Is sexual brutality maladaptive under high population density?

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Coercive copulation is frequent in promiscuous mating systems, generating both benefits (e.g. higher copulation rate) and costs (e.g. injuries and fewer foraging opportunities). The negative consequences of sexual harassment are expected to increase with increasing population density with male-biased operational sex ratio (OSR). This study offers an example in which the frequency and severity of the injuries inflicted on female tortoises during forced copulations increased with population density and biased OSR. Male Hermann's tortoises (*Testudo hermanni*) harass females during courtship, ramming and biting them until they eventually force mating. They also use their horny and mobile tail to stimulate females, sometimes damaging their cloaca. We compared the frequency and severity of cloacal injuries between two populations in the Republic of Macedonia. Under high density and balanced OSR at one site (Konjsko), 25% of females exhibited cloacal injuries. Under very high density and extremely biased OSR at another site (Golem Grad Island), 75% of females were wounded, often severely. Furthermore, exclusively on Golem Grad, many small and immature females were courted and wounded. This behavioural shift toward juveniles generated costs without benefits. Perhaps brutal reproductive behaviours in male Hermann's tortoises evolved under low or moderate population densities? Under very high densities, coercive mating seems maladaptive, negatively affecting females and possibly further skewing OSR.

ADDITIONAL KEYWORDS: cloacal injury – OSR – sexual coercion – *Testudo hermanni*

INTRODUCTION

Sexual selection provides a unitary framework to study the tremendous variation in animal reproductive traits (Andersson & Iwasa, 1996; Dall *et al.*, 2006). The respective fitness interests of females and males are expressed through a continuum of mating strategies ranging from collaboration (convergent interests) to antagonism (divergent interests) between the sexes (Chapman *et al.*, 2003). Strict monogamy characterized by tight cooperation between the sexes and strongly bonded pairs is rare (Bull, 2000). In most species, males invest less in offspring production than females, generating predominantly divergent interests. Promiscuity favours non-collaborative strategies and thus the emergence of sexual conflicts (Cordero, 1999; Blyth & Gilburn, 2006). Males often adopt forced copulation to resolve such conflicts, thereby inducing high mating costs (e.g. due to fewer foraging opportunities among harassed females) that in turn promote female resistance (Clutton-Brock & Parker, 1995; Fitze & Le Galliard, 2008).

Broadly, males can achieve forcible insemination via two main tactics with different evolutionary consequences (Clutton-Brock & Parker, 1995; Holland & Rice, 1998; Brennan & Prum, 2012). In species where males are physically stronger and can harm the females (e.g. large males that possess weapons), strength and intimidation are used to rapidly subdue and fertilize the greatest number of reproductive females. The resulting sexual antagonistic forces have been formalized as an evolutionary arms race where females develop defensive attributes to minimize fecundity costs induced by sexual coercion, or even repair the physical damage caused by males (Arnqvist & Rowe, 2002; Reinhardt, Naylor & Siva-Jothy, 2003; Muller *et al.*, 2007; Johns *et al.*, 2009; Hare, Wobber & Wrangham, 2012; Lange *et al.*, 2013;

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Michels, Gorb & Reinhardt, 2015; Peinert *et al.*, 2016). On the other hand, in species where females are larger (stronger), and cannot be immobilized or harmed, the males harass them through a war of attrition (Clutton-Brock & Parker, 1995). In this case females gain little by evolving specific traits against male brutality (Bisazza, Vaccari & Pilastro, 2001; Pilastro, Benetton & Bisazza, 2003). Instead they adopt defensive or escape behaviours, test male quality and thereby optimize sperm selection (Wang, Cummings & Krikpatrick, 2015). Intermediate, cryptic coercive strategies and subtle female choices provide abundant exceptions and complications to this dichotomous view (Reyer, Frei & Som, 1999; Pizzari & Birkhead, 2000; Shine, Langkilde & Mason, 2003; Parker, 2006; Knott *et al.*, 2010). Yet, theoretical models and empirical studies converge on the idea that at least one sex (generally both sexes) loses substantial fitness benefits from forcible insemination to permit maintenance of the mating strategy (Parker, 2006). Therefore, whatever the mating tactic, males target reproductive females and prefer those with the highest potential fecundity (McLain & Pratt, 1999; Low, 2004).

A male-biased operational sex ratio (OSR) promotes sexual harassment and female mortality in feral sheep and in captive lizards (Rèale, Boussès & Chapuis, 1996; Le Galliard *et al.*, 2005). These issues are less well documented in natural populations, however. Hermann's tortoise (*Testudo hermanni*) provides one of the few examples of free-ranging vertebrates where sexual harassment is influenced by population structure (i.e. population density and/or OSR; Hailey & Willemsen, 2000). Males are smaller than females; they achieve copulation through intensive harassment, and sometimes damage the female's cloacal region with their sharp horny tail (Hailey, 1990). In this species OSR is generally biased towards males (on average 1F/3.2M, N = 21 populations; reviewed by Bonnet *et al.*, 2016). In Greek populations, harassment of females intensified with an increase in density of males while OSR was strongly male biased: 1F/6.7M. This probably brings additional costs to females, possibly lowering their chances of survival (Hailey & Willemsen, 2000). In the current study we used a natural setting that provided two neighbouring populations exhibiting different OSRs and population densities: a balanced ratio and high-density population (~20 adults/ha and 1F/1M) versus one with extreme values for both parameters (~67 adults/ha and 1F/17.5M; Bonnet *et al.*, 2016). This extreme situation enabled us to examine the influence of population density and OSR on coercive behaviours. Does harassment level simply increase with population density and biased OSR, or does a behavioural shift in harassment tactics emerge when mating opportunities are extremely biased? For example, marked female scarcity may stimulate males

to harass individuals otherwise ignored in populations with a more balanced OSR. This potential shift can have profound impacts on the cohorts of individuals that are usually spared, either by promoting specific resistance or by inducing novel costs. Assessing these questions is important to better understand the evolutionary frame of coercive mating strategies.

MATERIAL AND METHODS

STUDY SPECIES

The mating system of Hermann's tortoises is characterized by promiscuity and coercion. During courtship, the males chase, ram and bite the females to exhaust them in order to eventually mount them (Willemsen & Hailey, 2003; Sacchi *et al.*, 2013). The bites inflicted to the females' legs sometimes cause bleeding wounds. Male tortoises have a longer and more mobile tail compared to females (Bonnet *et al.*, 2001; Djordjević *et al.*, 2011). In Hermann's tortoise, the horny extremity of a male's tail is elongated (Fig. 1; Willemsen & Hailey, 2003; Djordjević *et al.*, 2011). During mounting, males use the tail to stimulate the cloaca, and this behaviour can open wounds around the cloaca and in the supracuadal area (Hailey, 1990; Willemsen & Hailey, 2003; Fig. 1). Intromission of the penis into a female's cloaca generally requires long and intensive harassment with tail movements until the female surrenders, which apparently is a rare event (Hailey, 1990; Hailey & Willemsen, 2000). Therefore, most coercive behavioural sequences can last hours (G.A., personal observation) while the female typically continuously tries to escape.

POPULATION CHARACTERISTICS AND DATA COLLECTION

Data were collected from two neighbouring populations in the Prespa Lake region (Golem Grad Island and Konjsko village in the Republic of Macedonia), only 4.5 km apart from each other, albeit largely different in population density and sex ratio (Bonnet *et al.*, 2016). On Golem Grad Island (~18 ha, 40°52′N, 20°59′E) the population is dense with ~67 adults/ha. Furthermore, the sex ratio is extremely biased toward males (~95% male). In contrast, the Konjsko population (~20 ha, 40°54′N, 20°99′E) is characterized by a lower (albeit elevated) population density of ~20 adults/ha, and a balanced sex ratio (47% male). The two populations are genetically undistinguishable (our unpublished data).

Field surveys were performed in May, June and July 2016 and 2017. Individuals from both populations were captured, sexed, measured [straight carapace length (SCL) and body mass (BM)], marked and released at the

place of capture. Body size at maturity ranges between 130 mm and 150 mm (SCL) in this species (Hailey & Loumbourdis, 1990; Willemsen & Hailey, 1999; Bertolero *et al.*, 2007). In this study, we included both adult females (SCL > 150 mm) and smaller, presumably immature individuals (82 mm < SCL < 150 mm). We nonetheless included only small individuals that clearly exhibited sexually dimorphic characteristics (Willemsen & Hailey, 2003; Djordjević *et al.*, 2011). A photo of the cloacal region of each female was taken by gently pulling the tip of the tail (Fig. 1). Possible wounds in the supracaudal area were not clearly visible from photographs and were not included in the analyses. Some females were captured and photographed two or three times. The sample included photographs taken from 208 different individuals: 69 females from Golem Grad (May $N = 35$, June $N = 16$ and July $N = 18$) and 139 females from Konjsko (May $N = 20$, June $N = 100$ and July $N = 19$). All the procedures during data collecting were in accordance with the ethical legislature of Macedonia (Permit no. 03-246).

ANALYSES

Photographs were visually scored for cloacal swollenness (0: not swollen, 1: slightly swollen, 2: clearly swollen, 3: extremely swollen, Fig. 1) and for injury severity (0: no injury, 1: moderate injuries, 2: severely injured, Fig. 1). Because the cloaca is soft and exhibits a relatively labile shape, it is not measurable by classical morphometric methods, and we therefore used visual ranking (Hailey, 1990). To minimize the subjective nature of this method, photographs were randomly sorted into 15 sheets with 10–25 photographs each. This sample included 208 photographs corresponding to the 208 individuals examined. They were blindly categorized by two observers independently (i.e. each photograph was scored twice). In most cases, both scores were in agreement (swollenness: 51% total agreement, 42% slight disagreement, 7% partial disagreement, 0% full disagreement; injury levels: 66% total agreement, 33% partial disagreement, 1% full disagreement). Importantly, the overall proportions provided by each observer were very close considering
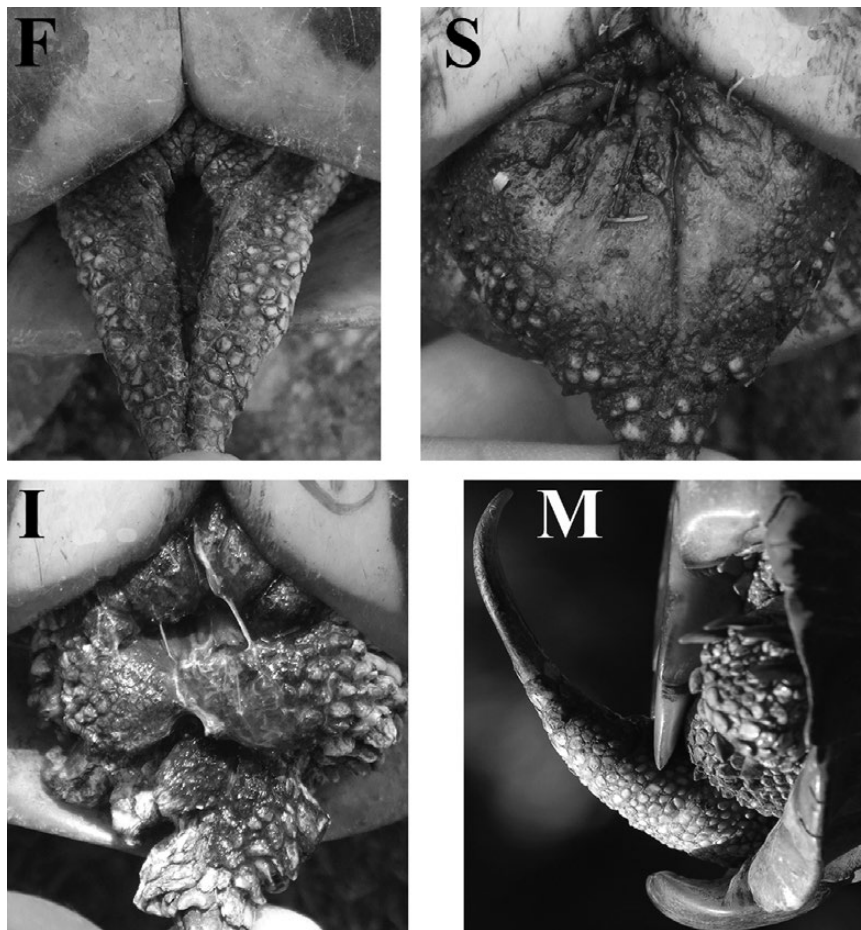

Figure 1. Photographs of female cloacal regions: normal cloaca (F), extremely swollen (S), and severely injured (I), and a photo of a male's long horny tail (M).

cloacal injuries, or provided relatively similar trends for swollenness (Table 1). For analyses we used average values from the double scoring, thereby generating additional intermediate values (e.g. 0.5, 1.5). Overall, we used seven levels of swollenness (0, 0.5, 1, …, 3) and five levels of injury severity (0, 0.5, 1, …, 2). For clarity of graphical reproduction, we used three injury levels: 0 (0–0.5 pooled), 1 (1.0) and 2 (1.5–2.0 pooled).

In practice, swollenness and injury levels provided similar trends (Fig. 2). Indeed, the average values of swollenness correlated positively with injury scores (Spearman's rank correlation r_S = 0.41, N = 259, P < 0.05), simply because injuries entail tissue inflammation. Yet, the level of injury scores probably better reflect the intensity of damage caused by males. For conciseness we emphasized injury level results. Proportions were analysed using contingency tables; comparisons of continuous variables among groups were assessed using ANOVA (alpha level set at 0.05 and all tests were two-tailed). Several continuous variables were not normally distributed (e.g. SCL), and therefore we used Box-Cox transformations. The resulting Henry's probability plots revealed linear patterns. Analyses were performed with Statistica.13 (Dell Inc., 2015, Dell Statistica version 13; www.dell.com.).

RESULTS

Injury severity differed significantly between the two populations (Fig. 2; contingency table, χ^2 = 16.51, d.f. = 4, N = 208, P = 0.002). At Konjsko, most females (77%) were either not injured or were moderately injured (mean score ranging from 0.0 to 0.5), and the number of injured females decreased sharply with injury severity. By contrast, on Golem Grad Island 51% of females were injured (mean score ranging from 1 to 2) and most females exhibited an injury score of 1 (Fig. 2). The proportion of clearly injured females (scores 1–2) was higher on Golem Grad Island than at

Table 1. Comparison of the blind scoring for each category of swollenness and injury level performed by two independent observers (Obs1 and Obs2) using photographs of the cloacal region of 208 female tortoises

Source	Level	Obs1	Obs2
Swollenness	0	82	86
	1	65	103
	2	41	14
	3	20	5
Injury level	0	116	113
	1	77	82
	2	15	13

Konjsko. Swollenness scores exhibited a similar pattern (Fig. 2; χ^2 = 24.86, d.f. = 6, N = 208, P = 0.001).

BODY SIZE AND LEVEL OF CLOACAL INJURY

Mean body size differed significantly between populations, with females at Konjsko being larger (ANOVA with Box-Cox-transformed SCL as the dependent variable, $F_{1,206}$ = 154.41, P < 0.001). Mean body size differed significantly among the five injury-level categories without interaction between populations; larger females experienced more severe injuries (Fig. 3; Table 2). Regarding swollenness, we found a significant difference in mean body size between the two populations ($F_{1,194}$ = 47.38, P = 0.001), merely due
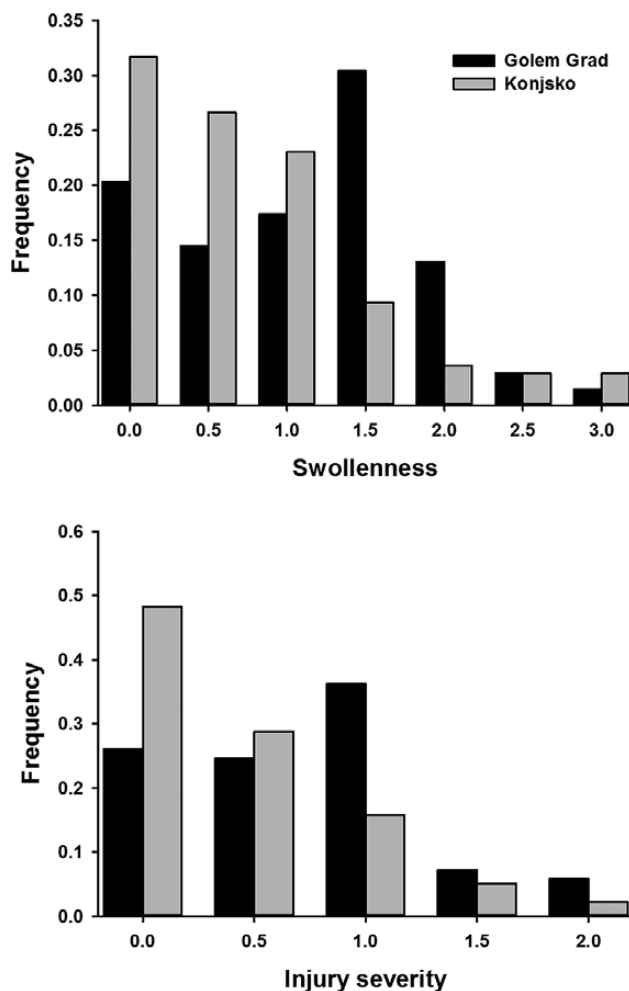

Figure 2. Comparison of the prevalence (frequency, *y*-axis) of sexual harassments between the two neighbouring tortoise populations. Two proxies of coercive mating in females were used (*x*-axes): levels of cloacal swollenness (upper panel) and levels of cloacal injuries (lower panel). See text for details and statistics.

to the greater size of Konjsko females, but not among swollenness categories ($F_{6,194} = 0.704$, $P = 0.646$).

SEXUAL MATURITY AND CLOACAL INJURY

In both populations, many large females (SCL > 170 mm) exhibited severe cloacal injuries (Fig. 4). However, on Golem Grad exclusively, smaller adult females (i.e. 150–170 mm SCL) were also severely injured. This was not the case for smaller adult Konjsko females that were spared from cloacal damage. Remarkably, many small females (130 mm < SCL < 150 mm) not easily classified as sub-adult or adult, along with several smaller clearly immature females (SCL < 130 mm; below the lower body size threshold for maturity), showed clear cloacal
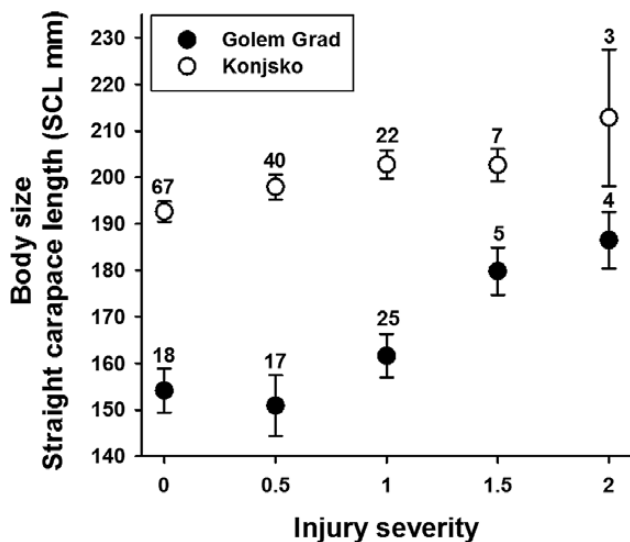

Figure 3. Relationship between body size (*y*-axis; mean ± SD, number above symbols denote sample size) and cloacal injury level (*x*-axis; the five categories correspond to increasing levels of injuries) recorded in female tortoises from the two populations. In both populations a similar trend emerges: severely injured females were larger (see Table 2 for statistics).

injuries on Golem Grad. Overall, the two populations exhibited strong divergences in the relationship between body size (and hence maturity) and the prevalence of cloacal injuries.

DISCUSSION

Our results confirm previous findings indicating that sexual harassment increases with population density and biased OSR (Cordero, 1999; Fitze & Le Galliard, 2008). More importantly, they revealed a shift in the harassment tactic employed by the males where body size (SCL), and hence body mass (BM) and maturity, played an important role. Indeed, previous studies suggested that intensive harassment seems to be limited to large and potentially most fecund females (Hailey, 1990), and our results from the moderately dense population with a balanced OSR (Konjsko) corroborate this. However, in the very dense population of Golem Grad and with a shortage of adult females, male coercion also targeted smaller presumably less fecund females, and remarkably, very small non-reproductive individuals. In this latter case, the resulting sexual conflicts do not benefit any sex: males waste their time and energy while the harassed non-reproductive females are exposed to potential costs without a fitness payoff. Indeed, offspring production – the raw material for female cryptic choice (e.g. via sperm selection), antagonistic co-evolution and more broadly sexual selection – is lacking. Below we briefly discuss these results.

POTENTIAL HARASSMENT COSTS

Harassment often entails long pursuits and repeated mating attempts (Willemsen & Hailey, 2003; Blyth & Gilburn, 2006; Adler, 2010), involves energy expenditure, generally decreases female fitness (e.g. lowering foraging opportunities and thus egg production) and sometimes has lethal consequences (Foott, 1970; Pratt, 1978; LeBoeuf & Mesnick, 1991; Rice, 1996; Stutt & Siva-Jothy, 2001; Adler, 2010; Reinhardt, Anthes & Lange, 2015).
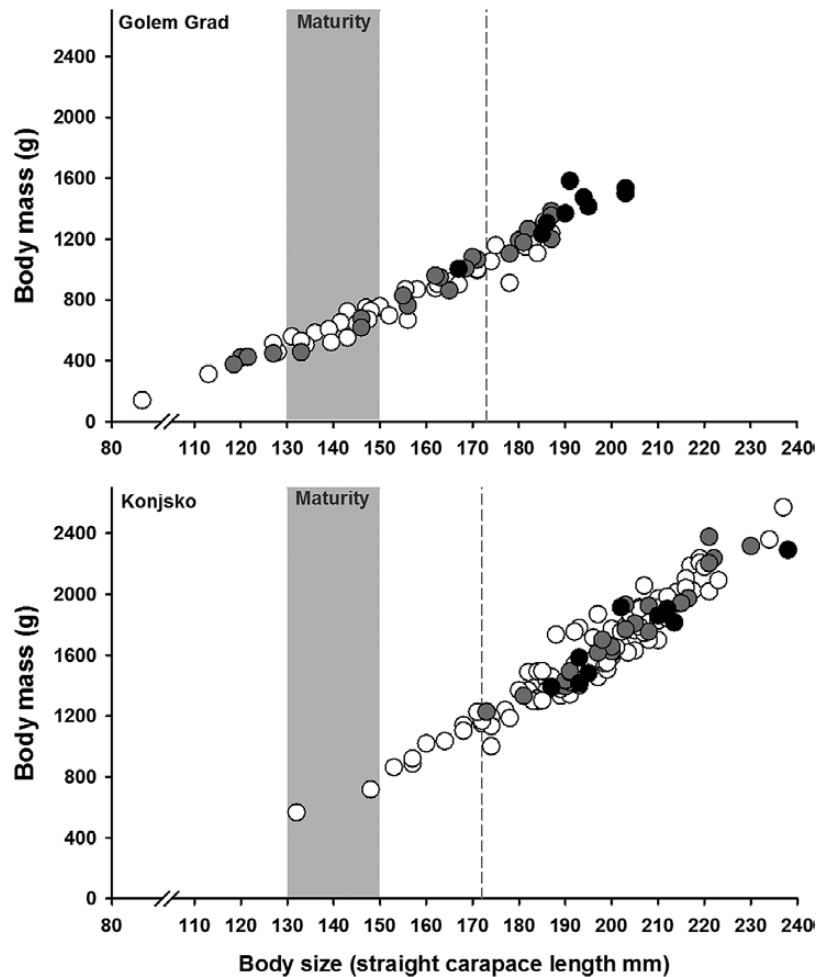
Table 2. Statistics from the ANOVA to compare the mean body size (SCL, Box-Cox transformed data) between two populations of tortoises (P: Konjsko vs. Golem Grad) and among the five categories of injury level (IL, three levels, see Table 1); in total, $N = 208$ individual females were used

Source	Sum of Squares (S Sq)	d.f.	Mean Squares (M Sq)	F	P
Intercept	7.394E+13	1	7.394E+13	1276.120	< 0.001
Population (P)	4.628E+12	1	4.628E+12	79.884	< 0.001
Injury level (IL)	1.208E+12	4	3.019E+11	5.211	< 0.001
Interaction (IL × P)	1.632E+11	4	4.081E+10	0.704	0.590
Error	1.147E+13	198	5.794E+10		

Figure 4. Relationship between cloacal injury level (white, grey, black pattern) as a function of body mass (*y*-axis) and body size (*x*-axis) recorded in two populations of free-ranging tortoises (total sample *N* = 208): Golem Grad (upper panel, *N* = 69) and Konjsko (lower panel, *N* = 139). For clarity, only three broad categories of injury levels are displayed: open circles for females without or with moderate injury (0–0.5), grey for average level (1) and black for strong injuries (1.5–2). The grey area indicates the range of body sizes at which maturity occurs in this species. The dashed vertical line, which indicates the minimal size for average injury level recorded in Konjsko females, facilitates comparisons between the two populations.

In Hermann's tortoises, courting insistence is associated with systematic escape attempts of the females. Furthermore, males inflict injuries to the females, and thus their mating system involves punishment and is somehow intermediate between coercive insemination based on physical domination and harassment followed by female surrendering. Although we did not quantify the costs of harassment in the Hermann's tortoise, our results strongly suggest that they do occur.

A recent study in an aquatic turtle species suggests that coercive mating does not inflict injuries to females (Keevil *et al.*, 2017). However, in terrestrial tortoises, males can bite females' legs to the point of bleeding and sometimes flip them onto their backs,

placing them in a perilous situation, notably because the females struggle to right themselves (Bonnet *et al.*, 2001; Golubović *et al.*, 2013). Although the cloacal region of the female is not armored, their hard skin is protected by keratinous scales (Fig. 1). This means that prolonged and intensive periods of harassment are required to produce high levels of swollenness and cloacal injuries. Indeed, in most tortoise populations, mated females do not show any sign of injury and in the current study many were not wounded despite having been observed copulating. In the two populations monitored, population density was elevated and therefore the likelihood for a female to not be courted and mated seems negligible. Thus,

the most injured females were probably subjected to repetitive and intensive harassment episodes. The two categories of cloacal injuries differ in their durability and possible biological effect. Swelling of the cloacal region could reveal ongoing inflammatory processes due to harmful courtship, but also due to other physiological processes (e.g. transmitted diseases). Such inflammations might heal relatively quickly, depending on the immune response of the individual, leaving no visible scar. By contrast, open wounds on the skin and surrounding tissues could easily become infected and subjected to necrosis, especially in the cloacal region (Hailey, 1990). These wounds could be slow to heal, and they often leave visible scars. Overall, major perturbations during foraging or basking caused by intensive harassment along with physical damage (loss of blood, injuries, infections risks, healing, etc.) will probably entail costs. Our data support the suggestion of Hailey & Willemsen (2000) that extreme harassment could lower female survival.

Shift of harassment tactic

In tortoises, males occasionally court small immature individuals (Hailey & Loumbourdis, 1990). Intensive harassment can result in substantial wounds. Females from the two studied populations were under different courtship pressures. At Konjsko, injuries were typically more frequent in larger individuals and were never observed in females smaller than 170 mm SCL and 17 years old or younger (age estimated from Arsovski et al., 2018: fig. 2). Thus, intensive coercive mating was concentrated on large females at least 5 years after maturity, revealing an important buffer age-span preventing harassment of small, possibly immature females. Conversely, small females on Golem Grad Island were often wounded long before they reached adulthood (Fig. 4), revealing a lack of body size threshold. The smallest wounded females on Golem Grad Island were estimated to be only 8 years old (Arsovski et al., 2018: fig. 2). The high population density and strongly male-biased sex ratio on Golem Grad triggers unusually intensive reproductive activity in males. Frustrated males not only court and mount females, but also other males (including immatures), dead tortoises, empty shells and even stones (Bonnet et al., 2016). These behaviours have not been recorded in other free-ranging tortoise populations (Bonnet et al., 2016). Consequently, a very high population density and skewed OSR not only increase the likelihood that a female will be courted, but also induce a behavioural shift in male mating tactics. This shift toward immature females may entail costs but cannot generate any benefit; in this case coercive mating was maladaptive.

CONCLUSION

Our results show that under unusual demographic conditions, behavioural mechanisms that otherwise optimize mating tactics (i.e. males intensively court the most fertile females) can be perturbed. In most situations, forcible insemination might be profitable to both sexes, and is probably advantageous under low population density with low encounter rate (Swingland & Stubbs, 1985; Hailey, 1990). This tactic enables males to fertilize (many) females, whilst long-term sperm storage (~ 3 years, Cutuli et al., 2013) may facilitate cryptic female choice. A war of attrition is demanding and costly for both partners, so behavioural mechanisms are expected to limit coercive mating to mature individuals. Males identify adult reproductive females using chemical cues, then chase and harass them using their powerful horny tail until they are able to mate (Galeotti et al., 2007). In populations with a balanced OSR, a threshold in female body size seemingly triggers harassment. Smaller adult females are thus automatically spared (Fig. 4). However, a high population density combined with a strongly skewed OSR seem to override this mechanism. In our study, a shift in male mating tactics was found to underlie the frequent maladaptive sexual behaviours. Further investigations are needed to explore the roles of hormones, pheromones and population structures in this perturbation (Bonnet et al., 2016).

Previous studies reported that increasing population density influences the occurrence of maladaptive coercive mating with deleterious population consequences, simply through an increase in the level of harassment (Rèale et al., 1996; Le Galliard et al., 2005). Yet, sexual conflicts do not necessarily provide benefits to any partner. In the elephant seal, bulls can kill coveted females, illustrating an extreme but seldom observed case in which coercive mating does not bolster reproductive success (LeBoeuf & Mesnick, 1991). Our results add another mechanism by which a behavioural shift can actually spread the negative consequences of maladaptive coercive mating to a wider range of age cohorts. The resulting worsening bias in OSR may further stimulate sexual harassment, creating a vicious circle.

ACKNOWLEDGEMENTS

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