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Population Structure and Activity Pattern in a Dalmatian Tortoise (*Testudo hermanni hercegovinensis*) Population

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Zusammenfassung

Während westliche Populationen von *Testudo hermanni* gut untersucht sind, gibt es vergleichsweise wenig Studien über jene der Balkanländer. Um mehr über die Populationsstruktur und die Aktivitätsmuster von *Testudo hermanni hercegovinensis*, einer Unterart, welche entlang der Küste von Montenegro, Kroatien und Bosnien und Herzegowina vorkommt, zu erfahren, konzentriert sich unsere Studie auf geschlechts- und altersspezifische Unterschiede der Körpergröße (SCL) und der Verhaltensmuster dieser Population. Im Mai 2014 und 2015 wurden Daten von insgesamt 500 wildlebenden Tieren gesammelt, welche in einem ±1,5 km² großen Untersuchungsgebiet gefunden und markiert wurden. Die Zahl der gefundenen Weibchen war etwa doppelt so hoch wie die der Männchen, weshalb das Geschlechterverhältnis bei 2,06 liegt. Individuen beider Geschlechter waren im Durchschnitt größer als aufgrund bisheriger Studien erwartet. Männchen waren durchschnittlich 2,49 cm kleiner als Weibchen und zeigten einen signifikanten Zusammenhang zwischen Größe und Mobilität. Während die Größenverteilung der Weibchen zeigte, dass die meisten von ihnen groß waren, zeigte jene der Männchen, dass diese meist mittelgroß waren. Dies könnte auf einen Kompromiss zwischen Beweglichkeit, intra- und interspezifischer Konkurrenz, Prädation und Metabolismus hindeutet. Die untersuchten Verhaltensmuster der Tiere, wie sonnen, ruhen, fressen oder in Bewegung waren nicht gleichmäßig über den Tag verteilt. Inaktives Verhalten (sonnen, ruhen) dominierte deutlich mit 60-80% der täglichen Beobachtungszeit. Es wurden keine signifikanten Unterschiede zwischen Männchen, Weibchen und Jungtieren bezogen auf ihre Verhaltensmuster festgestellt, mit einer Ausnahme, dass juvenile Schildkröten sich signifikant öfter sonnen als adulte. Dies könnte thermoregulatorische Gründe haben.

Abstract

Only a few field studies of *Testudo hermanni hercegovinensis*, a subspecies of *Testudo hermanni*, have been carried out so far. In order to learn about the population structure and daily activity patterns of this species, we focused on sex and age specific differences in body size and behaviour. In May 2014 and 2015 we collected data of 500 individuals within a study area sized ±1.5 km² near Dazlina/Croatia. In contrast to other studies, the sex ratio was strongly female-biased (2.06) and individuals of both sexes were in general larger than expected. Males were on average 2.49 cm smaller than females and showed a significant relationship between size and mobility. They also were mostly medium-sized, which indicates that there might be a compromise between mobility, inter- and intraspecific competition, predation and metabolism. Females, on the other hand, were mostly large-sized. Regarding activity patterns, we observed that behaviour types such as basking, resting, moving or foraging were not evenly distributed throughout the day. We found that inactive behaviour dominated with 60 - 80% of the daily observation hours. With the exception of basking which was most frequent in juveniles, no significant activity differences between males, females and juveniles were found.

Introduction

Population composition and demography depends on a variety of factors including ecological ones (Fahrig & Paloheimo, 1988), inter- and intraspecific competition (Lin & Batzli, 2001) (Waser, 1985), predation or parasites (Cramer & Cameron, 2006) (Schwanz et. al 2010) (Barbault 1988). One important parameter shaping but also depending on demographic traits like population growth or density, sex ratio, or age composition is body size. Thus body size is a very important life history parameter of organisms (Angiletta et. al, 2004) and body size relations being representative for other aspects of an animals biology like morphology, speed, respiratory or metabolic rate. Demographic traits and body size vary between homeotherms and ectotherms (Gillooly et. al, 2001). An important factor in relation to body size (mass) is gravity, particularly in individuals following a terrestrial lifestyle (Berry & Shine, 1980).

In turtles and tortoises, a huge diversity in body size (Jaffe et al., 2011) and life histories (Willemsen & Hailey, 2000) was found with the smallest species, *Homopus signatus*, sized about 8 to 10 cm (Loehr et al., 2004) and the largest living species, *Dermochelys coriacea*, showing an SCL (straight-line carapace length) of 130 to 170 cm (Zug & Parham, 1996), whereas prehistoric species such as *Archelon ischyros* grew up to a size of 4.6 m (Jaffe et al., 2011).

Besides a general difference between terrestrial and aquatic species as well as species-specific deviations, body size can also differ between sexes. A sexual size dimorphism can be observed, which also, according to Berry and Shine (1980), correlates with the habitat conditions of a species. Their study suggests that males in Testudines are larger than females, when it is important for them to be successful in male-male competition over female fertilization and to coerce females into copulations. Nevertheless, males tend to be smaller than females, when it is essential to find females and having less to deal with male-male competition, because a smaller size facilitates mobility. Thus, sexual size dimorphism is a good indicator for sexual competition and reproductive strategy in a given population.

In comparison with the larger nominate form, both sexes in the Dalmatian tortoise show a small to medium body size (Fritz et al., 2006) with females being bigger than males (Fasola et. al 2002) (Vetter, 2006). Rogner (2012) found a maximum SCL of 17 cm in females and of 14.8 cm in males.

Schweiger (2006) suggests that the smaller body size in *T. hermanni hercegovinensis* might be artificially biased and not a result of evolutionary processes. He believes that intensive collecting of large sized individuals by pet traders during the 1970s and 1980s might have diminished the actual sexual dimorphism of this species. Occasionally, larger individuals were found, which indicates that this suggestion is worth considering.

Seventeen populations of nominate *T. hermanni* were studied in Greece by Willemsen and Hailey (1999), which resulted in the conclusion that females of *T. hermanni* are always larger in size than males. Just like Fasola et al. (2002) they also discovered that populations native to cooler regions showed a larger body size than populations in warmer areas. This interestingly corresponds to Bergmann‘s rule, which suggests that endothermic individuals tend to be larger

in cooler landscapes, due to better heat conservation and it matches the results of Ashton & Feldman (2003), which postulates that many ectotherms follow the reverse Bergmann's rule, although turtles and tortoises do not for thermoregulatory reasons.

In previous studies on *T. hermanni* a slightly male-biased sex ratio (1.33 males per female) was recorded in Croatia (Vetter, 2006), therefore, we suspected a similar sex ratio of *T. hermanni hercegovinesis* within our study area.
A male-biased sex ratio might be a consequence of an increased need of mobility in males. During spring and early summer (reproductive period), males are constantly searching for mating partners and are therefore more active and mobile (Rogner, 2012) (Calzolai & Chelazzi, 1991). However, Hailey (1989) discovered that females in *T. hermanni* showed more activity (movements) during the day than males, but with variation between months.

The diurnal activity pattern in *T. hermanni* is set by sunrise and sunset (Vetter, 2006) and to season of the year (Fasola et al., 2002) (Rogner, 2012). One of the most crucial behaviours detected for tortoises is basking. After basking in the morning sun to reach a body temperature of about 29-30 °C (Vetter, 2006), they start moving around, most likely to look for food and in spring, males additionally search for mating partners.

In Greece, activity (movements) varied seasonally between 4.8 h a day during May/June and only 0.4 h in November (Cheylan, 2001). Fasola et al. (2002) found, that in terms of the daily time budget, basking is with 70 % the most time consuming activity, which prevailed more or less constant over the eight month-study (Vetter, 2006). As soon as the temperature rises in spring, activity increases, with a peak of movement and foraging in May (Rogner, 2012) (Vetter, 2006).
In spring, the daily activity peak was around 9 am and decreased towards noon. Individuals hide in shrubs, as soon as temperatures rise above 26.4 ± 8.6 °C (Vetter, 2006) or the sun does not reach the soil anymore in the late afternoon (Rogner, 2012). During the hot summer months, they are only active from around 7-10 am and again from 3-5 pm, with a long break at noon to avoid the midday sun (Vetter, 2006). Based on these previously conducted studies, we predict similar activity patterns within our study area.

Since studies of wild populations of *T. hermanni* in the Balkan area are still quite rare (Djurakíc et. al, 2011) our study focused on *T. hermanni hercegovinensis*, which shows the northern most habitats of tortoise distribution in Europe and was known to occur in a reasonable density in the study area.

In order to study local adaptations and distributions in body size, daily activity patterns and differences in age and sex, in comparison to life history data of the nominate Hermann's tortoise *T. hermanni*, the Dalmatian tortoise (*T. hermanni hercegovinensis*), was studied in its natural environment and distribution during spring, in which the species is most active.
Besides being ectothermic, tortoises are an ideal model species because they have a rather small home range, are slow moving and hence easy to find and handle.

Material and Methods

Study species

The Dalmatian Tortoise *Testudo hermanni hercegovinensis* occurs along the coast of Bosnia and Herzegovina, Croatia as well as Montenegro and is a subspecies of the Hermann's Tortoise (*Testudo hermanni*) (Vetter, 2006). It is characterized by a yellowish-green colour (Rogner, 2012) as well as by the lack of inguinal scutes and bright spots on the back of its head (Wegehaupt, 2005), which makes it distinguishable from other subspecies (Perälä, 2002). Furthermore, in *Testudo hermanni*, supracaudal scutes are usually divided (Amiranashvili, 2000). Both males and females of the Dalmatian tortoise show a small to medium body size (Fritz et al., 2006) with males usually not growing bigger than 14.8 cm (Rogner, 2012).

Study site

Data were collected in May 2014 and 2015 in an area of approximately 1,5 km2 near Dazlina (Fig. 2), a small village in coastal Croatia south of Zadar. A big part of the area is used for extensive farming, the rest of the land is unused.

Fig.1a: The typical landscape of the study area shows olive groves (upper left), grassland with shrubs (upper right), fields (lower left) and Macchia (lower right). ©Karoline Bürger

The small-scaled landscape mostly contains small fields, grassland with shrubs and hedges, macchia, olive groves and vineyards (Fig.1a). Additionally, at least five ponds are situated within the area as well as many scattered stonewalls. Unsealed field paths can be found throughout the whole study area. The hardly managed grassland is occasionally grazed by sheep and goats. The area shows Mediterranean climate with hot and dry summers. The breeding season starts as soon as the amount of rain decreases in late April or May (Fig.1b).

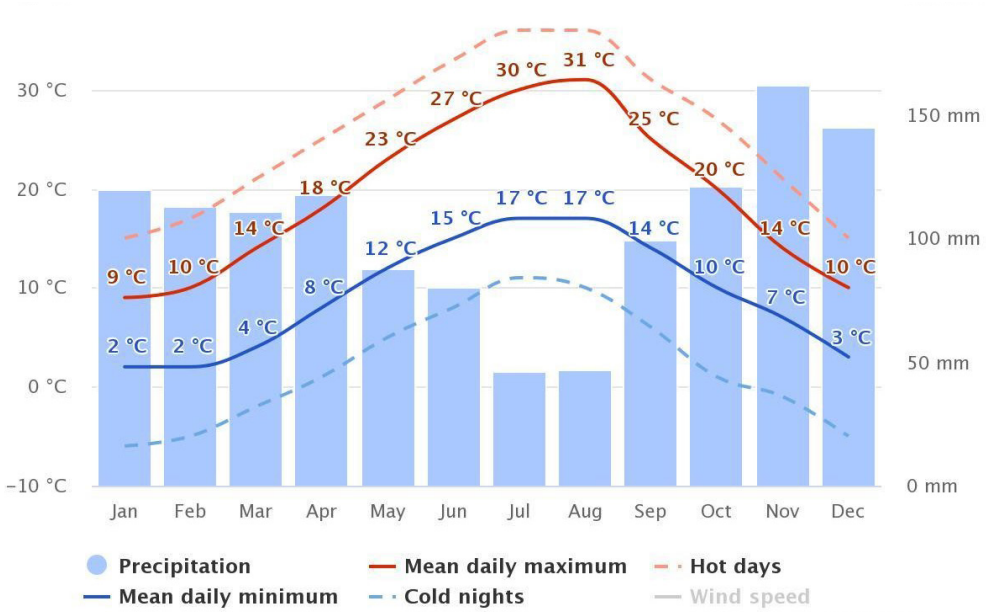

Fig.1b: Climate graph for the study area in Croatia based on 30-year global history with hourly weather data derived from the global NEMS weather model at 30 km resolution collected at Dazlina. ©www.meteoblue.com

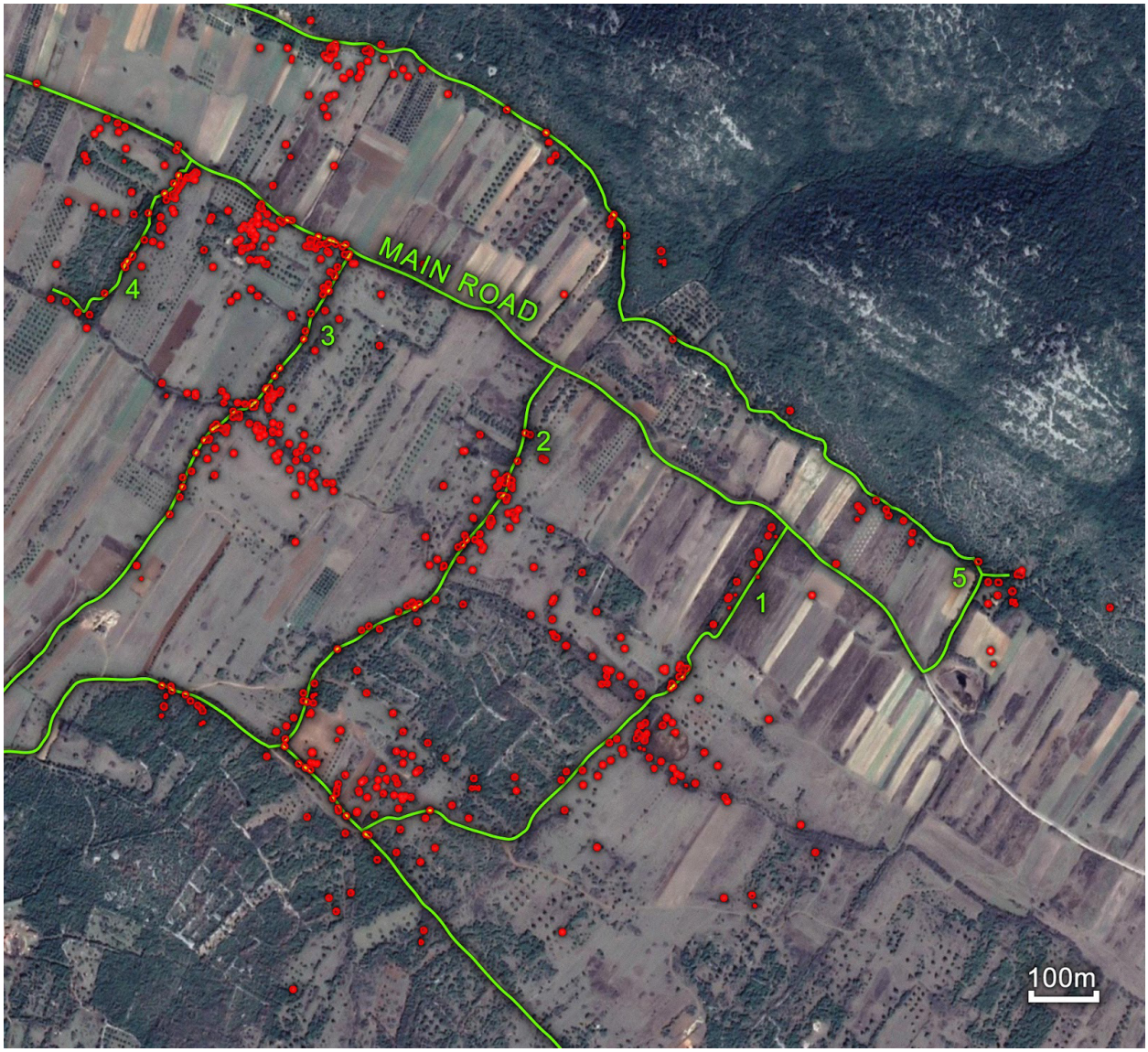

Fig 2: Overview of the study area, sized about 1.5 km², near Dazlina, Croatia. Every dot represents one individual, which was marked at the finding site with a GPS point.

Methods to determine number, density and distribution of tortoises

In order to achieve comparable data, searching effort was evenly distributed within the study area. The method used was transect sampling. This was done usually by two, sometimes three or four people in parallel in a distance of around 20 m. Each person scanned an area of about 10 m to the left and to the right. The scanned distance and hence distance between observers differed depending on the habitat. The distance covered per observer was longer for open habitats e.g. meadows, open fields with bare ground or vine yards) but much shorter (5 m or less) e.g. with dense vegetation cover like the macchia. The whole study plot was therefore scanned in a stratified manner namely according to habitat (fields, orchards, meadows etc.). Thus during transect sampling one field was finished before moving on to the next adjacent spot, which could be the same (the next field) or a different habitat (e.g. a meadow). In this way, the whole study area was scanned for individuals and when finished, transect sampling started over again. During the observation period of each year, the whole area was scanned at least ten times. To finish the whole study site took about three days but varied depending on the observers involved and/or weather conditions. For each run (one completed transect for the whole study plot) the stratified field sites were randomly selected to avoid a bias in the observation time and hence circadian information gathered.

Five pathways of the local farmers crossed the study area and were used for orientation within the area (Fig.2).
During the study period (May 1st - May 31st 2014 and 2015) data collection was done every day from around 9 am to 6 pm depending on weather conditions. Most of the animals, due to the high temperatures, stopped being active around noon on warm and sunny days to hide in hedges and shrubs from around 12:30 pm until 2:30 pm. After that, their activity usually lasted until 6 pm and data collection was stopped. On cloudy days, the duration of their retreat around noon was shorter. At temperatures around 20 °C or below and especially on windy days their activity was very low. The tortoises were hard to find and usually hiding very well.

Parameters sampled

Basic parameters

For every individual, the position of the first sighting was registered and noted with a GPS device. Additionally date, time, weather conditions, individual position (e.g. exposure to sun) and habitat were noted. Some individuals were recovered more than once. The recaptures are not included in the analyses.

Individual specific data

For each individual, sex and body size in terms of SCL (straight carapace length), CCL (curved carapace length), body weight and the type of activity was noted. Furthermore general condition characteristics like injuries, parasites, missing or damaged scuted were registered as well.

Sex determination

The determination of the sex was only possible when a certain size and maturity was reached (Rogner, 2012). Therefore, as a lower threshold for sex determination we used individuals with a

SCL ≥ 10 cm. For smaller individuals, sex determination was uncertain or not possible at all and therefore individuals sized smaller than 10 cm were classified as juveniles.
In general, males were smaller than females and showed a different habitus, such as broader marginal scutes and most important, a longer tail.

Behavioural determination

Six different behavioural categories were distinguished for the analyses: basking, resting, moving, foraging, copulating and egg-laying. Basking and resting were separated according to the position to the sun. An individual was considered resting, when it was found in the shadow without showing any other activity. Basking was considered when individuals were resting in the sun. Moving was noted when an individual was found walking. Foraging was noted when an individual was encountered with food in its mouth and/or chewing. To describe the time budget tortoises were inactive, basking and resting were pooled and to get an estimate for the time budget they were active, foraging and moving were pooled.
Furthermore, copulations or copulation attempts as well as egg-laying were noted, but both behaviours were rarely observed and therefore not included in the statistical analyses.
To measure body size we used specially designed callipers to the nearest of millimeter and body weight to the nearest of gram using an electronic balance. All individuals were marked with a continuous number, using a black permanent marker pen (Fig.3). For identification, the dorsal and the ventral side of each individual was photographed to ensure that individuals they could be recognized even when the mark disappeared between seasons. Therefore, a photo album with pictures of all individuals was additionally established in 2015 to identify any individual recovered from the previous year by its unique shell colour pattern.

Fig.3: Individual marking at ventral (left) and dorsal (right) side (individual no. 18)
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Statistical analyses

To express results usually means and standard errors of the mean (s.e.) were given otherwise indicated in the text. A Oneway χ2 - goodness of fit test was used to compare proportions in different contexts. Generalized linear models in combination with a stepwise regression design were used to examine the importance of size for the use of different behaviours.
All the collected data were processed through SPSS 20.0.

Results

i) Population composition

Based on the individuals found (n = 500) at the study site, the results revealed an adult biased population composition. 389 (78%) of all individuals were determined to be adults, 111 (22%) were juvenile individuals (□10 cm) ($\chi2 = 218.2$, df = 2, $p < 0.0001$). The adult population was significantly female biased (χ2 - test, $\chi2 = 643.1$, df = 2, $p < 0.0001$). We found over twice as many females than males with a ratio of 2.06. Of all individuals found and marked, 262 were females (52%) and only 127 (26%) males (Fig.4).

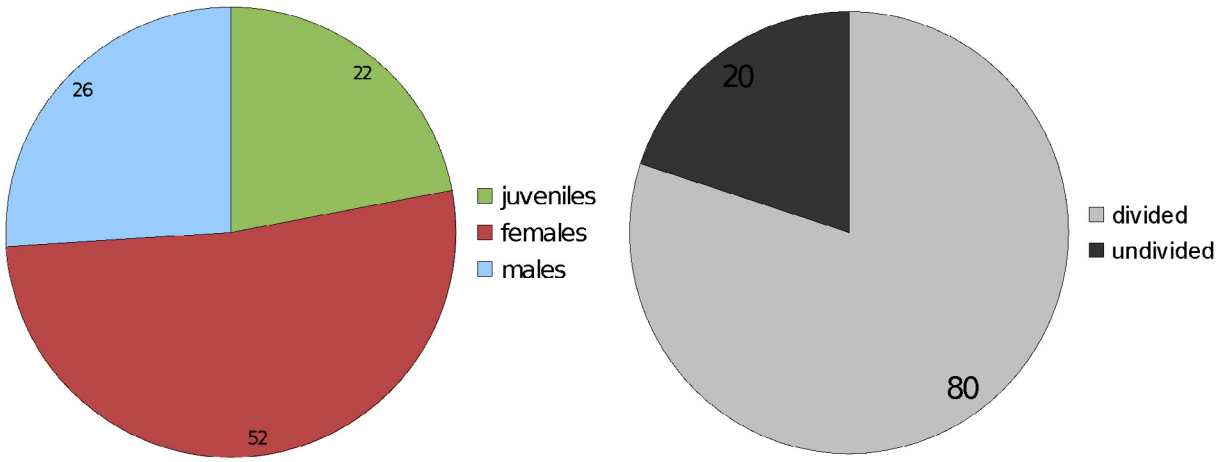

Fig. 4: Proportion (%) of juveniles, males and females at the study site (left pie) and individuals having a divided or undivided supracaudal scute (right pie). Data are based on 500 individuals, namely 262 (52%) females, 127 (26%) males and 111 (22%) juveniles ($\chi2 = 218.2$, df = 2, $p < 0.0001$).

ii) Size composition in relation to age and sex

a) Juvenile size distribution

The size composition of juvenile tortoises followed a normal distribution (Kolmogoroff-Smirnov test: $z = 0.16$, $p > 0.2$) with most juveniles being 6 cm (modal value) and a juvenile population average of: 6.9 cm + 0.16 s.e, (n = 111). (Fig.5). Smaller and bigger juveniles were less abundant, with the distribution slightly right-tailed (skewness = 0.11) and steeper towards smaller individuals (Kurtosis = -0.783).

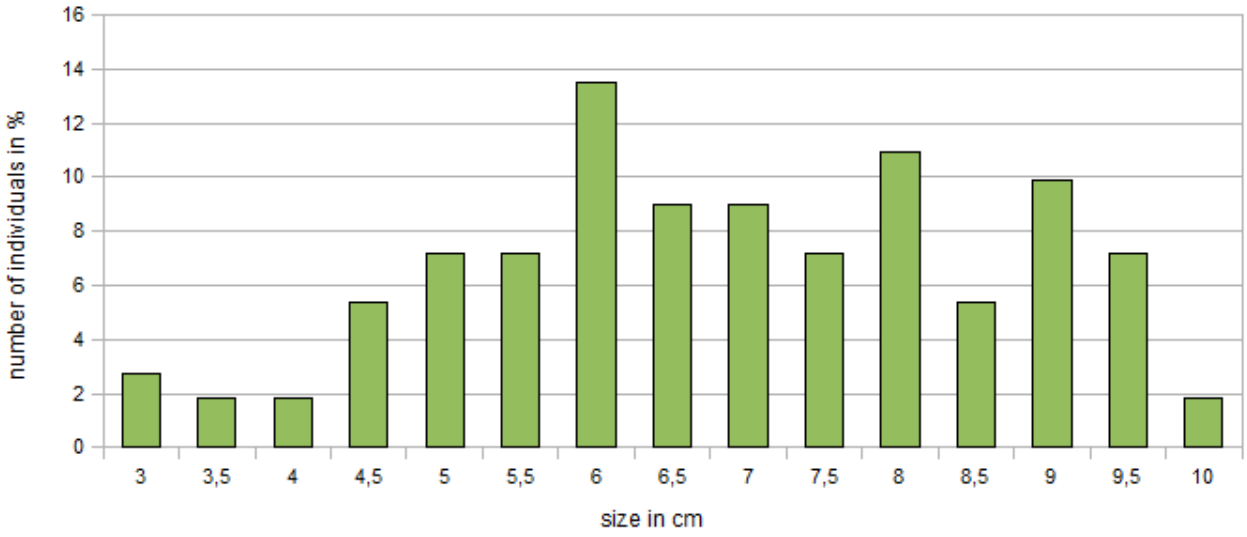

Fig.5: Body size distribution (SCL) of juvenile Dalmatian tortoises found in the study area (n=111).

b) Adult size distribution

Males were significantly smaller than females (t-test, t = -12.6, p < 0.0001, df =387) (Fig.6). Similar to juveniles (Fig.5), male size composition in the population followed a normal distribution (Kolmogoroff-Smirnov test: z = 0.18, p > 0.2) (Fig.7). The biggest male found measured 16.5 cm (Fig.7). The majority (54%) of the 127 males were within a medium-sized size range of 12 to 14 cm (on average: 13.25 cm + 0.14 s.e., n = 127). Females were on average 2,49 cm larger than males.

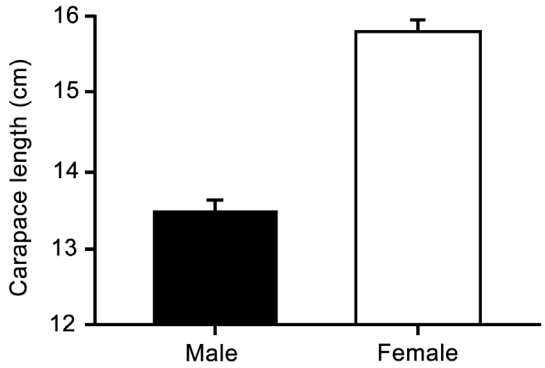

Fig.6: Mean carapace length (SCL) of males and females in cm.

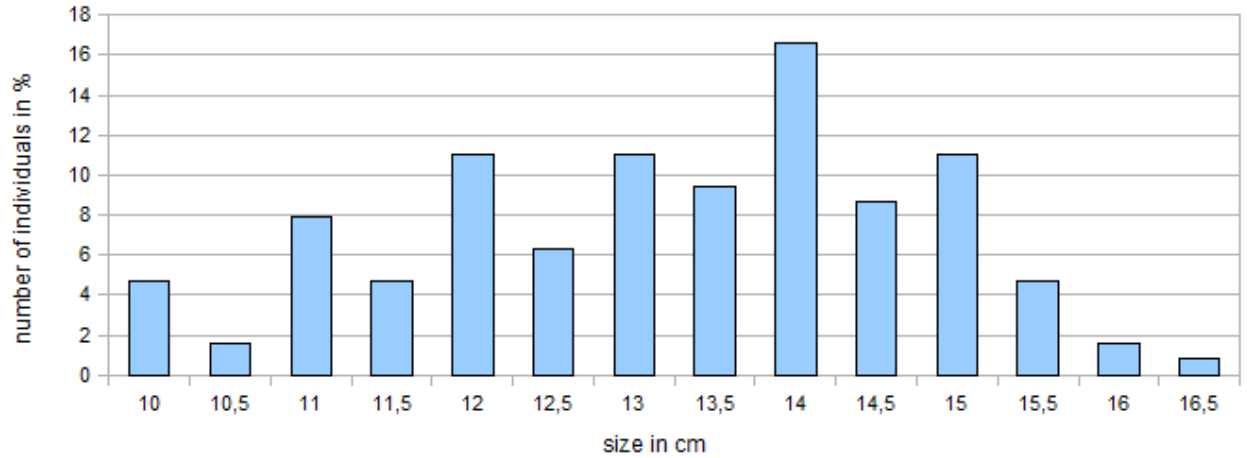

Fig.7: Body size distribution (SCL) of male Dalmatian tortoises found in the study area (n=127)

In the study population, females were generally larger (average = 15.736 + 0.118, n = 262). The largest marked female was 18 cm in length. In contrast to males (Fig.7), female size distribution clearly deviated from a normal distribution (Kolmogoroff-Smirnov test: z = 3.91, p = 0,032) and was significantly left-tailed (Fig.8). Almost half (46%) of the 262 marked females were larger than 16 cm and therefore as big as or bigger as the biggest males in the population. In contrast, medium-sized and smaller individuals were rather rare.

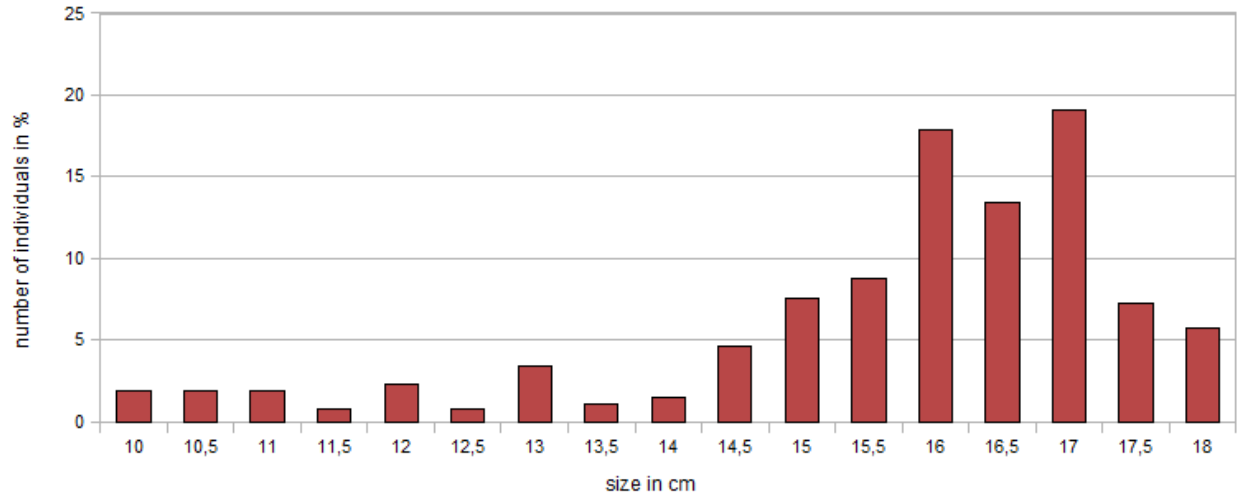

Fig.8: Body size distribution (SCL) of female Dalmatian tortoises found in the study area (n=262)

iii) Daily activity budget in relation to age and sex

For most of the daily observation hours, Dalmatian tortoises were inactive, namely between 60-80% of the daily observation hours (Fig.9), whereby males were found to be most and juveniles least active. Thus, a bias towards being inactive rather than active throughout the day was most obvious for juveniles (Fig.9). In spite of that, the difference between the groups (juveniles, males and females) in being inactive was not significant ($\chi 2 = 3.45$, df = 3, p = 0.18).

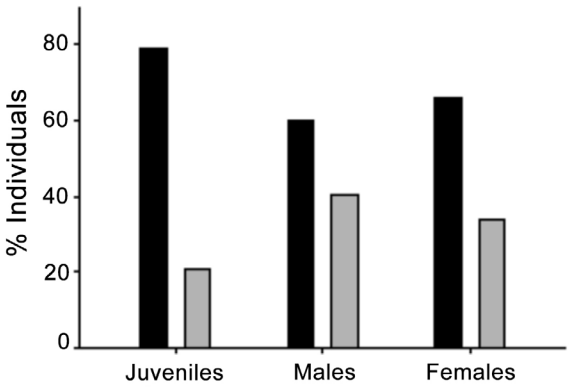

Fig.9: Inactivity (black) vs. activity (grey) in % throughout the daily observation hours in juveniles, males and females (n=500)

Inactivity was defined as individuals either basking or resting. Comparing the two behaviours separately, revealed that for resting no obvious difference between juveniles or adult males or females existed ($\chi 2 = 0.3$, df = 3 p = 0.86). However, basking differed significantly between the three groups ($\chi 2 = 8.94$, df = 3, p = 0.0114), which was most frequently observed in juveniles and least in males (Fig.10a). The amount of time in which tortoises were active was quite low (Fig.9).

Considering only active behaviour stages, tortoises were most frequently observed walking around. Still, this made up a rather small part of their observed daily activity budget, and did not differ between the three groups ($\chi 2 = 2.95$, df = 3, $p = 0.228$) (Fig.10b).
The time individuals spent foraging was less than 10%, and there was no significant difference between juveniles, males and females ($\chi 2 = 2.83$, df = 3, $p = 0.243$) (Fig.10b).
Finally, the results revealed significant differences between the four most common types of behaviour observed in all three groups (for juveniles: $\chi 2 = 42.12$, df = 3, $p < 0.0001$; for males: $\chi 2 = 29.67$, df = 3, $p < 0.0001$; for females: $\chi 2 = 48.4$, df = 3, $p < 0.0001$) (Fig.10a and 10b).

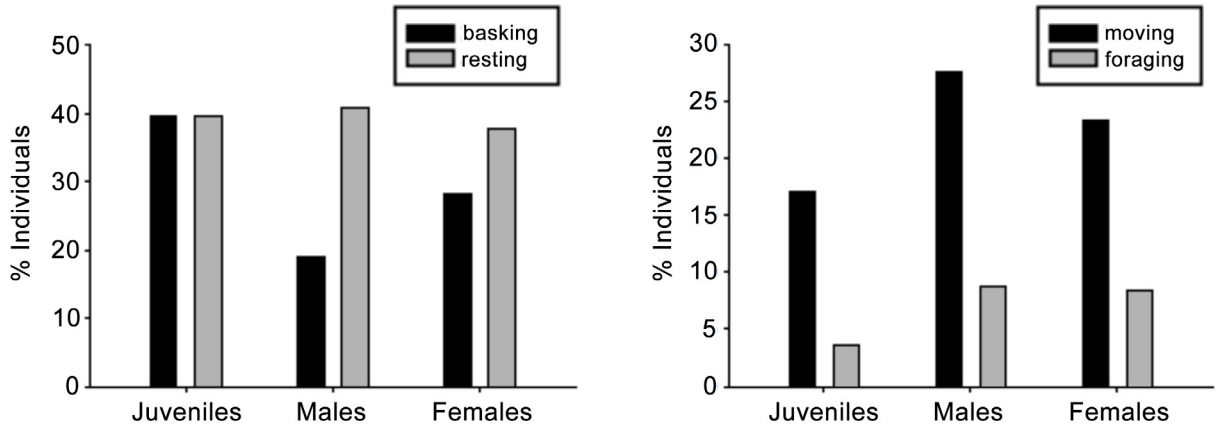

Fig.10a and 10b: Differences between juveniles, males and females regarding the most common types of behaviour: inactive behaviour (upper graph) and active behaviour (lower graph)

iv) Daily distribution of behaviours

The behavioural categories basking, resting, moving and foraging were not evenly distributed throughout the day (Fig.11). Basking clearly decreased over time. Basking was observed to be the most important activity in the morning for both sexes as well as juveniles (Fig.12), regardless of age (Fig.11) or size (Table X,Y,Z).

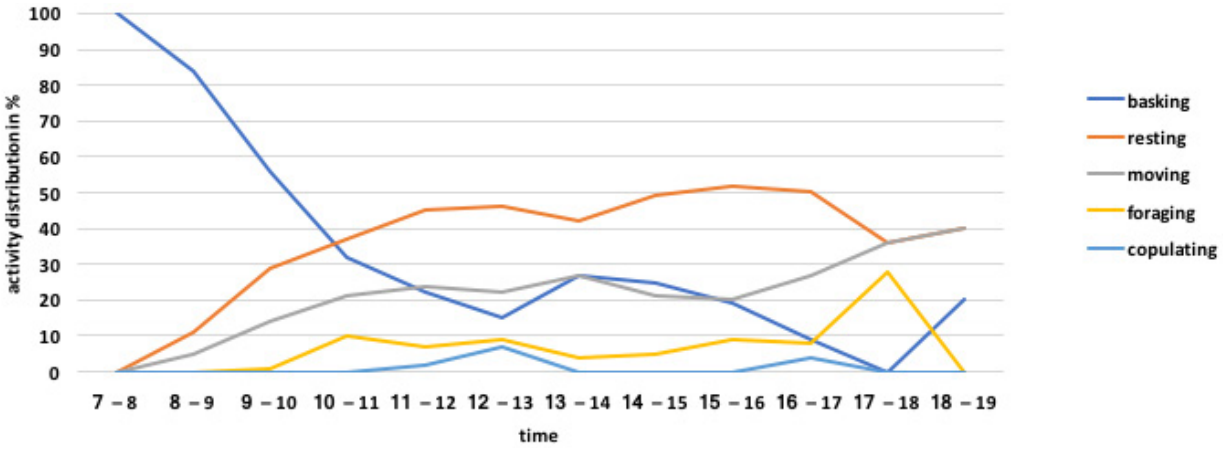

Fig.11: Distribution of daily activity pattern combined for all individuals marked (n = 500)

Resting behaviour increased throughout the morning, reached a plateau in the late morning and approximately maintained this level with a frequency of about 40% to 50% (Fig.11). Moving around in the habitat increased with the morning hours and maintained a level of about 20% to 30% throughout the daily observation hours (Fig.11). Finally, mobility showed a peak in the late afternoon (4 pm to 6 pm).

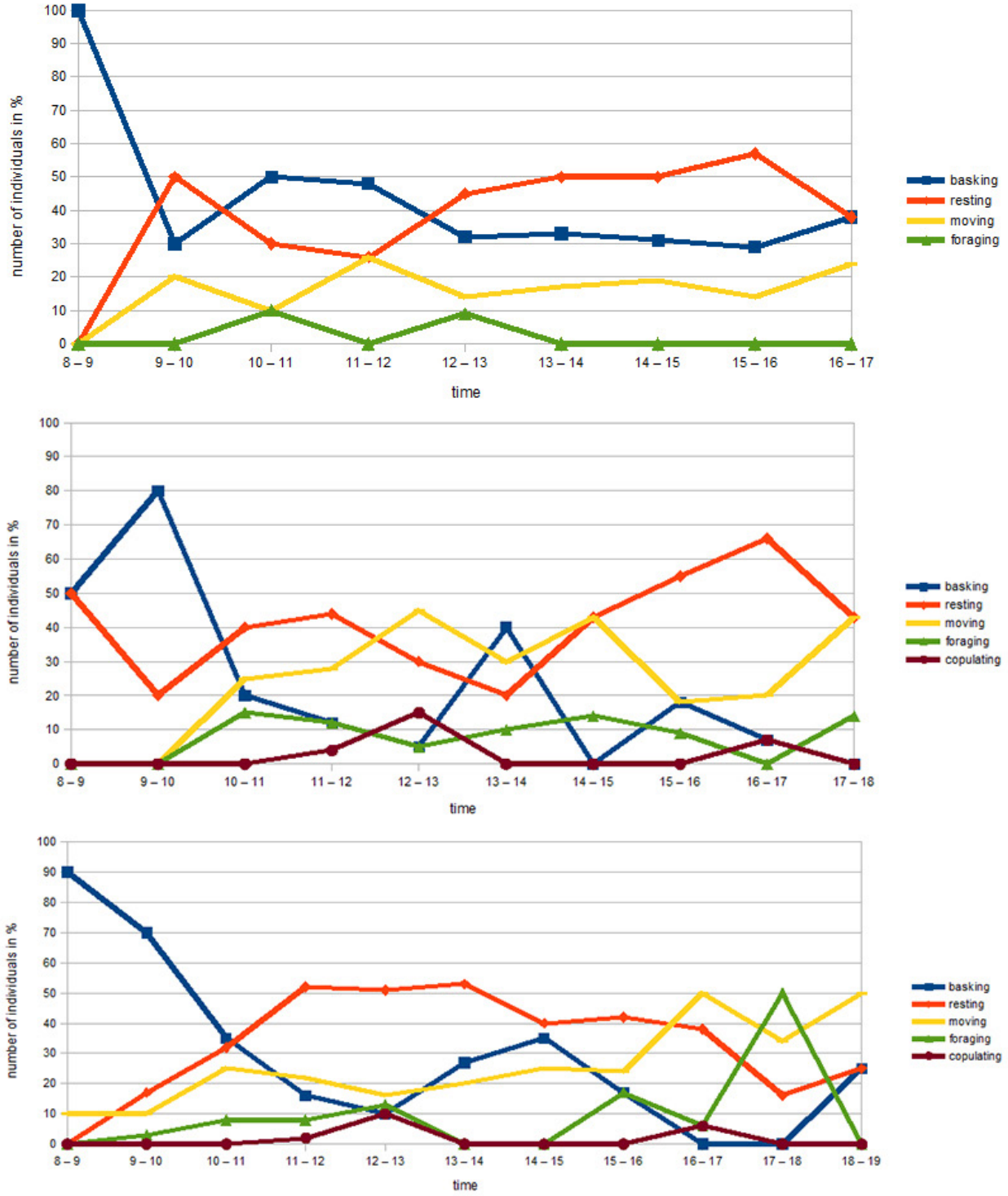

Fig.12: Distribution of different behaviours for juveniles (upper graph), males (middle graph) and females (lower graph) along daytime, based on the respective number of marked individuals (juveniles: n=111, males: n=127, and females: n=262)

Foraging was observed after 9 am and remained at a constant level with a frequency between 5% to 10% throughout the daily observation period. In the late afternoon a peak reaching almost 30% was noted (Fig.11).

Finally reproductive behaviour in terms of copulations, was restricted to two periods, namely around noon and in the late afternoon (Fig.12).

Examining the behavioural categories separately for juveniles, males and females revealed similar results. Except that for adult individuals basking showed two peaks. One in the morning (for both

sexes about 80%) and another one at noon (for both sexes about 40%) (Fig.12). In juveniles, basking decreased towards noon and stayed at a more constant level throughout the rest of the day (between 30 and 50 %).
Males and juveniles also did not show a peak in resting, and therefore remained on a constant level throughout the day, whereas females rested more during the hotter time of the daily observation period and were more active (moving and foraging) in the late afternoon.
In general males started moving later (at about 10 am) and walked around more frequently throughout the whole day. This is contrary to females, who started being active earlier in the morning. They increasingly moved around until they reached a peak in the late afternoon. Males and juveniles spent less time foraging and did not show such a clear peak (Fig.12). Furthermore, the time cost in relation to reproductive behaviour was minimal (Fig.12). Copulation behaviour made up 3.9% of their daily time budget and the time during which females were observed egg-laying (not shown in the graph) made up 0.5%.

v) Behaviour in relation to body size

In juveniles, we found no relation between body size and behaviour. The four behaviours were not differently represented in relation to different size categories (GLM $F = 0.309$, $p > 0.865$, $df = 3, 110$; Fig.10) and there is no directional trend (table X)

Table X: Relationship between body size and juvenile behaviours

Model	Unstandardized Coefficients		Standardized Coefficients			Correlations
	B	Std. Error	Beta	T	Sig.	Partial
Basking	-0,021	0,435	-0,015	-0,048	0,962	-0,015
Resting	0,062	0,424	0,057	0,145	0,888	0,046
Moving	0,519	0,680	0,293	0,763	0,463	0,234
Foraging	0,096	1,482	0,020	0,065	0,950	0,020
Dependent Variable: Juvenile carapace length						

Males (Table Y) show a significant relationship between size and mobility ($F = 9.158$, $df = 1$, $p < 0.009$). The relationship is positive as suggested by partial correlation coefficient.

Table Y: Relationship between body size and male mobility

Model	Unstandardized Coefficients		Standardized Coefficients			Correlations
	B	Std. Error	Beta	T	Sig.	Partial
1(Constant)	12,634	0,717		17,612	0,000	
Moving	0,431	0,142	0,629	3,026	0,009	0,629
Dependent Variable: Male carapace length						

In females, similar to juveniles, no significant relationship between body size and behaviour could be detected ($F = 1.344$, $p > 0.334$). The partial correlation indicates a positive relation between size and movement and a negative with resting and basking (Table Z).

Table Z: Relationship between body size and female behaviours						
Model	Unstandardized Coefficients		Standardized Coefficients			Correlations
	B	Std. Error	Beta	T	Sig.	Partial
Basking	-0,465	0,340	-0,375	-1,368	0,208	-0,435
Resting	-0,432	0,257	-0,569	-1,682	0,131	-0,511
Moving	0,361	0,264	0,494	1,367	0,209	0,435
Foraging	0,583	0,508	-0,342	-1,148	0,284	-0,376
Dependent Variable: Female carapace length						

Discussion

i) Population composition

The results suggest a healthy population with a female bias in size, a female biased sex ratio and a strongly adult biased population composition (Fig.4). Different behaviours show clear diurnal patterns but differences between sexes and age categories are minimal.
With a minimum of 500 individuals per 1 km2, individual density is higher than expected, although the uneven sex ratio might be an indication for a declining population (Celse et al., 2014) (for details see Bürger in prep.) Population density is similar to some other populations of *T. hermanni*. In Croatia, most areas show a density of up to 10 tortoises ha-1, whereas up to 80 individuals ha-1 can be found, if habitat conditions are very advantageous (Celse et al. 2014) (Meek, 1985) (Meek, 1989). Hailey & Willemsen (2000) found individual density ranging from 3.7 – 77 tortoises ha-1 in Greece and Stubbs and Swingland (1985) found densities ranging between 45 to 100 tortoises ha-1 in France.

We found individuals with divided as well as undivided supracaudal scutes. With 80% the proportion of individuals with divided scutes was significantly higher (Fig.4). Previous studies led to similar results, with divided scutes being more abundant than undivided ones (Ljubisavljevic et al., 2012). Divided scutes are typical for *T. hermanni* and undivided ones in *Testudo graeca ibera*. However, the expression of the supracaudal scute alone is still not sufficient for a precise species determination (Amiranashvili, 2000). Although their geographic range does not overlap at the study site, it is well known that hybrids of the two species do occur, e.g. in Bulgaria (Amiranashvili, 2000).

The population composition is biased towards females. About twice as many females than males were found (Fig.4), which is surprising since a previous study on *T. hermanni hercegovinensis* in Croatia found the opposite, namely more males than females (see Vetter, 2006). Since the sex

ratios of healthy populations are usually balanced (Celse et al., 2014), both populations might show signs of change or decline. Female biased sex ratios could be also influenced by climate conditions given that temperature is known to be an important sex determinant in many reptile species (Eendebak, 1995) (Bull, 1980) and warmer temperatures lead to a higher number of females during egg incubation (Lambert, 1982). Eendebak (1995) found that only females hatch, if a temperature of 33-34°C prevails for 5-7 days straight. Since there has been an ongoing rise in air temperature for the past two decades as well as a tendency to extreme weather conditions in Croatia (Simac & Vitale, 2012) and temperatures above 30°C are common in our study area (Fig. 1b), the effect of temperature on the sex ratio might be worth considering.

Another influence on the sex ratio could be habitat characteristics (for details see Bürger in prep.), although there are no previous reports of sex specific differences in microhabitat use in *T. hermanni* (Del Vecchio et al., 2011) (Stojadinovic et al., 2017) .

Assuming that females are the more productive sex (Charnov, 1982) and more stationary (Rogner, 2012) (Chelazzi & Francisci, 1979), habitat characteristics could affect rather female than male abundance. The habitat should provide more or less optimal foraging (grassland with preferably *Asteraceae*, *Fabaceae* and *Plantaginaceae*) (Cheylan, 2001) (Vetter, 2006), hiding (shrubs, hedges) and reproductive conditions, like high occurrence of loose and sandy soil with favourable humidity conditions (Vetter, 2006), within a small range, as well as a moderate diversity and a high heterogeneity (see Bürger in prep.). Also inbreeding or differences in sex specific behaviour in *Testudo hermanni* could influence the sex ratio (Hailey, 1990). However, the study area is not isolated by fragmentation or affected by any other obvious factors that might cause inbreeding.

Studies in Greece also showed a sex specific difference in age. Males were mature for 56% and females for 42% of their lifetime (Hailey, 1989).
Besides a clear females biased ratio, there is also an adult bias in our study population. The number of marked juveniles (Fig.4) was much lower (22%) compared to the number of adult individuals (78%). However this could be partly due to the fact that it is more likely to overlook smaller juveniles. In fact, the smallest individual found had an SCL of only 3.2 cm.

ii) Size composition in relation to age and sex

a) Juvenile size distribution

If search failure is only size dependent, one would expect a continuous increase with body size. The distribution regarding juvenile size is indeed slightly left tailed (Fig.5). However, many juvenile individuals turned out to be medium-sized, about 5.5 to 7.5 cm (see Fig.5). Hence, this peak in medium juvenile body size is unlikely due to individuals being overlooked, but could be explained by a higher reproductive success in some years, as a result of, for example, beneficial weather (warm temperatures, advantageous soil humidity, little rainfall during the first and second trimester of egg incubation) (Vetter, 2006) and/or foraging conditions e.g. due to higher food availability or better quality food. Since individuals of *T. hermanni* sized 5.5 to 7.5 cm are usually aged between 1-3 years (Vetter, 2006), we studied weather data of the study area from the years 2010, 2011

and 2012. In 2011 and 2012, temperatures were higher than usual, in 2010 on a normal level. Considering the climate graph of Dazlina (Fig. 1b), the precipitation was particularly low in 2011, with only 95 rainy days and a daily maximum precipitation of 71 mm. In 2010, there were 156 rainy days and 185 mm precipitation in Dazlina and 117 rainy days and 102 mm precipitation in 2012 (https://www.visualcrossing.com/, 16/01/21). Given that 2010 was abundant with rain so the soil was moistened and loosened up, and 2011 and 2012 were lower in precipitation but warmer, the conditions for egg incubation were most likely very beneficial and resulted in a higher outcome, since rainfall delays embryonic development (Vetter, 2006). These weather conditions might have also led to a beneficial food availability and juveniles may have profited from the low number of rainy days and warmer temperatures in 2011, which possibly resulted in a peak in medium-sized juveniles during our study (Fig.5).

In our study many juveniles were found resting exposed in the sun or right next to adult individuals of either sex. Since *T. hermanni* is considered to show mostly solitary habits (Sovrano et al., 2018), it was surprising that many individuals, especially such a high number of juveniles were found in close proximity to adults. A possible reason might be, that since the study area is used for extensive farming with many unmanaged areas in between, the landscape is very diverse and high in heterogeneity, which provides a variety of habitats close to each other and facilitates optimal conditions regarding habitat use within a small range. Since *T. hermanni* is considered to be a non-territorial species (Celse et. al., 2014), beneficial microhabitat conditions might lead to an accumulation of individuals.

b) Adult size distribution

Males were on average 2.49 cm smaller than females (Fig.6), which is well known and supported by previous studies (Rogner, 2012) (Fasola et. al 2002) (Vetter, 2006) and also matches the theory of Berry and Shine (1980), that in our studied population, mobility is more important than male-male competition over mating success.

In contrast to other species, such as *Testudo marginata*, where males are larger than females (Willemsen & Hailey, 2003), males in *T. hermanni hercegovinensis* are smaller than females (Fig.8). This could be a compromise between size and mobility. If males were too large, moving around to find females would become too energy-consuming. If they were too small, they would hardly or not at all be able to copulate with a large female.

In our study, the majority of male individuals were medium-sized (Fig.7). In relation to the sex specific size dimorphism, one basic assumption is, that with increasing size and weight, mobility becomes more costly in energetic terms, which holds for endothermic as well as ectothermic species (Blanckenhorn, 2000) (Fenchel, 1974).

Male body size seems to be a compromise between mobility, inter- and intraspecific competition, predation and metabolism (Fasola et. al, 2002). In line with this, also juvenile individuals move around less than adult ones. Males searching for females in order to mate might also be an explanation for the higher mobility in bigger and older individuals, given that body size and age correlate (Table Y).

The results suggest that for males, being medium-sized is optimal (Fig.7), because it means that they are large enough to mate, but small or light enough to move around without spending too much energy. Thus, the female biased sex ratio in combination with the female biased sexual dimorphism suggest, that male-male competition does not play a crucial role in this species (Berry & Shine, 1980).

Since there were twice as many females within the study area, the selection pressure might not be on female availability but rather on spatial and resource availability. This suggests that also smaller, more agile males get a chance to copulate, without having to compete directly with a stronger and/ or larger male. The left-tailed size distribution in females (Fig.8) indicates a selection pressure towards large females given that larger individuals produce more eggs and hence offspring than smaller ones (Rogner, 2012).

Therefore, large female body size might be an indicator for attractiveness. Besides, only males of a certain size and fitness are able to mate with large females, which produce more eggs and therefore contribute more offspring to the population. However, Cutuli et al. (2014) suggest that in *T. hermanni* hermanni all males, independent of their body size, have equal access to large females and size-assortative mating is absent.

Since predator pressure strongly decreases with increasing body size and age in this species (Vetter, 2006), a larger size is more advantageous. Our observations and previous studies suggest that males are more on the move and therefore tend to be more exposed to risk than females, especially during the mating season (Rogner, 2012) (Ramsey et al., 2002). Thus males might be at a higher risk of being captured by a predator at a young age and smaller size than females.

This theory might also be an explanation for the sex ratio found (Fig.4).
Body size for the largest male found was 16.5 cm (Fig.7), and for the largest female 18 cm (Fig.8), This is comparable to body sizes of a study by Willemsen and Hailey (1999) conducted in Greece, where females were always larger than males. Body size information found in the literature on Dalmatian tortoises suggest that individuals of our study area are generally larger, since they found maximum sizes of 14.5 cm in males (Vetter, 2006) and 17 cm in females (Rogner, 2012).

The high abundance of *T. hermanni hercegovinensis* suggests that the population in our study area was less affected by the exploitation of pet traders in the past than other areas (see Schweiger 2006). Thus larger individuals could stay in the gene pool.

iii) Daily activity budget in relation to age and sex

Dalmatian tortoises spent the majority, namely 60 - 80% of the day inactive (basking or resting) (Fig.9). Similar results were found in other studies (Fasola et al., 2002) (Vetter, 2006). There are slight, yet not significant differences between sexes or age categories. Results suggest that males tend to be most and juveniles least active (Fig.9). In general, right after hibernation, tortoises tend to be less active and mobile than during the rest of the season, with a peak of activity in May and June (Fasola et al., 2002).

While there are no obvious differences between the three groups regarding resting, there are significant differences in basking. Juveniles were observed basking the most and males least (Fig.10a). An explanation for this might have to do with thermoregulation. The smaller body size of juveniles could be disadvantageous in this context. They may need to spend more time basking to maintain body temperature in a range of being active. Males, in contrast, spend a lot of their time searching for females (see also Calzolai & Chelazzi, 1991), which might result in less time available for basking. Thus there might be a body size dependent trade-off between these two behaviours.

Thus only after reaching a certain body temperature, the performance of various other activities, such as moving can happen. When the environment and hence body temperature reach an upper level the tortoises start to hide and rest in the shadow to avoid health damage. Even though moving around was the most frequent active behaviour found, it still makes up a rather small part of their daily time budget (Fig.10b). Fasola et al. (2002) observed very similar behaviour patterns in a Northern Italian population of *Testudo hermanni*, where moving was also the most frequent activity.

iv) Daily distribution of behaviours

Tortoises adjusted their behaviour to the weather conditions. On warm and sunny days, for example, when there were no or hardly any clouds, basking started early in the morning and stopped around 12 pm, when the day time temperature reached its maximum. From that time onwards, they disappeared in the shrubs until about 2:30 pm. After that, they started again with basking and then moving around looking for mates and/or food (Fig.11). Observations of copulations were restricted to around noon and in the late afternoon (Fig.11). Copulation behaviour and egg-laying were observed very rarely and hence the daily patterns have to be taken with care.

Foraging was most commonly observed in the afternoon and evening, but less than 10% of their day time is used this way (Fig.10b) (Fig.11).
Low food intake is typical for the metabolism of ectotherms, since they can survive quite well with little amounts of food, in contrast to endotherms, which need a lot of energy to maintain their body temperature (Bennett & Ruben, 1979).
In both cases, moving and foraging, no significant differences between the three groups could be found (Fig.10b). Thus one may conclude that foraging is not constraint at all and there is probably no need to trade foraging with other behaviours.

The diurnal activity patterns of *T. hermanni hercegovinensis* (Fig.11) suggest that they do not evenly spread activities throughout the day. It clearly showed, that basking in the morning is the most important activity regardless of sex (Fig.12), age or size (Table X,Y,Z). This is also consistent with the results published by Fasola et al. (2002). Since tortoises are ectothermic animals, basking is of significant importance to build up body temperature to start being active, which allows them to move around and perform other essential activities. Peak mobility on the other hand is in the late afternoon and is mainly mediated by the search for food (Fig. 11). Thus mobility in general and foraging behaviour shows a similar distribution.

Males and juveniles are quite similar in some respect. The results reveal no significant age or sex specific difference in basic behaviours. Examining the behavioural categories separately for juveniles, males and females revealed similar results. Basking in adults showed two peaks, whereas juveniles tend to remain basking at a more constant level throughout the day. This may have to do with thermal conditions (body size), discussed earlier or may be partly due to the fact that adult individuals have learned e.g. to find more efficient basking sites or to apply more efficient basking postures to warm up, or may simply need to spent their daytime for other activities like searching for mating partners, which is not the case for juveniles.

Males and juveniles rested at a constant level throughout the daily observation period, whereas females rested more during the hotter time of the observation period and were more active in the late afternoon. Males and juveniles spent less time foraging and did not show such a clear peak (Fig.12). One explanation might be that females need more energy for egg production, which may result in an increased food intake during the early mating and egg laying period.
The fact that females do not actively search for mating partners (Rogner, 2012) may also explain why females are less mobile. Their activity was focused on the late afternoon and is mainly dedicated to foraging. Males started moving around at about 10am), and were mobile for a large part of the day (Fig.12).
Fasola et al. (2002) found that males were active earlier in the morning than females during post-hibernation (March-April), whereas later both sexes showed similar morning activity throughout the season. Our observations showed that females started being active earlier in the morning than males during spring. They increasingly move around on a constant level until they reach a peak later in the afternoon.

v) Behaviour in relation to body size

The results suggest a correlation between size and behaviour of males, i.p. mobility, namely mobility increases with body size in males (Table Y). This correlation could be explained by an increasing motivation to find mating partners the bigger and more mature a male individual gets. Also, it is easier for larger sized individuals to move around in their environment, than for small sized.

In females (Table Z) and juveniles (Table X), there is no indication for a relationship between body size and mobility.

Our results on activity patterns are basically in line with other studies on tortoises and this species in particular (Vetter, 2006) (Rogner, 2012) (Fasola et al., 2002) (Meek, 1988).
Therefore, our expectations based on literature matched our results of the study. On cloudy days, their activity strongly depends on the temperature. When cloudy, but warm, they only took short breaks in shrubs around noon. On hot days they often disappeared for two or more hours at noon. Their behaviour, especially basking, became infrequent, just as observed in previously conducted studies (Meek, 1988). On cloudy and cool days, they tended to be very inactive and were quite hard to find. When it was raining or very windy, they were almost impossible to find, since they hid deep within hedges or bushes, but also under branch wood. Even an old sofa, which somebody

dumped in the area was good enough for a small group of tortoises to seek shelter. Although our study took place in May, they already showed behaviour usually expected in the hot summer months (Vetter, 2006).

At this point, it is important to mention that these studies were solely conducted in spring during their reproductive time, hence the most active period of the year. During the mating period as already pointed out, the animals moved around more and therefore were also easier to find.

Therefore in the future studies, it would be interesting to focus on their behavioural patterns but throughout the year. Long-term monitoring over several years might also be interesting to examine the population development. Furthermore, recoveries within and between years may provide us with more details about home range size, territoriality and habitat use and hence habitat requirements of that species. Finally, gathering information on the population structure, such as kin relationships would be very important. There is no study so far on that topic and it could be achieved by using non-invasive DNA-sampling.

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