

# Sex divergence in space utilisation in the steppe tortoise (*Testudo horsfieldi*)

Fredéric Lagarde, Xavier Bonnet, Brian Henen, Arnaud Legrand, Johanna Corbin, Ken Nagy, and Guy Naulleau

**Abstract:** In animal species without parental care, the fitness of males should increase with the number of females encountered, court, and fertilise, and the fitness of females depends strongly on the quantity and quality of resources acquired. This should translate into a marked sex differences in the patterns of space utilisation. We analysed the sex divergences in home range and movements pattern in the steppe tortoise (*Testudo horsfieldi*) in Uzbekistan. From the radio-tracking data of 36 individuals throughout the active season, the home range of the male steppe tortoise was estimated to be smaller than that of the female (24 vs. 57 ha), even when the analysis focused on the mating season only. During the mating season, males intensively patrolled a small area, going back and forth within their territory, thereby covering greater distances than females. The females movements were more unidirectional, resulting in large loops over a very extended home range. We proposed several nonexclusive hypothesis for such a pattern.

**Résumé :** Chez de nombreuses espèces animales dépourvues de soins parentaux, le succès reproducteur des mâles dépend du nombre de femelles qu'ils rencontrent, courtisent et parviennent à féconder et celui des femelles dépend fortement de la qualité et de la quantité des ressources trophiques qu'elles acquièrent. Cela se traduit souvent par des différences marquées dans les modes d'occupation de l'espace développés par chaque sexe. Dans cette étude, nous analysons les divergences sexuelles dans les domaines vitaux et les déplacements chez la tortue des steppes (*Testudo horsfieldi*) en Ouzbékistan. A partir d'un suivi par radio-tracking de 36 individus tout au long de la saison d'activité, le domaine vital des mâles s'est avéré plus petit que celui des femelles (24 contre 57 ha), même lorsque l'analyse est restreinte à la période d'accouplements. Ce résultat surprenant est partiellement clarifié lorsque la nature des déplacements est prise en compte. Durant la saison des accouplements, les mâles patrouillent intensivement un petit domaine vital, en réalisant de constants allers et retours, parcourant de plus grandes distances que les femelles. Les femelles réalisent de plus petits déplacements quotidiens, s'enchaînant en de larges boucles couvrant un domaine vital étendu. Différentes hypothèses non exclusives sont proposées pour expliquer ce pattern d'occupation de l'espace.

## Introduction

In mobile animals, space utilisation, home range, and movement patterns are strongly influenced by both the temporal and spatial distribution of the resources, as well as the state (sex, age, condition, and health) of the individuals (Bury 1979; Savitz et al. 1983; Ims 1987; Macartney et al. 1988). Broadly speaking, essential resources fall into several major categories: physical, chemical, and biological resources (i.e., food, mates, etc.; Morreale et al. 1984; Gibbons and Semlitsch 1987; Gregory et al. 1987; Gibbons et al. 1990). In the vast majority of animal species, females and males optimise their fitness through a sex-specific utilisation of the available

resources. For example, in oviparous species, a laying site is a more fundamental "resource" for females than for males. Hence, sexual divergence in space utilisation may reflect divergences in the nature, distribution, and (or) quantity of the essential resources available for males and females. Therefore, comparison between the sexes within a given species is a straightforward way of examining the relationship between resource availability and space utilisation, as it is not confounded by phylogenetic distance between individuals. Several conceptual problems, however, may obscure the analyses at the species level; in particular, a marked sex divergence in the ecological niche leads to a complex ecological picture. For example, if females and males differ in their habitat, predator avoidance strategy may also differ, and such divergence may interact with the pattern of space utilisation strictly related to the acquisition of resources. The methodological and analytical challenge is then to tease apart the different components, i.e., primary components that are directly dependent on the acquisition of the resources vs. secondary ones such as predator avoidance, all of which will contribute to the optimisation of space utilisation by each sex. By studying species in which both females and males occupy the same habitat, feed on the same food items, suffer from the same predation, and are comparable in size and body shape, we may expect that any sex divergence in space use will be the product of their respective ways to optimise the

Received 10 July 2002. Accepted 15 January 2003. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 26 March 2003.

**F. Lagarde,<sup>1</sup> X. Bonnet, A. Legrand, J. Corbin, and G. Naulleau.** Centre d'Etudes Biologiques de Chizé, CNRS, 79360 Villiers en Bois, France.

**B. Henen.** Smithsonian Institution, National Zoological Park, Department of Zoological Research, 3001 Connecticut Avenue, Washington, DC 20008, U.S.A. **K. Nagy.** Department of Biology, University of California, Los Angeles, CA 90095, U.S.A.

<sup>1</sup>Corresponding author (e-mail: [lagarde@cebc.cnrs.fr](mailto:lagarde@cebc.cnrs.fr)).

relationship between resource acquisition and reproductive success. Also, in the absence of parental care, there should be little overlap in the respective role of females and males in the production of the offspring (Emlen and Oring 1977; Davies 1991). In most animal species, females do not search for mates, but egg production is energetically expensive and reproductive success is often strongly influenced by foraging success and nesting success. The gametic contribution of the male usually requires less energy, and fitness is more influenced by mating success. These strong sexual divergences in reproductive role should translate into strong divergences in daily movements patterns and home ranges between males and females, at least during the mating season.

We analysed the sex-specific space utilisation pattern in the steppe tortoise (*Testudo horsfieldi*), a polygynous species, not exhibiting parental care, and without noticeable ecological differences between the sexes.

## Materials and methods

### Study area

The field site is situated at the Djeiron Ecocenter, which is near the Kyzyl Kum desert (40°N, 65°E) in Uzbekistan. This area is characterised by a continental climate, and air temperature averages 1.6°C in January and 28.8°C in July. Mean annual rainfall averages 175 mm, almost all of which (96%) falls between November and May (Pereladova et al. 1998). Annual rainfall varies considerably, for example, from 96 mm in 1996 to 271 mm in 1998. The study area is semidesert, with perennial shrubs (*Haloxylon aphyllum* and *Astragalus* spp.) and annual plants (*Hypocoum parviflorum*, *Papaver parvoinum*, *Roemeria* sp., *Ceratocephalus falcatus*, *Alyssum desertorum*; Pereladova et al. 1998). The whole Djeiron Ecocenter area covers more than 5000 ha. For the purpose of this study, however, we limited the investigations to a smaller study zone of ~100 ha confined at one of the extremities of the reserve. This study zone, protected by a fence and a channel on two sides, is open to the rest of the natural reserve.

### Study animals

The steppe tortoise is a widespread terrestrial tortoise; its distribution extends from southeast Russia to northeast Iran, Afghanistan, northwest Pakistan, and western China (Iverson 1992). Several studies have provided important background information on the ecology of *T. horsfieldi* (Paraskiv 1956; Korotkov 1967; Brushko 1981; Brushko and Kubykin 1982; Kubykin 1995). The extreme environment constrains the activity of *T. horsfieldi* to about 3 months per year, from mid-March to mid-June (Ataev 1997; Lagarde et al. 1999, 2002). Upon emergence, males exhibit intense sexual behaviour, including frequent male-male combat, and devote the greater part of their activity to searching for a mate (Lagarde et al. 1999). The females nest from late April to late May (Ataev 1997; Henen et al. 1999). From late April until the end of June, ambient temperatures increase markedly and rainfall decreases, resulting in a severe and prolonged drought. Consequently, daily activity declines noticeably and the tortoises are constrained to aestivate underground. Males bury themselves in the sandy soil by the end of May, followed by the females in mid-June. Activity during summer or autumn is

extremely rare (Ataev 1997; Lagarde et al. 1999, 2002). The tortoises remain buried until the following spring and emerge in March.

### Measurements

From 1996 to 2000, 851 individuals were captured in the field. Body weight and carapace length were recorded and the animals were identified by incising notches in the marginal scutes. For long-range identification, the animals were numbered on the carapace with a nontoxic paint. The sex of mature animals can also be distinguished, even at long range; the male has a longer tail than the female (Bonnet et al. 2001). Females and males were considered mature if they were observed engaging in mating activities and (or) when the mid-line carapace length exceeded the minimum size for maturity (102 mm in males, 124 mm in females; Lagarde et al. 2001).

### Telemetry

A total of 36 tortoises were monitored every day throughout the active season (7 adult males and 6 females in 1997 and 10 males and 13 females in 1998). Tortoises were fitted with electronic transmitters (Telonics Inc., Mesa, Ariz. or P2PL AVM Instrument Co., Colfax, Calif.; 5 to 40 g) early in their active season (late March) and were monitored to the onset of the inactive period (mid-May to mid-June, depending on individuals). The transmitters were glued on the back of the carapace using a Fiberglas resin. The mass of the transmitter plus the resin never exceeded 10% of the body mass of the tortoise and caused no detectable disturbance as all the monitored individuals foraged, mated, and buried themselves in the soil as did "normal" individuals. After initial capture, each animal was quickly fitted and released at the exact site of capture (identified in the field with a plastic marker). Each tortoise was relocated at least daily, often 2-3 times a day, generally in late afternoon and occasionally at night. For the analyses, we took into account only the last position for the day. A map of the study area was drawn, and a grid of 5 x 5 m squares was superimposed. In the field, we installed a set of 200 round plastic markers (10 cm in diameter, 1 m above the ground) every 100 m along the paths that we used routinely. We used another set of plastic markers, one of which was placed at each new location along the route followed by each radio-tracked tortoise when the nearest marker was more than 100 m away. These plastic markers were used to determine, with reasonable precision ( $\pm 1$  m), the linear distance travelled by the tortoise between fixes and to determine each location (i.e., the geographic position of a radio-tracked tortoise) on the map with a  $\pm 5$  m accuracy. Distance between a given position and the nearest marker was measured with a laser telemeter (Bushnell Range Finder, Bushnell Corp., Cody, Wyo., accuracy  $\pm 1$  m); the direction (deviation from the magnetic north,  $\pm 3^\circ$ ) was measured with a handheld compass. All of the tortoises exhibited strictly diurnal activity; they started in the morning and buried themselves at dusk. Estimating the distance travelled only during the day is thus a good estimator of the locomotor activity in this species. As a result, however, the distance travelled was underestimated, as tortoises did not move in a straight line from one position to the next. Such a bias was greater in those individuals that changed their direction more frequently during the course of displacements.

### Home-range and displacement estimates

Because terrestrial tortoises do not rely on agility or speed to escape predators, we assumed that all of the series of fixes gathered were representative of activities other than predator avoidance. For example, tortoises moved only very short distances to hide themselves when they were aware of our presence. Consequently, we had no reason to exclude the 5–10% of fixes that are sometimes considered as "exotic" in telemetric studies (White and Garrott 1990), and we included all fixes for the analyses.

Home-range estimators vary greatly in their robustness, suitability, and power, and none is perfect (White and Garrott 1990; Anderson 1992). We estimated home ranges using the minimum convex polygon (MCP) method as it has been used intensively in the past. We also used the adaptive kernels (AK) method to increase the accuracy and robustness of the analysis (Worton 1989, 1995). If an animal patrols intensively a given area, its home range can be established sooner than that of a wandering individual. To test the rate at which a tortoise saturated its home range, we calculated the proportion of the surface area represented by cumulative fixes over time relative to the total home-range area including all fixes. We also calculated the proportion in a stepwise manner by counting the total number of displacements necessary to estimate 25 (HR25), 50 (HR50), and 75% (HR75) of the total home-range area for each animal. Although focal observations (unpublished) indicated that daily paths were not linear, to simplify, we calculated the daily displacement as the distance in metres from one fix to the next. We also calculated 2-week displacements (the sum of the daily displacements over 14 consecutive days) from the beginning of April to mid-June. The rationale for this procedure was to obtain an index of locomotor activity that matches the different periods of activity in our study zone. The mating period (MP) was restricted the first 2 weeks of activity and was followed by the post-mating period and nesting period for females (PMP).

### Statistics

All data were tested for normality, and home ranges were log transformed before analysis. In practice, log-transformed data for home ranges were homoscedastic (Levene's test,  $P > 0.09$  for each group tested). We analysed the effects of sex, year, and period (mating vs. post-mating period) on home-range size. In a radio-tracked animal, each location potentially influences the next location, for example, if an individual crosses a large area, we may obtain a suite of long and straight displacements. Hence, there was the likelihood of a strong dependence among repeated fixes (and the associated calculations of distance and speed) recorded on the same individual. Consequently, we used repeated-measures analyses of variance (ANOVA) to complete most of the analyses (O'Brien and Kaiser 1985). Simple ANOVA were performed when data groups were independent. Home-range saturation in males and females was compared using a non-parametric test (Mann-Whitney rank-sum test). Because of the relatively small sample size within each year, the relationship between body size and other variables were analysed using Spearman's correlation. Statistics were performed with Statistica 5.1.

## Results

### Home range

Pooling 1997 and 1998 and both sexes into a single analysis ( $N = 36$  tortoises), the MCP and AK procedures provided very different values to estimate home ranges: the values were  $18 \pm 19$  ha (mean  $\pm$  SD) and  $42 \pm 42$  ha, respectively. Such a strong discrepancy between the results obtained with the two methods held true in all subsequent analyses. Be-cause it is widely accepted that the AK method provides a more accurate estimate, we present here only those home ranges estimated by the AK procedure.

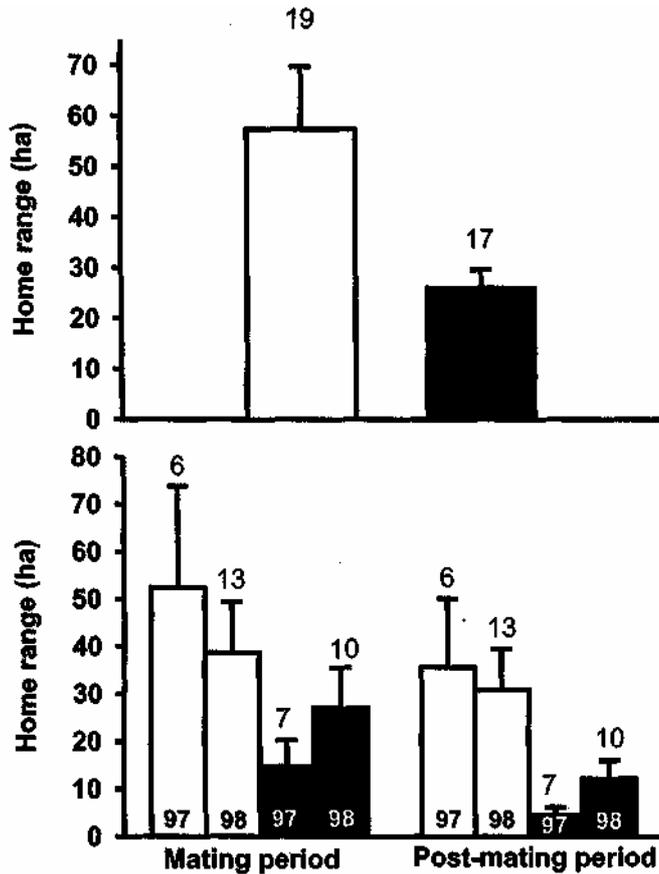
Home ranges were much larger in females ( $57 \pm 53$  ha) than in males ( $24 \pm 15$  ha) (one factor ANOVA,  $F_{[1,34]} = 4.93$ ,  $P = 0.03$ ; Fig. 1a). Such a difference between sexes held true when the possible effect of years was taken into account (two factors ANOVA with sex and year as the independent variables: sex,  $F_{[1,32]} = 10.12$ ,  $P = 0.003$ ; year,  $F_{[1,32]} = 0.20$ ,  $P = 0.65$ ). We found, however, an interaction between these two factors (sex by year interaction,  $F_{[1,32]} = 9.91$ ,  $P = 0.003$ ), probably because male home range tended to increase from 1997 ( $14 \pm 8$  ha) to 1998 ( $33 \pm 14$  ha), whereas female home range showed the reverse tendency ( $88 \pm 63$  ha in 1997 and  $42 \pm 44$  in 1998).

Although overall mean home range was larger in females than in males, there remained the possibility that the reverse pattern may have occurred transitorily during the mating season. Males may have travelled over significantly larger surface areas during the brief mating period and then greatly reduced their activity afterwards, leading to deceptive overall results on the size of the home range. We examined such a possibility by estimating, separately, home-range size during the mating and the post-mating season. Surprisingly, the sex difference detected in the overall activity period (above) was also observed when either the data from the mating period or from the post-mating period were included in the analyses (Fig. 1b; repeated measures over time with sex as the factor and subsequent home ranges as the dependent variables: Wilks'  $\lambda = 0.76$ ,  $F_{[2,33]} = 5.07$ ,  $P = 0.001$ ; specific sex effect:  $F_{[1,34]} = 8.21$ ,  $P = 0.007$ ). This analysis also revealed a strong, and somewhat expected, decrease in the area of home ranges from the mating to the post-mating period (specific (time) period effect,  $F_{[1,34]} = 23.32$ ,  $P < 0.001$ ). The inclusion of 2 years of the study as an additional factor did not change any of these results. Interestingly, when the analyses were performed independently on each sex (to minimise the variance), we found a significant decrease in males home range from the mating to the post-mating periods (Wilcoxon's test,  $U = 3.38$ ,  $P < 0.001$ ), but not in females (Wilcoxon's test,  $U = 1.77$ ,  $P = 0.07$ ). This suggests that after the mating season, the surface prospected by the tortoises decreased more sharply (or only) in males relative to females.

### Home-range saturation

Males saturated their home range more rapidly than did females. Less fixes were necessary to estimate 50 and 75% of the total home range in males (Wilcoxon's test,  $U = 93.50$ ,  $P = 0.018$ , and  $U = 82.50$ ,  $P = 0.007$ , respectively; Fig. 3). This feature could be explained by two different

**Fig. 1.** Mean ( $\pm$  SD) home ranges for female (open bars) and male (solid bars) *Testudo horsfieldi*. The upper graph illustrates the mean values estimated over the whole active season and pooling the 2 years (1997-1998). The lower graph provides details considering the 2 years and the two main (mating (MP) and post-mating (PMP)) periods separately. The size of the home range was estimated by the adaptive kernel (AK) method; the numbers above the bars indicate the sample size.

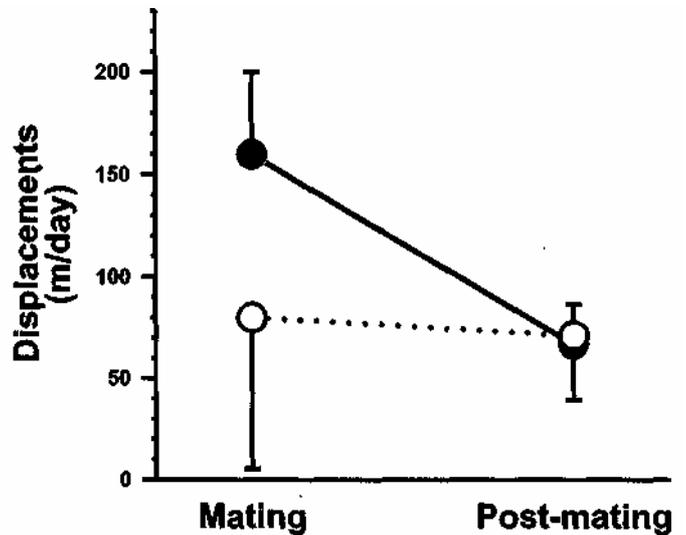


effects: firstly, the size of the home range and, secondly, the pattern of the displacements (direction or celerity) of the radio-tracked animals. Importantly, these effects can act in a very complex way: independently, in synergy, or even antagonistically. For example, that the mean home range of males is the smaller may explain the sex difference in the saturation rate. Alternatively, greater and faster displacements of males can produce the same result. It is even possible to imagine that females are more active than males, but that they cannot rapidly saturate their immense home range. Many other scenarios could be envisaged if one included, for example, the effect of the directional changes in the course of displacements. To tease apart some of these factors, we quantified the movements of the tortoises.

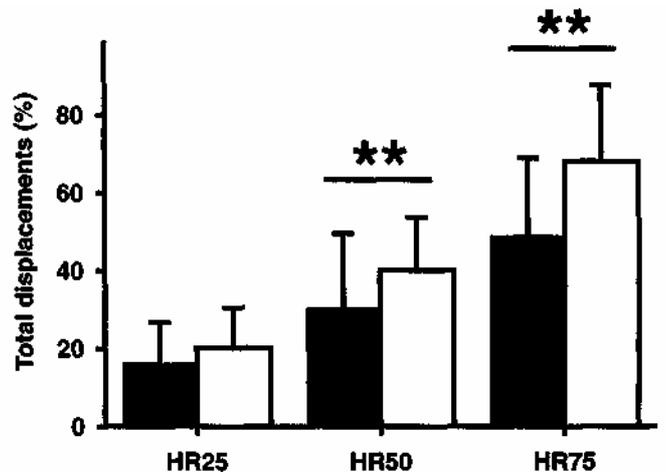
**Movements**

The daily displacements travelled by each sex did not differ when the entire active period (from winter hibernation to summer aestivation) was considered ( $F_{[1,34]} = 0.02, P = 0.84$ ). Repeated measures over time, with sex as the factor and subsequent distances travelled in the mating and post-

**Fig. 2.** Mean ( $\pm$  SD) distance (m) covered per day by 19 free-ranging female (O, dotted line) and 17 male ( $\bullet$ , solid line) *T. horsfieldi*. The graph shows the values measured during the mating season and during the post-mating season.



**Fig. 3.** Contribution (in percentage of the total number of fixes) necessary to explain 25, 50, and 75% of the total home range (HR25, HR50, and HR75, respectively) in female (open bars) and male (solid bars) *T. horsfieldi*. The asterisks indicates that a



mating periods as the dependent variables (Wilks'  $\lambda = 0.67, F_{[2,33]} = 7.29, P = 0.02$ ), revealed a significant sex effect ( $F_{[1,34]} = 12.42; P = 0.001$ ) and a time effect ( $F_{[1,34]} = 29.81, P < 0.001$ ). During the mating period, males travelled over longer distances ( $159.7 \pm 40.1$  m/day) than did females ( $79.8 \pm 74.5$  m/day), and this trend disappeared during the post-mating period ( $66.6 \pm 27.5$  m/day in males,  $70.9 \pm 15.4$  m/day in females; Fig. 2). Considering the sexes separately, daily displacements tended to decrease after the mating period in males (Wilcoxon's paired test,  $U = 3.57, P < 0.001$ ) but not in females (Wilcoxon's test,  $U = 0.48, P < 0.62$ ).

We also found marginal yearly effects, but they did not alter the main results and added no further information.

**Table 1.** Influence of body size on home range and daily displacements in 36 radio-tracked female

Sex	Statistics	Home range	Displacements
Females ( <i>n</i> = 19)	<i>r</i>	-0.003	0.42
	<i>P</i>	0.89	0.06
	Power	0.05	0.45
	Relaxed power	0.10	0.58
	Sample size	>10 000	55
Males ( <i>n</i> = 17)	<i>r</i>	0.005	0.17
	<i>P</i>	0.44	0.48
	Power	0.05	0.10
	Relaxed power	0.10	0.17
	Sample size	>10 000	359

**Note:** Tortoises were monitored during 2 consecutive years (*n* = 13 in 1997, *n* = 23 in 1998) over the whole active period (see text). Coefficient of correlation (*r*) and  $\alpha$  (*P* value) and  $\beta$  (power = 1 -  $\beta$ ) errors are given above. Relaxed power corresponds to a power calculated with an error relaxed to 0.1. The required sample size to have detected an eventual significant ( $\alpha < 0.05$ ) influence of body size is also indicated (sample size).

### Influence of body size

Body size has a significant effect on most aspects of an animal's biology. However, despite the large variations in size of the tortoises monitored (females: 15-18 cm in shell length, 807-1229 g in body mass; males: 11-15 cm in shell length, 412-667 g in body mass), we did not detect any positive correlation between home ranges, or daily displacements, and body size (Table 1). We note, however, that a correlation test has little power when the sample size is small, which was the case in all of our analyses (Table 1). In such a case, it makes sense to relax an error beyond 0.05 (i.e., 0.10) and to check if a reasonable power can be achieved. In doing this, the power of the analyses was not markedly improved in our data (Table 1). We also calculated the sample sizes that would be required to detect a "significant" effect at low  $\alpha$  and  $\beta$  error rates (0.05 and 0.10, respectively). These calculations suggest that despite the low power of the tests, body size had probably no influence on the size of the home ranges and perhaps a weak influence (in females?) on the distance covered per day by the tortoises. Finally, considering years (1997-1998) and periods (mating vs. post-mating period), further analyses of these data did not provide any additional information (all *P* > 0.1; except a positive correlation (*P* = 0.04) between home-range and body size in females, but with a low power (0.60) impeding any conclusion to be drawn). Certainly more data are necessary to detect any possible effect of size on space utilisation in the steppe tortoise.

### Discussion

Our study shows that the home range of the steppe tortoise (18 ha, using the MCP method) is noticeably large when compared with that of other Testudinidae species; all of which have a home range of only a few hectares (Rose and Judd 1975; Bertram 1979; McRae et al. 1981; Stubbs and Swingland 1984; Naulleau 1988; Calzolari and Chelazzi 1991; Diemer 1992; Smith 1995; Hailey and Coulson 1996; Huot-Daubremont 1996; Smith et al. 1997).

Large home ranges appear to characterise the larger Testudinidae species (e.g., *Geochelone* (Hailey and Coulson

1996; Smith et al. 1999)), as well as the desert species (e.g., *Testudo kleinmannii* (Geffen and Mendelssohn 1988) and *Gopherus agassizii* (Burge 1977; Barret 1990; O'Connor et al. 1994; this study)). A large home range of desert-dwelling tortoises may reflect the paucity of feeding resources (Geffen and Mendelssohn 1988).

### Males intensively patrol their territory

The male steppe tortoises exhibit a typical pattern of activity during their short 3-month activity period. Almost immediately after winter emergence, they are highly mobile and 70% of their active time during the day is spent devoted to prospecting for mates, some form of sexual activity (courtship, mating) and male-to-male agonistic behaviours (Lagarde et al. 2002). The male is therefore highly mobile during the mating period and covers a much greater distance compared with the female (Fig. 2). As a result, they patrol a large territory, moving back and forth, and rapidly saturate their home range (Fig. 3). Hence, a body of data suggest that during the mating season, males intensively patrol and vigorously defend their territory to maximise the number of matings that they can obtain during the brief favourable period.

During the post-mating period, 30% of their daily activity is devoted to foraging, and virtually all sexual activity ceases (Lagarde et al. 2002). The result is a marked decrease of locomotor activity and a reduction in their home range. Such a shift has been documented in many other species (Chelazzi and Francisci 1979; McRae et al. 1981; Geffen and Mendelssohn 1988; Calzolari and Chelazzi 1991; Diemer 1992; O'Connor et al. 1994; Diaz-Paniagua et al. 1995; Weatherby 1995; Jones 1996).

### Why do females exhibit such large home ranges?

Female steppe tortoises have a much larger home range than that of their conspecific males. This result held true throughout the 2 years of the study and in every period of activity under focus. It should be noted here that our method of recording the movements most likely underestimates the distance travelled by the tortoises. Using only one fix per day, the zigzag trips of males are more sensitive to the loss of information than are the relatively straight trips exhib-

ited by the females. Thus, more frequent monitoring should reveal an even greater difference between the sexes with regard to their locomotor activity than is reported here (Bon-net et al. 2001).

However, even during the brief and very intense mating period, females prospected larger surface areas than did males. The larger body size of females relative to males cannot explain the sex difference in their respective home range; in-deed, we did not detect any body-size effect on the area prospected by these tortoises. Therefore, the space utilisation pattern undertaken by the females seems puzzling and we can only propose a set of nonexclusive hypotheses relating to three different kinds of resources.

Firstly, the high-energy requirements for the production of eggs plus the larger body size of the females probably require the females to forage more than the males. Nevertheless, we estimated that the biomass (expressed as dry matter) represented by the plants upon which tortoises feed is ~700-900 kg/ha and that a typical 1-kg tortoise consumes roughly 400-700 g per active season (Lagarde et al. 2003). Given a density of 5 tortoises/ha, food availability is clearly high enough for the tortoises to avoid travelling long distances in a purely energetic perspective. Perhaps reproductive females have to prospect a large area to cover special dietary requirements (e.g., vitamins, minerals, etc.).

Secondly, the very large home ranges of the females during the mating period overlap many males' territories, suggesting that the females may be "gene shopping" in order to optimise possible sperm competition. Sperm storage in females' genital ducts is very common in tortoises and turtles (Gist and Jones 1989; Brown and Brooks 1993), providing ample possibilities for sperm competition to occur (Schuett and Gillingham 1986; Stille et al. 1986; Barry et al. 1992; Galbraith 1993; Galbraith et al. 1993). Multiple paternity may enhance female fitness, as it has been documented in other reptiles (Loman et al. 1988; Madsen et al. 1992).

Thirdly, the very large home ranges of the females during the post-mating period may result from the dispersion of suitable nesting areas and (or) may be due to a strategy of predation risk reduction (Wilbur and Morin 1988). A steppe tortoise lays an average of three clutches per year, and the time elapsed between each clutch is approximately 15 days (Henen et al. 1999).

### Conclusion and perspectives

*Testudo horsfieldi* show marked sexual differences in home ranges and daily movements. The home ranges of the females were much larger than those of the males. A closer examination revealed that although the males are more mobile than the females during the mating season, their directional movements are such that they patrol a more limited territory than do females. Males probably optimise their fit-ness through an intensive locomotor activity during the mating season. However, the very long trips undertaken by the females throughout the activity period are more puzzling, suggesting a need for further investigations on mating behaviour, sexual selection, nest selection, and feeding ecology to clearly understand such sexual divergences in space utilisation pattern in steppe tortoises.

### Acknowledgements

Financial support was provided by PICS (International Program for Scientific Collaboration between Uzbekistan and France, No. 266), granted by the French CNRS, and the Ministère des Affaires Étrangères. Additional funds were provided by the French Embassy of Tashkent and SOPTOM (Gonfaron, France). Grants for K.A. Nagy and fellowships for B.T. Henen (Friends of the National Zoo and Visiting Scientist for the Smithsonian Institution) enhanced their contributions to this project. We also thank Antoine Sempéré, Goulom Djoumaiev, Aziz Kasimov, Paul Carpentier, Karim Bahloul, the IFEAC, and the "Conseil Général des Deux Sèvres" for logistical help and Felicity Bradshaw for great assistance with the manuscript.

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