

Gender Differences in Seasonal Movement of Dice Snakes in Histria, Southeastern Romania

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Abstract. An archaeological excavation site among ancient ruins in Histria, south-eastern Romania, that harbours several thousand dice snakes (*Natrix tessellata*), is the focus of various ongoing studies. The current work evaluates seasonal variation of gender specific movements. Seasonal movements were estimated from captures of adult snakes over four years. Visible abundance of snakes among the ruins was largest in early spring and autumn. Summed over one entire season, the capture rates were similar for both sexes. During April males were more frequently captured than females. However, the proportion of males decreased later during the mating period in spring and until the end of June, only to rise again in August. Capture rates of gravid females continued to remain high in the vicinity of the ruins throughout vitellogenesis until ovulation, for which they mainly stayed near the hibernation area, which is also favoured for ovipositing. At the onset of hibernation in October, the ratio of males to females was consistently 0.4 across all years of study. We suggest that the skewed sex ratio among captures is due to gender-specific behaviours rather than to a naturally uneven sex ratio or capture artefacts. Males generally emerge earlier from hibernation in order to maximize their chances to reproduce. Consistent with our data, we suggest that in autumn males may be entering hibernation dens over a longer period than do females. Arguably, males do not have the same energy requirements as females, which could be expected to exploit the feeding season maximally, due to their higher-energy reproductive investment.

Key words. Squamata, *Natrix tessellata*, dice snake, seasonal movements, activity patterns, sex ratio

Introduction

Movement in animals over different seasons has been studied across a wide range of taxa, e.g. birds (BOISVERT et al. 2005), mammals (TIERSON et al. 1985, BEST & SCHELL 1996), fishes (LUCAS & BATLEY 1996), insects (BISHOP 1995), reptiles and amphibians (PHELPS 1978, PLUTO & BELLIS 1988, PILLIOD et al. 2002). Several studies of snake migration and dispersal patterns have been conducted (e.g. BONNET et al. 1999, KEOGH et al. 2007, DUBEY et al. 2008), as well as studies of seasonal movements (e.g. VIITANEN 1967, MADSEN 1984, DURNER & GATES 1993, BRITO 2003, GERALD et al. 2006, ROTH et al. 2006). GIBBONS & SEMLITSCH (1987) distinguish between two different seasonal activity patterns in temperate snake species: (1) A unimodal peak of activity, usually in the summer or (2) a bimodal activity pattern with peaks in spring and autumn. Several species of snakes show a bimodal activity pattern with reduced activity in summers following the spring mating, e.g. the natricine *Thamnophis radix* and *Rhabdophis tigrinus* (GIBBONS & SEMLITSCH 1987). During autumn, the snakes' activity, respectively its detectability, increases again prior to the onset of hibernation. Autumn movements around the hibernacula are similar to those observed in early spring (GIBBONS & SEMLITSCH 1987). Autumn matings also occur occasionally in some species of water snakes, e.g. *Thamnophis sirtalis* (SCHWARTZ et al. 1989), *Nerodia harteri paucimaculata* (GREENE et al. 1999), *Natrix maura* (SANTOS & LLORENTE 2001), and have also been

documented for *Natrix tessellata* (GRUSCHWITZ et al. 1999, STREET 1979).

The majority of studies on spatial movements in snakes point towards a higher activity in the male gender, especially during the mating period (e.g. VIITANEN 1967, MADSEN 1984, SHINE et al. 2001a, PEARSON et al. 2005). In addition to being more active, males generally move longer distances than females to actively search for females in the mating season (VIITANEN 1967, PHELPS 1978, WEATHERHEAD & PRIOR 1992, GRUSCHWITZ et al. 1999, KEOGH et al. 2007). However, males of *T. sirtalis* remain at the hibernation site for a long period to mate, whereas females emerge later and disperse directly after mating (GREGORY 1974, SHINE et al. 2001a). The females move also farther away from the hibernation area than males (SHINE et al. 2001a). A higher activity is also indicated in female pythons of *Morelia spilota imbricata* which have larger annual home ranges than males (PEARSON et al. 2005). Other studies have also suggested that females are more mobile than males, but later in the season, e.g. during the summer in *Natrix natrix* (MADSEN 1984). PARKER & PLUMMER (1987) suggested the reasons lie in sexual differences of habitat preferences or foraging behaviour.

Several studies have shown that snakes of both or either sex move to a feeding habitat at a certain time of the year (SHINE et al. 2001a, SUN et al. 2001, ROTH et al. 2006). For example, in the adder *Vipera berus* in Finland, only males and non-gravid females move to a summer feeding habitat, whereas gravid females remain

at or near the hibernation area (VIITANEN 1967). Furthermore, gravid females of *Natrix natrix* are less mobile than males (MADSEN 1984). We hypothesize that there is a gender difference in seasonal movements also in *N. tessellata*.

Natrix tessellata is threatened by habitat destruction and water pollution across many areas of its distribution in Europe (NECAS et al. 1997). The population investigated herein is considered to have been substantially larger in the past (A. SUCEVEANU, pers. comm.), although thousands of *N. tessellata* still utilize the ruins for hibernation and oviposition (CARLSSON et al. 2011, Fig. 1). The excavated stonewalls likely provide suitable sites for thermoregulation and protection from predators in addition to being sites for oviposition in summer and hibernation in winter.

Relatively few investigations have been conducted about the ecology and life history of *Natrix tessellata* (reviewed in MEBERT 2011). As far as we are aware, large scale studies of *N. tessellata* involving thousands of individual captures have not been published before except for one study in central Italy (LUISELLI et al. 2007, CAPULA et al. 2011). Although studies of movement patterns of snakes are preferably performed using methods of

radio-telemetry (e.g. MADSEN 1984, WEATHERHEAD & PRIOR 1992, SHINE et al. 2001a), including *N. tessellata* (CONELLI & NEMBRINI 2007, CONELLI et al. 2011, NEUMANN & MEBERT 2011, VELENSKÝ et al. 2011), we believe that the large sample size of the current research allows for elucidating gender-specific patterns of movement by analyzing capture rates.

Material and Methods

The study area is located in the southeast of Romania (44° 54' N, 28° 77' E) approximately 40 km north of Constanța, situated at the shore of brackish Lake Sinoe, which is connected to the Black Sea. Adjacent to the lake lie the excavated ruins of Histria, encompassing seven hectares of house ruins, stonewalls and stone paved streets among unexcavated areas of meadows with grass and angiosperms (see pictures and map in CARLSSON et al. 2011).

Field research was conducted from April to July 2005, from March to October 2006 and from April to October in 2007 and 2008. Snakes were caught, marked, measured and sexed according to CARLSSON et al. (2011). The



Fig. 1. A gravid female creeps around a column in the ancient ruins in Histria. Photo: SIMON KÄRVEMO

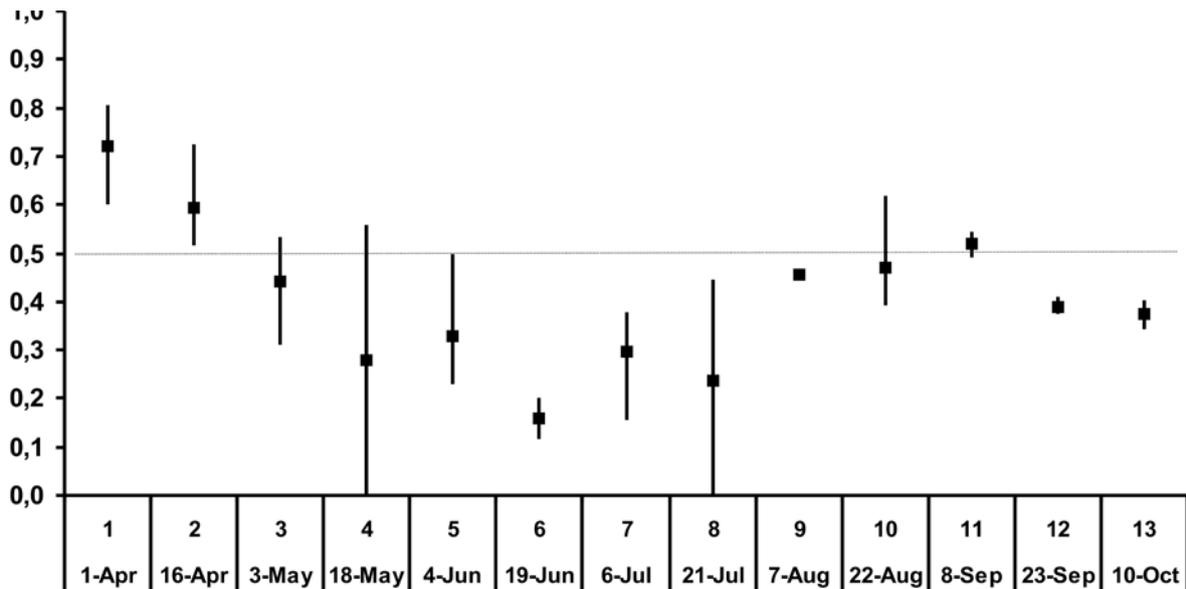


Fig. 2. The proportion of males of *Natrix tessellata* caught in Histria for each 16-day time interval (initial day indicated). Black squares show the average proportion of males for each time interval of four years of study. The vertical lines include the range of proportions. The horizontal line shows an equal sex ratio. Time intervals are explained in Table 1.

Tab. 1. Field season divided into time intervals and periods of activity to evaluate seasonal movements of *Natrix tessellata*.

Period	Activity periods	Start	End
1	Spring matings	01 Apr	16 Apr
2		17 Apr	02 May
3		03 May	18 May
4	Vitellogenesis peak	19 May	03 Jun
5		04 Jun	19 Jun
6		20 Jun	05 Jul
7	General foraging	06 Jul	21 Jul
8		22 Jul	06 Aug
9		07 Aug	22 Aug
10	Autumn matings	23 Aug	07 Sep
11		08 Sep	23 Sep
12	Onset of hibernation	24 Sep	09 Oct
13		10 Oct	25 Oct

snakes were captured by hand mainly inside the ruins and along the adjacent shoreline of Lake Sinoe. In order to compare differences in seasonal movements between the sexes of *Natrix tessellata*, the field season was divided into 13 intervals of 16 days each, spanning the same dates every year (Fig. 2). These intervals were pooled into five different periods of activity phases: (1) spring mating, (2) vitellogenesis peak, (3) general foraging, (4) autumn mating and (5) onset of hibernation (Tab.1).

Unsexed individuals, subadults and juveniles have been excluded to prevent uncertainty in gender alloca-

tion. A minimum snout vent length of 48 cm in males and 55 cm in females was applied to define adults according to LUISELLI et al. (2007). These lengths conform to our own measurements of snakes, which were either mating or contained embryos (CARLSSON et al. 2011).

Results

Throughout the four years of research 4129 individuals were adults when first captured. More snakes were caught in spring and autumn (CARLSSON et al. 2011) and show a bimodal peak of activity, i.e., an increased abundance of snakes in spring and autumn (Fig. 3). In total, significantly more males ($n = 2181$; 53%) were sampled than females ($n = 1948$; 47%) ($\chi^2 = 13.15$, 1 df, $P = 0.0003$). On an annual basis however, only snake captures from 2006 had significantly more males (1233 males and 970 females), ($\chi^2 = 31.40$, $P < 0.0001$) (Tab. 2).

Generally, the sex differences in seasonal pattern of visible abundance were relatively consistent across all years (Fig. 2). The majority of males (63% males) were captured during the spring mating period from 1 April to 18 May (Fig. 2, Tab. 3), i.e., with three of four years yielding a significant difference, whereas females were usually more often encountered (68% females) during the periods of vitellogenesis peaks and general foraging, from 19 May to 22 August, also significant in three of four years for both periods, respectively (Tab. 3). The frequency of males per period fell to a minimum of 0.2 at the end of June and beginning of July (interval 6), which was consistent over the years (Fig. 2). Capture ratios remained biased towards females until the beginning of autumn matings (intervals 10–11) at the end of

Tab. 2. The total number of snakes caught; separated by sex and year.

	Sex	<i>n</i>	%	X ²	P
2005	M	326	50%	0.03	0.8751
	F	322	50%		
	Total	648			
2006	M	1233	56%	31.40	>0.0001
	F	970	44%		
	Total	2203			
2007	M	222	45%	4.32	0.0377
	F	268	55%		
	Total	490			
2008	M	404	51%	0.51	0.4762
	F	384	49%		
	Total	788			

August, when gender differences were equal for all years of sufficiently collected data (Fig. 2 and Tab. 3). Later in October (intervals 12 and 13) the frequency of males dropped to a stable ratio of 0.4 (Fig. 2), i.e., significantly more females were visible towards the end of the active season (Tab. 3).

Discussion

Seasonal variation in movement patterns is common in many species of snakes (e.g. MADSEN 1984, GREGORY et al. 1987, SHINE et al. 2001a, BRITO 2003). This study provides comprehensive data of seasonal differences of the activity pattern in a population of *Natrix tessellata* from Histria. This population shows a bimodal spring/autumn peak of activity, with the majority of snakes being observed in spring when all snakes exit hibernation and most matings occur, as well as in autumn with their return to the hibernation sites. The low frequency of captures of both sexes during the summers may not only be an effect of the absence of snakes in the immediate proximity to the hibernation site, but possibly also due to low activity and even subterranean aestivation (see e.g. BROWN & WEATHERHEAD (2000)).

There are established activity differences between males and females in the literature. For *N. tessellata* and many other species of snakes in the temperate zone, males are often observed to exit hibernation prior to females (SEIGEL & FORD 1987), and remain near the hibernation site in order to reproduce with females as they emerge (PHELPS 1978, GARSTKA et al. 1982). As in some other natricine taxa, e.g. *Thamnophis sirtalis* (ALEKSIUK & GREGORY 1974) and *N. maura* (SANTOS & LLORENTE 2001), the maturation of the spermatozoa and follicles in *N. tessellata* occur in the late summer or fall, prior to entering the hibernation, i.e., postnuptial spermat-

ogenesis and vitellogenesis increases (SEIGEL & FORD 1987, BENDEL 2001). In some other species of temperate snakes, e.g. *Vipera berus* (VIITANEN 1967, NILSON 1980), males emerge in advance of females to bask and complete spermatogenesis prior to the mating season. At our study site matings were observed just after emergence from hibernation (e.g. 30 March 2006) and we suggest that here too, male *N. tessellata* generally emerge earlier from hibernation than females to maximize their reproductive success by increasing their chances to encounter reproductive females, which is consistent with our observations of a male predominance among captures in early spring (at least 72% during interval 1, Figs. 2 and 4.). The same pattern has previously been recorded for other temperate natricine species, such as *N. natrix* (MADSEN 1984), and SHINE et al. (2001b) observed 75% of Canadian *T. sirtalis* being males during early spring. A higher frequency of males than females after emergence from hibernation has been observed in *N. tessellata* elsewhere (GRUSCHWITZ et al. 1999, MEBERT 2001, 2007) with the exception of a population in Germany (LENZ & GRUSCHWITZ 1993a).

Females of *N. tessellata* differ in reproductive traits in comparison to males, in that females have a later reproductive age (ZIMMERMANN & FACHBACH 1996) and a large proportion might not mate every year (LUISELLI & ZIMMERMANN 1997). Consequently, females may opt to leave the hibernation site directly after emergence, if non-reproductive, or shortly after mating if reproductive (e.g. SHINE et al. 2001a). We suggest that the rapid spring movements of females away from the hibernation site occur as a result of: (1) avoidance of courting males due to increased energy costs and interference with feeding and basking (ALDRIDGE et al. 2005 and references therein), (2) the high predation risk where many snakes are aggregated (GREGORY et al. 1987), and (3) movements in order to initiate foraging in the nearby lake. If so, males should be more likely to be encountered around the hibernation area than females, where they remain active and exposed. Indeed, almost half (2023 individuals) of all snakes in this study were caught during April (intervals 1 and 2), of which 66 % (1330) were males.

Later in the mating season, from May until June, the proportion of males decreases (intervals 3–6). This is probably caused by male movements to summer foraging habitats in adjacent lakes, whereas gravid females remain in the vicinity of the ruins to thermoregulate and forage in the nearby lake during their vitellogenesis peak (Figs. 2, 4, 5). According to our data, end of June to early July is the period of ovipositing in this population. This is also the time when the males are least visible, with a consistent proportion of 0.2 for all study years (Fig. 2). Thermoregulatory activities and search for suitable ovipositing sites might increase the visibility of females and, hence, their detectability (MADSEN 1987). In addition, large numbers of males may be absent, because they have moved to foraging habitats or simply remain

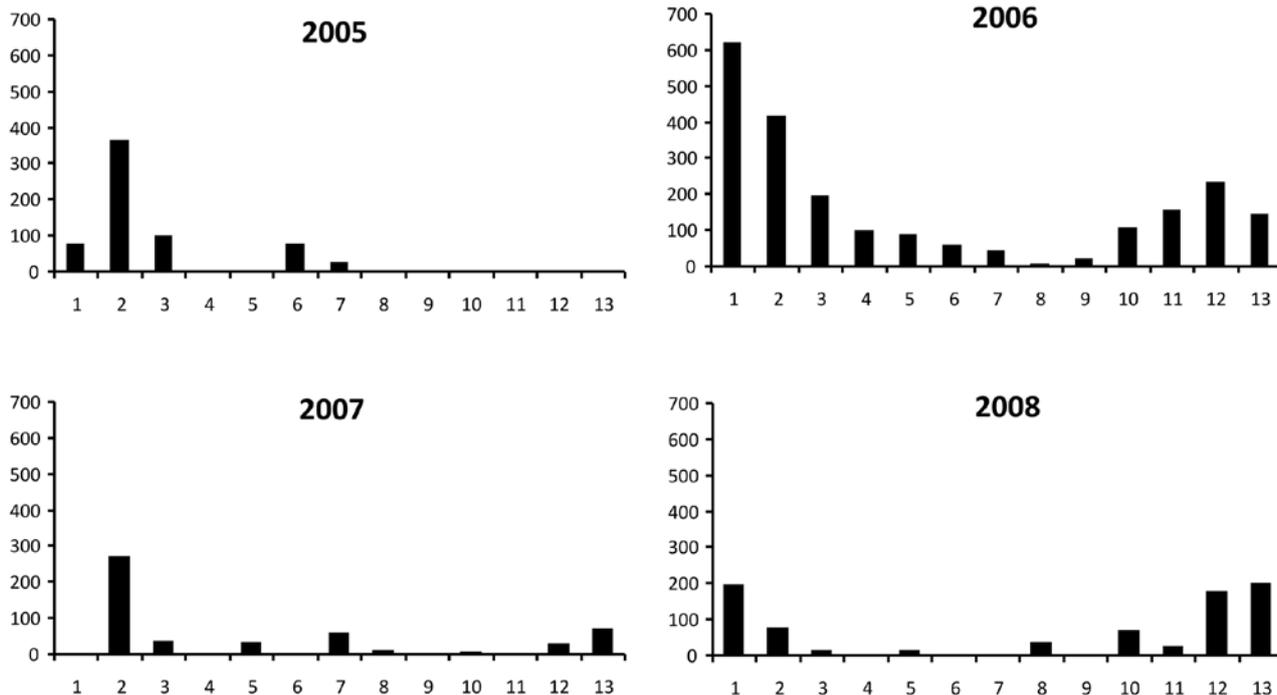


Fig. 3. Total number of *Natrix tessellata* caught during each interval and year. Missing bars indicate intervals without fieldwork. The periods on the x-axis are explained in Tab.1.

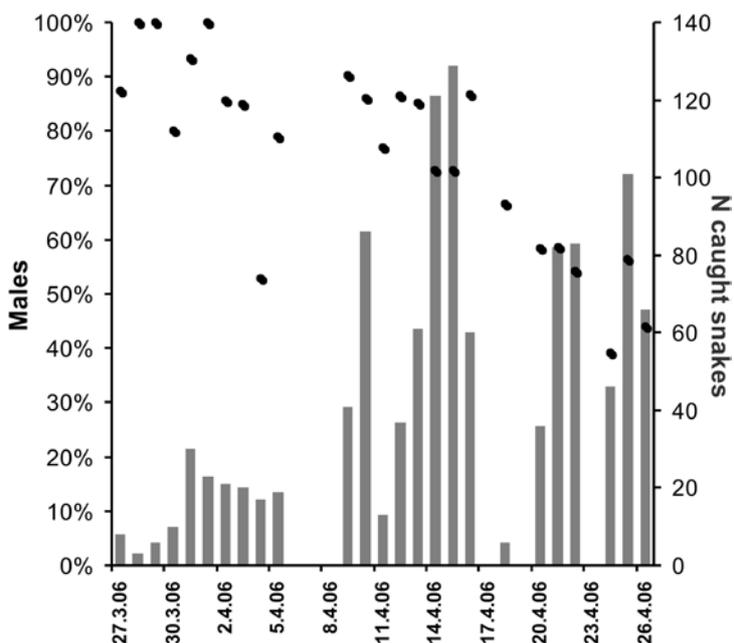


Fig. 4. The daily percentage of males (dots) and the total number of snakes caught (bars) during the periods of emergence from hibernation and mating, late March to late April in 2006 (the year of the most extensive field work).

elsewhere (PRESTT 1971, VELENSKÝ et al. 2011). A presumed proximal cue for the initiation of autumn activity is suggested by GIBBONS & SEMLITSCH (2001); "...movement to winter denning areas presumably occurs during the late summer or autumn in response to photoperiod regardless of environmental temperatures..."

The sex ratio for all data combined is close to a 1:1 ratio (53% males and 47% females). The slightly higher

proportion of males might result from the majority of snakes being captured in spring, when more males are encountered. We presume that the proportion of males would increase further if the field work had started earlier in the spring (see below). GRUSCHWITZ (1986) determined a sex ratio of 71% females and 29% males in a German population of *N. tessellata*. This highly unbalanced sex ratio is difficult to explain, although differ-



Fig. 5. A dice snake in July 2006 with a syrman goby (*Neogobius syrman*) from the lake Sinoe, Histria. Photo: SIMON KÄRVEMO

ences in observed sex-ratios of snakes vary considerably between years (PARKER & PLUMMER 1987). A later study of the same *N. tessellata* population showed a more balanced sex ratio (LENZ & GRUSCHWITZ 1993b), supporting the conclusions of PARKER & PLUMMER (1987). Variations in captures of males and females between different investigations are not surprising, given that sex ratios in snakes can differ depending on the season or in what habitat the collections are performed (PARKER & PLUMMER 1987). However, we cannot exclude that the observed total sex ratio for all years combined in the Histria population (53% males to 47% females) indeed corresponds to a factual skew in the sex-ratio. Nevertheless, until more information is available, we consider the observed annual fluctuations of the sex-ratio and the slight skew overall to be artefacts from fluctuating field-work success (CARLSSON et al. 2011).

The consistently larger proportion of females captured (0.6 females to 0.4 males, Fig. 2) in late September and early October for all years deserves some attention. During this period snakes are almost exclusively encountered in the immediate surroundings of the actual hibernation dens. As all snakes must hibernate, it is reasonable to assume a balanced sex ratio. The consist-

ent between-years difference in the sex ratio of captured snakes towards the end of the season may be a result of unequal capture probability at the hibernation site. It can be argued that females are more likely to be captured than males during this time of year. Females are generally larger in size and arguably easier to spot and catch for a field worker. If so, the proportion of males might have been underestimated to some extent throughout the study. This rationale, however, is in contrast to findings in a North American natricine species. It has been shown that females of the Northern watersnake, *Nerodia sipedon*, have a greater flight propensity (flight initiation distance) than males and juveniles when approached by a human (COOPER et al. 2008). This might suggest that adult males are easier to catch than females. Naturally, the results from the Northern water snake do not necessarily apply to *Natrix tessellata*, as it is a different species with a potentially different behavioural repertoire. But if sex does affect flight propensity, we should expect a reversed gender specific capture ratio to that observed here. The overall skew in observed sex ratio for all years combined, does allow for the possibility of males being easier to catch than females, especially given that big snakes are predominantly females. In contrast, the

consistently reversed and much more pronounced skew during autumn appears not as artefactual, but in need of some biological explanation. Several explanations for finding a larger proportion of females in autumn have been proposed: (1) females have finished their oviposition and are more active when not gravid (GREGORY et al. 1987). (2) Females may initiate hibernation one or two weeks before males (LENZ & GRUSCHWITZ 1993b). Consequently females could have a larger probability to get caught earlier in the autumn compared to males. This implies that a large proportion of late males may have been missed in our study. Finally, (3) females may linger at the hibernation site, and exploit opportunities to bask, as thermoregulation may be more important for the females' next reproductive investment than the males' spermatogenesis (BONA-GALLO & LICHT 1983). In a study about the reproductive cycles in female *N. tessellata*, BENDEL (2001) suggested that their annual reproductive investment continues in August with the follicular maturation. With any of the three explanations listed above being true, one arguably would expect to encounter more females than males in late autumn, especially in sunny weather. Because, field work was terminated before the end of October, we can not fully assess the second explanation, whether more males than females enter hibernation later in October or early November. However, field work was conducted until about two weeks after the last foraging snakes were observed and we consider it unlikely that we would have missed enough males to account for the skewed sex ratio in late autumn. Time constraints have precluded fieldwork until the very end of snake activity. Yet, data and observations from subsequent years suggest that although the sex ratio tends to become equalised in late October, less snakes are also encountered in late October –early November compared to early-mid October (M. CARLSSON unpublished, M. TUDOR pers. obs.). We believe our data fits a combination of explanations 1 and 3 above. Females may remain active longer and exploit basking opportunities to a higher extent than do males. Further, given lower metabolic requirements than females, males may be entering hibernation over a longer period, at a low but steady rate, starting already in August. This hypothesis rests on the premise that females experience a greater need than males to maximize their food intake in order to recover from the energy drain of pregnancy, prepare for reproduction the following year or simply to maximize growth. Thus, we expect that at the time when foraging activity in the water had ceased and hibernation could no longer be postponed, more females than males should be expected to enter into hibernation.

In conclusion, our results show that *Natrix tessellata* has two seasonal peaks of activity around the hibernation area, one in spring and one in autumn. In addition, our study suggests that there is a gender difference in activity and movements of *N. tessellata*. In early spring, males leave the hibernation prior to females to maximize the mating success. They remain near the hibernation site for several weeks before moving to foraging

habitats. The females, however, leave the area after mating, but remain in the vicinity for oviposition and thermoregulation. During summer foraging, males may disperse farther than pregnant females or aestivate, given their lower energy requirements. Towards the end of summer an increase of males encountered may be due to autumn mating activity and/or a male-biased early retreat into hibernation, leaving females to be the more frequently encountered gender in September and October.

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