

SEXUAL SELECTION IN THE TORTOISE *Chelonoidis denticulata*: DOMINANT PARTNER OR HEALTHY PARTNER?

Raiane Costadelle Cavalheiro ¹ & Eduardo Bessa ^{2*}

¹ Universidade do Estado de Mato Grosso (UNEMAT), Campus de Tangará da Serra, Departamento de Ciências Biológicas. Rod. MT 358 km 7, Jd. Aeroporto. Tangará da Serra, MT, Brasil. CEP: 78300-000

² Universidade de Brasília (UnB), Ciências Naturais, Laboratório de Ecologia Comportamental da Reprodução (LECR). Área Universitária 01, Vila Nossa Senhora de Fátima, Planaltina, DF, Brasil. CEP: 73.345-010
E-mails: raianecostadelli@hotmail.com, prof.bessa@yahoo.com.br

ABSTRACT

Sexual selection consists of differential reproductive success due to individuals choosing mates who provide more direct or indirect benefits. When partners present conflicting advantages, it is unclear how animals decide with whom to reproduce. *Chelonoidis denticulata* have a hierarchical society defined by ritualized fighting whose winners have access to limiting resources, however, they also harbor large amounts of ticks, which cause diseases and can affect partners' choice. In this study we tested which is more important in mate choice: dominance hierarchy or parasite biomass. We observed 57 individuals kept in semi-captivity; compared mating success in different hierarchical levels and ectoparasite load. Successful males were not more dominant, but had fewer parasites. We conclude that, when parasitism and hierarchy are in conflict, female tortoises choose a healthy partner over a dominant male.

Keywords: ectoparasites; healthy male hypothesis; hierarchy; mate choice; yellow-footed tortoise.

INTRODUCTION

Behavioral ecology can be defined as the study of the adaptive value of certain behaviors (Davies *et al.* 2012). It is related to the third form of behavioral causation described in the seminal paper by Niko Tinbergen (1963), in which he relates the survival value of a behavior as a distal evolutionary reason for it to occur. Although more than 50 years have passed since its publication, Tinbergen's four questions are still important in the study of animal behavior (Bateson & Laland 2013). Our study is especially interested in the adaptive value of partner's selection in tortoises. Sexual selection is an example of natural selection that consists of an individual choosing another for mating based on some differential attribute presented by the chosen one (Andersson & Simmons 2006). Alternatively, sexual selection may also be viewed as the reproductive success of an individual in relation to the quantity of available partners (Wade 1979).

There are many hypotheses about how females choose a specific partner among many (Andersson & Simmons 2006), such as good genes (females choose a partner who will offer her offspring good genes),

sexy son (females choose a partner whose attractive characteristics will be present in her sons), direct benefit (females choose partners who will offer her some resource in exchange for the mating), sensory bias (females choose males whose characteristics exploit some sensory bias they already have) and the healthy male hypothesis. The latest predicts that females use ornaments and courtship behaviors to assess its partners' immune quality (Hamilton & Zuk 1982). This has a double effect; females have a direct benefit, avoiding contamination by sexually transmitted parasites. Furthermore, there is an indirect benefit when females' selection increases the chances that her offspring will inherit its father's "good genes", those who guaranteed him his health against those parasites (Hamilton & Zuk 1982). Parasites are organisms that totally depend on another individual (the host) to survive, bringing damage, but seldom killing it (Zelmer 1998, Neves 2005); nevertheless, the effect of the parasite on the fitness of the host varies greatly with the species.

Besides health, females may obtain direct benefits searching for males who are hierarchically dominant (DeRussy *et al.* 2013). In some mating

systems in which males control access to limiting resources, choosing a dominant male is the only way a female can access such resources, providing the female with a direct benefit (Andersson & Simmons 2006). Many hypotheses on sexual selection are not exclusive, including the healthy male and the dominant male hypotheses (Brooks & Griffith 2010). Despite that, if there is a negative correlation between hierarchical position and parasite load, we expect a dilemma to arise. Females will have to opt between a healthy and a dominant partner. Such situation occurs in tortoises.

The yellow-footed tortoise *Chelonoidis denticulata* (Testudinidae) is distributed throughout Brazil in humid and dense forests (Tortoise & Freshwater Turtle Specialist Group 1996). Females use odor cues to search for partners during the reproductive phase, which varies according to the geographic region, but usually concentrate between October and January (Molina *et al.* 1998, Teixeira 2009). At least some tortoise societies are hierarchical, with ritualized combats defining the dominant male, who is usually the larger and heavier one (Mann *et al.* 2006, DeRussy *et al.* 2013). Females have been reported to select dominant partners (Teixeira 2009, Barros *et al.* 2012). Moreover, *C. denticulata* may host large quantities of ectoparasites (Neves 2005), especially when exposed to inadequate hygiene and environment (Rodrigues 2011). Ticks are important indicators of health status in tortoises because they reach high densities (Ehlers *et al.* 2015) and work as vectors of numerous pathogens, such as hemorrhagic fever (Tótoky *et al.* 2014) and *Rickettsia bellii* (Erster *et al.* 2015). In *C. denticulata*, dominant males carry more parasites than submissive males because they get infected by dispersing ticks more often while persistently patrolling the territory (O'Connor *et al.* 1994). According to the healthy male hypothesis, this could affect female choice for partners and allow for testing it against the dominant male (direct benefit) hypothesis.

Due to its wide distribution, docility and ease of observation, *C. denticulata* is a good model to study the trade-off between sexual selection for health and status. Thus, in this study we tested the healthy male hypothesis against the dominant male hypothesis by

evaluating which factor influences more the success in mating: ectoparasite biomass or social dominance. We also included a comparison between size and parasitism between males and females because this difference is expected in a sexual selection scenario.

MATERIAL AND METHODS

Study area

Our study was accomplished in an urban natural park in Tangará da Serra, Mato Grosso, Brazil (14° 37' 39.61" S; 57° 29' 35.29" W). The area consists of 11.8 ha of transitional vegetation between Cerrado (savanna) and Amazon forest (Melz & Tiago 2009). Tortoises live in semi-captivity and *ad libitum* supplementary food is offered daily. Although precise data is unavailable, a population of *C. denticulata* has inhabited the area for the last 20 years at least, according to the municipality environmental agency (Figure 1). The population was founded by abandoned domestic animals, but reproduction does occur in the area.

Data collection

All the individuals living in the area were tagged with numbers on the shell. With that we did an inventory of the males and females that inhabit the study area, using the shape of the plastron (plain = female; concave = male) to determine the sex of individuals (McRae *et al.* 1981). Although this method allows for misidentification of juvenile males, it did not affect our main objective since we were interested only in mounting, therefore, sexually mature males. We measured the shell and weighted the tagged animals. Weight and shell length were used as a proxy to social status, since they are strongly linked to success in ritualized combats, according to numerous studies (*e.g.*, Berry & Shine 1980, Niblick *et al.* 1994, Mann *et al.* 2006, DeRussy *et al.* 2013). We also collected *Amblyomma dissimile* ticks, the most common ectoparasite species in the area, from each individual, counting them and measuring their weight in a precision scale to obtain the ectoparasite biomass for each individual.



Figure 1. *Chelonoidis denticulata* in the study area a) individual with *Amblyomma dissimile* tick under the head; b) Mounting couple. Photographs by Ana de Medeiros Arnt.

From January to December 2013 we searched for mounting individuals and identified which males copulated and which did not. Observations occurred from 8 to 12 a.m. once a week, summing about 200 h of observations. Scans (*sensu* Martin & Bateson 2007) took place on feeding sites where the animals aggregate at about 0.3 individuals/m². Vocalizations were also used to spot courting and mating couples. Our methods were in accordance with national environmental policy and animal welfare guidelines (ASAB 2006).

Statistical analysis

We evaluated differences between the sexes in size, weight and parasite biomass using a Student's *t*-test (Zar 1999). To test which factor affects more the mate choice we compared parasite biomass, shell length and total body mass of individuals that did or did not copulate using another *t*-test (Zar 1999) on measures of each male (sample unity). We also tested for correlation between size and weight with parasite biomass using a Pearson test (Zar 1999). For all the tests we accepted a confidence level of $\alpha = 0.05$ for type I error.

RESULTS

During our study we tagged 57 individuals of *C. denticulata* of different sizes, a density of 483 individuals/km². The sex ratio was 1.85 males (total of 37 males) for each female (total of 20 females).

We also observed 43 copulations. Only 18 males were seen copulating (32.6% of the population), all of them larger than 46 cm of shell length.

Males had a mean (\pm standard deviation) shell length of 53 ± 5.80 cm (44-67 cm min-max values). They weighted 12.08 ± 3.49 kg (7-20 kg min-max values). Meanwhile, females were slightly smaller (46 ± 5.06 cm), and lighter (10.34 ± 3.61 kg) than their mates (39-55 cm and 5-17 kg min-max values, respectively). The statistical value for such comparison showed us a significant difference in size ($t_{55} = 4.640$; $p < 0.001$), but not weight ($t_{55} = 1.744$; $p = 0.087$). Males are also more subject to ectoparasites than females. Males presented 0.49 ± 0.73 g of ectoparasites, while females presented 0.27 ± 0.27 g of ectoparasites biomass ($t_{55} = 2.086$; $p = 0.041$). We found no correlation between parasite biomass and shell size ($p = 0.210$; $p = 0.157$; $N = 47$) or total weight ($p = 0.208$; $p = 0.160$; $N = 47$).

Our main question, though, was whether females prefer healthy males or dominant males. The mating success of males was not significantly affected by size ($t_{45} = -0.279$; $p = 0.782$) or weight ($t_{45} = 0.264$; $p = 0.793$). It was not the larger or heavier male who copulated (Figures 2 and 3, respectively).

Alternatively, when considering parasite biomass and sexual selection, the male reproductive success was inversely related to the presence of ectoparasites ($t_{45} = 3.526$; $p < 0.001$; Figure 4). This allows us to affirm that the females of *C. denticulata* will accept less parasitized males more often than larger or heavier males.

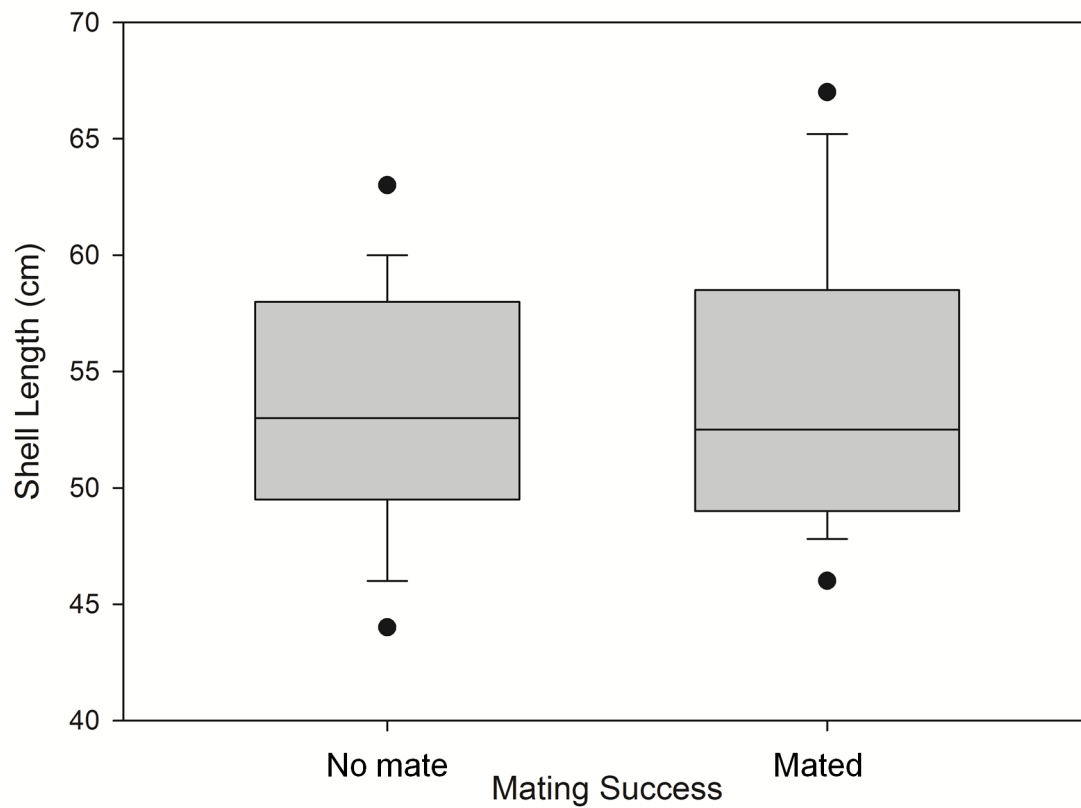


Figure 2. The shell size of *Chelonoidis denticulata* males does not predict his mating success. Central lines are the mean value, boxes are standard deviation and points are the maximum and minimum values.

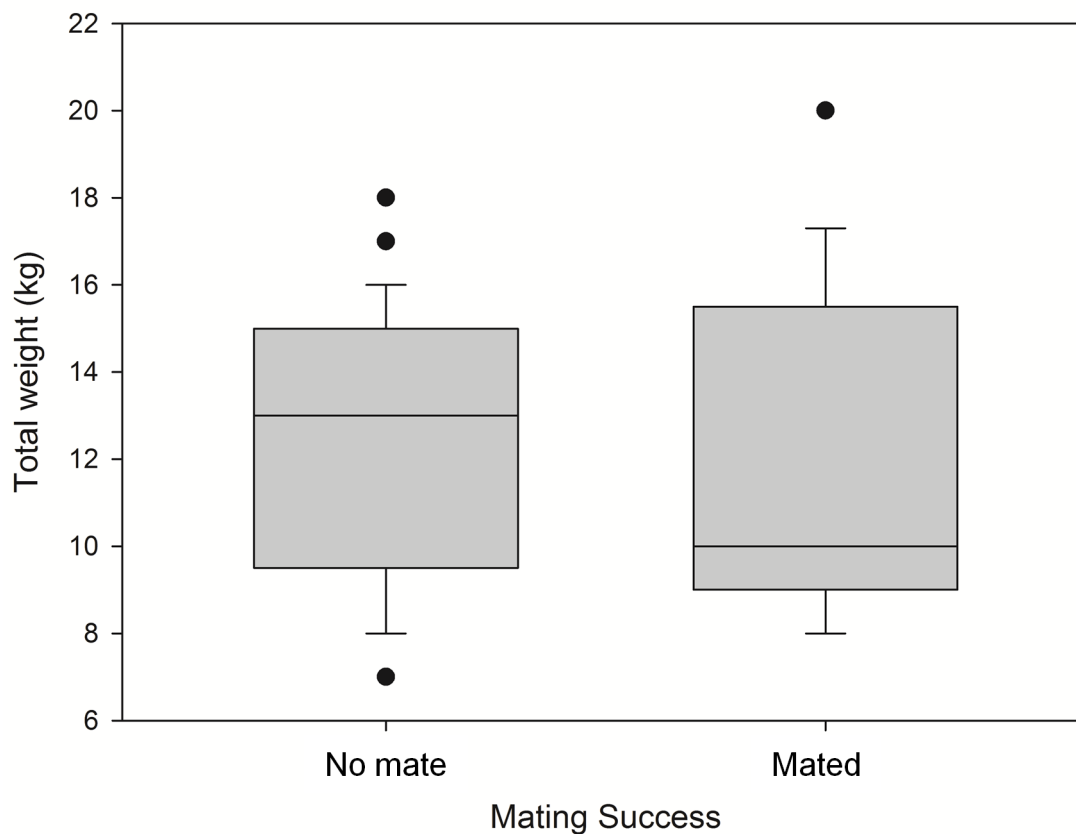


Figure 3. The weight of the male does not predict his success in copulating for *Chelonoidis denticulata*. Central lines are the mean value, boxes are standard deviation and points are the maximum and minimum values.

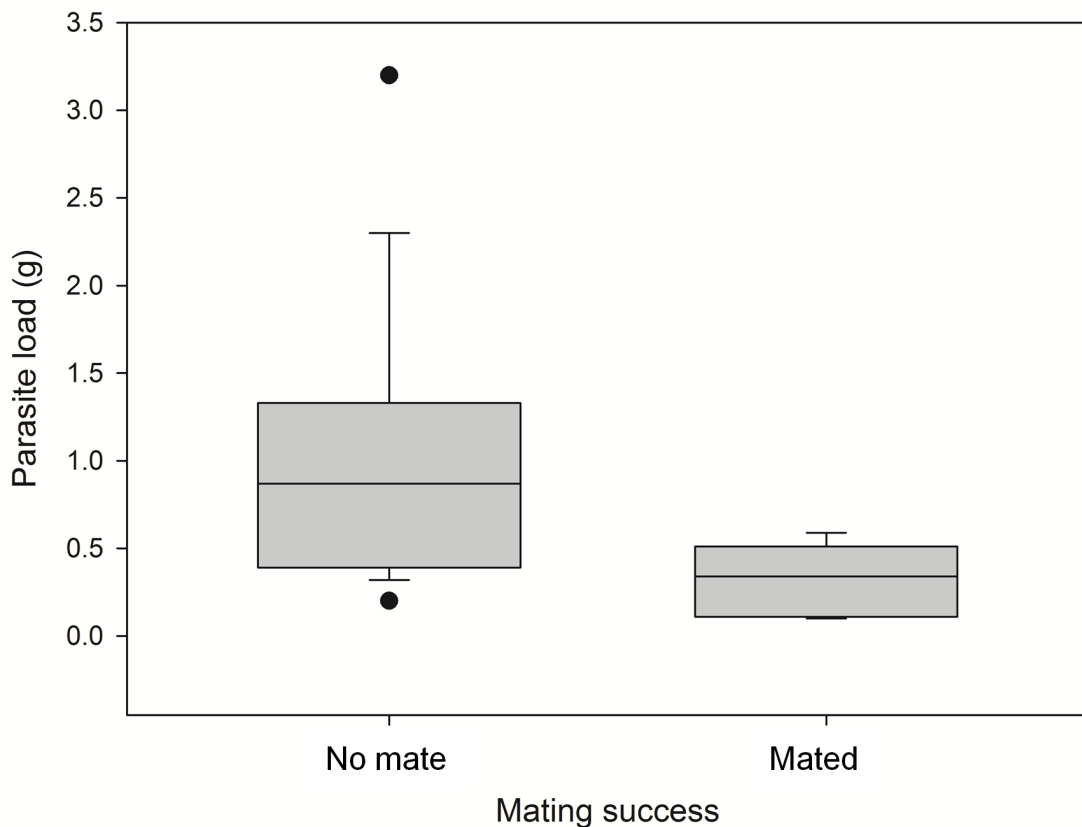


Figure 4. Males that copulated have less *Amblyomma dissimile* parasites (biomass) than males that did not copulate in *Chelonoidis denticulata*. Central lines are the mean value, boxes are standard deviation and points are the maximum and minimum values.

DISCUSSION

Our results indicate that parasite biomass influences the female choice for a partner more than male size or weight, a proxy for social dominance in the yellow-footed tortoise *C. denticulata*. Dominant males can offer their partners access to resources, while healthy males can offer good genes for the offspring and less parasite transfer to the female. In a semi-captivity environment such as our study area, with supplementary food, no natural predators and a high population density living close to humans, health becomes more important than resource-holding hierarchy, explaining our observations.

We found an average of 483 individuals/km² in our study area. This is about ten to twenty times denser than wild populations of the same species (Moskovits 1985, Stevenson *et al.* 2007). Such high density should only increase competition and contests if the disputed resources are limited (Wilson 2000). On the other hand, the dissemination of pathogens and ectoparasites should

be increased with host density (Wang *et al.* 2015). This turns health into a more urgent problem than social hierarchy in the study area.

Males of *C. denticulata* are larger, but not heavier than females. According to Molina (1992), this difference in size is one of the main factors that produce sex dimorphism in Testudines. A size difference is common in tortoises with dominance hierarchy and ritualized combats (Berry & Shine 1980), although there are several species with female-biased sexual size dimorphism, *i.e.*, females larger than males (Willesden & Hailey 1999, Gosnell *et al.* 2009), probably due to egg housing (Kaddour *et al.* 2008). In the *Gopherus agassizii* turtle, the larger the males, the higher they are in the dominance scale, which guarantees him access to better nests and more mates (Niblick *et al.* 1994). Mann *et al.* (2006) observed the same in their study on males of the tortoise *Chersina angulata*. Nevertheless, besides being larger, males are usually heavier too. Originally we expected the same to occur in *C. denticulata*, but our data indicates that males

are larger, but not heavier than females. During combats, males are often flipped upside-down by their contestants. The lighter the male, the faster he will return to the upright position (Kaddour *et al.* 2008), he is also more likely to move faster to forage, patrol his territory and locate females.

Females of *C. denticulata* did not prefer larger or heavier males in our study. Various studies report females with preference for larger and heavier males in many species (*e.g.*, Gonçalves-de-Freitas *et al.* 2009 for fish and Tsuji 2004 for amphibians, but see Wogel & Pombal Jr. 2007, for exception), including tortoises (Niblick *et al.* 1994, Mann *et al.* 2006, DeRussy *et al.* 2013). Male gigantism, as that observed in *C. denticulata*, is common in species with male-male competition, which occurs in *C. denticulata*, and with forced copulations, unreported in this species (Berry & Shine 1980). This result weakens the dominant male hypothesis for sexual selection.

Using size and weight as a proxy for dominance and aggression agrees with previous studies (Berry & Shine 1980, Craig 1986). By preferring a dominant male, the female will consequently opt for access to ecologic resources (Hamilton & Zuk 1982). An example of this behavior can be seen in the desert tortoise (*G. agassizii*), who chooses the most dominant partner because he controls the feeding grounds and shelters from the sun (Niblick *et al.* 1994). Moreover, social dominance can be an inheritable characteristic in social animals both by parental intervention (Engel *et al.* 2000) or expression of a phenotype more likely to reach the dominant status when adult (Moore 1990). Because of male's aggression, females are often forced to mate with high-rank individuals (Gonçalves-de-Freitas *et al.* 2009). Nevertheless, when females have the chance to choose, they may have reasons to avoid dominant males, as reviewed by Qvarnström & Forsgren (1998).

This is what we saw in our study. Females preferred to mate with the male with lower ectoparasite's biomass. According to Hamilton & Zuk (1982), the female preference for healthier males is a common trait. With this choice, she protects herself from being infected by the male's parasites, besides ensuring that her offspring receives genes for resistance to these diseases. In response to the

parasites, the animal suffers morphological and behavioral changes that may result in rejection by the female (Zuk *et al.* 1998). For example, males of the Hermann's tortoises (*Testudo hermanni*) in poorer health condition perform courtship displays and vocal callings that are negatively selected by the females (Galeotti *et al.* 2005). The same might be occurring with *C. denticulata*, although we cannot pinpoint how the female access information on her partner's parasite biomass.

Several species of parasites host on reptiles, one of the most common ectoparasite in the group are ticks (Cançado 2008, Fischer *et al.* 2009). According to Cançado (2008), the tick found in the study area, *A. dissimile*, is very common on tortoises. They adhere to the host with their mouthparts, the parasite's saliva release toxins that weaken the host, possibly killing it (Barbosa *et al.* 2006). Captivity conditions make tortoises more susceptible to infection with parasites (Barbosa *et al.* 2006). Therefore, in a semi-captivity condition such as the one observed in the study area, parasitism may be a stronger factor affecting the animal's survival than acquisition of ecological resources.

Our results indicate that social dominance will not guarantee reproductive success in *C. denticulata*. This has been reported before for *T. hermanni*, in which female post-copulatory sexual selection reduces the effect of social hierarchy on reproductive success (Cutuli *et al.* 2014). Why then is social hierarchy maintained in the studied tortoises? It is possible that a male's status can bring other benefits, such as access to shelters and preferred food, as pointed by other studies on social turtles (Boice 1970, Auffenberg 1978, Schneider *et al.* 2010). In many tortoises a good shelter can increase survival, providing reproductive sites and a suitable micro-climate for this ectothermic animal to hide (DeRussy *et al.* 2013). Therefore, even though social dominance will not provide more partners, reaching a high rank is still advantageous.

In the present study we tested the healthy male hypothesis against dominant male hypothesis for sexual selection in *C. denticulata*, a species with strong social hierarchy in a semi-captivity, high-density condition. Although the male's social dominance may be important for his survival, it is the ectoparasite load that

guarantees success with the females. Further studies are needed on this vulnerable species to evaluate what benefits arise from social dominance and how ectoparasites affect its survival.

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