differences between males and females in time spent above ground, the amounts of time devoted to different activities (foraging, walking, etc.) by males and females were comparable. Males allocated a large proportion of their daily activity to conspicuous sexual behaviours (fighting and courting) and consequently devoted less time to feeding or resting than did females. During the mating period, males travelled greater distances than females, intensively patrolling their territory (10 ha, on average; Lagarde et al. 1999). In contrast, females made larger loops and had larger territories (30 ha, each overlapping the territories of several males), but moved more slowly than males (Lagarde et al. 1999). When a female was courted by a male, she usually continued to walk and feed, ignoring her suitor(s); typical sexual behaviours (such as acceptance of mating) were generally observed only when a male tried to copulate. Then, the sexual activity of females tended to be cryptic. The intensive feeding of females during the mating period is important to fuel vitellogenesis and growth (Fig. 6). The egg-laying period occurred from late April to the end of the active season (Henen et al. 2000). During that time, both males and females spent much time foraging, presumably because there was a strong need to ac-cumulate energy for 9 months of fasting. A proportion of the energy gathered during that period by females may also be invested in egg production, which may explain the early de-crease in body condition observed in females between the beginning and end of the postmating period. Termination of the males' active season corresponds to the end of the rainy season and food availability. Females may remain active until they lay the last eggs they produce that year. Female in our study area can lay 9 eggs per year, separated into 3 clutches, the last one being deposited in June (Henen et al.

2000). For females exposed to hot climatic conditions, only scarce dry food resources are then available.

Body-mass variations are difficult to interpret in tortoises because body mass depends not only on body fat reserves but upon the amounts of water stored in the bladder and food in the gut (Nagy and Medica 1986). The bladder capacity of steppe tortoises is not known, but we suspect it is less than the 30% of body mass found in *G. agassizii* (Nagy and Medica 1986). Despite intensive mate-searching and court-ship activity, males increased their body mass dramatically during the mating period, and thus probably restored their body reserves well before the beginning of the long aestivation/ hibernation period. In contrast, despite intensive foraging, females seemed to allocate a large amount of energy gained during the active season to egg production. In 1998, when data on reproductive output were available, all females were reproductive (Henen et al. 2000); several females even lost mass, which suggests that they were in negative energy balance. These results suggest that female steppe tortoises may balance their resource budgets (water, energy, etc.) on a pluri-annual basis, exhibiting a bet-hedging reproductive strategy as documented in *G. agassizi* (Henen 1997).

Near the Kyzyl Kum Desert, steppe tortoises must cope with great environmental variation (Fig. 7). In a drought lasting 2 or more years, tortoises may find it difficult to restore their body reserves and (or) reproduce. Complex interannual effects between climatic conditions, body reserves, and activity budget should arise. For example, we may expect that body condition at the beginning of the active season may depend largely upon the BCI at the end of the previous season. Also, the rate of recovery of body reserves during the active season will depend upon climatic conditions in the current year. The amount of energy available for reproduction is a function of the interaction of body condition at the beginning of the season and foraging conditions during the cur-rent active season (Fig. 7). The intermixing of short-term and long-term effects provides an excellent opportunity to study energy-acquisition and -allocation processes in a long-lived species in a harsh environment.

Acknowledgements

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