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Reproductive state affects hiding behaviour under risk of predation but not exploratory activity of female Spanish terrapins

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ABSTRACT

Female investment during reproduction may reduce survivorship due to increased predation risk. During pregnancy, the locomotor performance of gravid females might be diminished due to the additional weight acquired. In addition, egg production may also increase thermoregulatory, metabolic and physiological costs. Also, pregnant females have greater potential fitness and should take fewer risks. Thus, females should ponder their reproductive state when considering their behavioural responses under risky situations. Here, we examine how reproductive state influence risk-taking behaviour in different contexts in female Spanish terrapins (*Mauremys leprosa*). We simulated predator attacks of different risk levels and measured the time that the turtles spent hiding entirely inside their own shells (i.e. appearance times). We also assessed the subsequent time after emergence from the shell that the turtles spent immobile monitoring for predators before starting to escape actively (i.e. waiting times). Likewise, we performed a novel-environment test and measured the exploratory activity of turtles. We found no correlations between appearance time, waiting time or exploratory activity, but appearance times were correlated across different risk levels. Only appearance time was affected by the reproductive state, where gravid females reappeared relatively later from their shells after a predator attack than non-gravid ones. Moreover, among gravid females, those carrying greater clutches tended to have longer appearance times. This suggests that only larger clutches could affect hiding behaviour in risky contexts. In contrast, waiting time spent scanning for predators and exploratory activity were not affected by the reproductive state. These differences between gravid and non-gravid females might be explained by the metabolic-physiological costs associated with egg production and embryo maintenance, as well as by the relatively higher potential fitness of gravid females.

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1. Introduction

One major concern in ecological studies is the estimation of the costs derived from reproduction (Renzick, 1985, 1992). Costs of reproduction may impact fecundity, survival or both (Bell, 1980; Brodie, 1989; Landwer, 1994; Shine, 1980). With respect to survival costs, optimality models predict that prey with greater initial fitness should be more cautious against predators (Cooper and Frederick, 2007). This prediction matches the “asset-protection principle” (Clark, 1994) that predicts that individuals with lower fitness would take higher risks than those with higher fitness, which would become asset protecting.

The cost of reproduction is defined as the negative trade-off between current reproductive investment and future reproductive output (Reznick, 1985; Roff, 1992; Stearns, 1992). In this way, current reproductive effort might represent a cost of reproduction expressed, for example, as diminished locomotor performance and lowered survivorship to the next clutch (Miles et al., 2000). In reptiles, some studies have suggested that decreased locomotor capacity of gravid females could be due to the additional weight of the clutch (Shine, 1980; Van Damme et al., 1989). Nevertheless, locomotor impairment of gravid females might be also due to physiological changes associated with pregnancy rather than a direct effect of physical burden (Brodie, 1989; Olsson et al., 2000). Gravid females may also change their behaviour independently of their increased weight (Cooper et al., 1990; Schwarzkopf and Shine, 1992). Along the same lines, because in ectotherms body temperature before ovoposition influences developmental rates as well as phenotypic traits of the resultant offspring (Shine, 2006),

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gravid females require basking at higher frequencies and for longer periods to reach optimal temperatures for correct embryo development (Blázquez, 1995; Braña, 1993; Brent Charland and Gregory, 1995). On the other hand, energy reserves allocated to reproduction might be important in terms of fecundity (Doughty and Shine, 1998). Metabolic rates tend to increase during gestation in pregnant female lizards due to embryogenesis (Angilletta and Sears, 2000; Robert and Thompson, 2000). In the same way, egg load occupies a great part of the body cavity that might compress internal organs, such as lungs, incurring a high energetic cost of breathing (Munns, 2013). Thus, switching behaviour in risky situations associated with gravidity in females might be also driven by thermoregulatory, metabolic and physiological requirements derived from egg production.

The main aim of our study was to test whether the reproductive state of female terrapins *Mauremys leprosa* imposes a cost in their risk-taking behaviour (i.e. hiding into their shells to avoid predators) and/or exploratory behaviour in a novel environment. This species is a predominantly aquatic turtle that remains submerged in water most of the time, but needs to bask and nest in terrestrial habitats (Andreu and López-Jurado, 1998). Turtles usually bask during long periods until they detect any potential predator and quickly dive into water reducing the probability to be captured (López et al., 2005a,b). The main turtle predators of this species come from terrestrial environments, mainly mammals and birds (Martín and López, 1990). We simulated predatory attacks under different levels of risk in the laboratory and measured the hiding response of gravid and non-gravid female turtles inside their shells. We also measured the exploratory activity of female turtles in a novel environment. Because these turtles may assess risk level and predator persistence after a simulated attack (Martín et al., 2005; Ibáñez et al., 2014), we expected that gravid females should modulate their hiding behaviour after the predator attack by considering their higher costs in terms of performance, thermoregulation and metabolism in comparison with non-gravid females. In addition, gravid females have higher potential reproductive value and hence they should act more cautiously than non-gravid ones (Clark, 1994; Cooper and Frederick, 2007). Thus, we predicted that gravid females should spend longer times hidden inside their shells until they decide to switch and escape actively to a safer refuge. In the same way, we also predicted that reproductive state should affect exploratory activity behaviour in a novel environment. We expected that gravid females should be less explorative than non-gravid ones due to their lower degree of mobility and their more constrained thermoregulation and metabolism. Alternatively, the opposite pattern could also be expected because the reduced manoeuvrability of gravid females could force them to increase their inspective behaviour to obtain detailed information of the surroundings and successfully escape from possible predators (Frommen et al., 2009).

2. Material and methods

2.1. Animals of study and husbandry

We captured 20 adult female *Mauremys leprosa* turtles during the spring of 2011 in several small streams, ponds and tributaries of the Gadiana River located within dehesa oaklands (Alconchel and Olivenza, Badajoz province, SW Spain). We used a modified version of the traditional underwater funnel traps, which include a mesh chimney that reaches from the body of the trap to the surface, allowing the turtles to come to the surface to breath (T and L Netmaking, Mooroolbark, Victoria, Australia; Kuchling, 2003). We baited traps with sardines and protected them from terrestrial predators by waiting in the proximity. We checked the traps every

hour to collect turtles. All collected turtles were alive and did not show any sign of being stressed inside the traps.

The turtles were transported in plastic cages (80 × 40 cm and with a height of 50 cm) to “El Ventorrillo” Field Station, near Navacerrada (Madrid province) where experiments were conducted. They were transported by car and the journey lasted four hours, during which a constant temperature of 23 °C was maintained to avoid heat stress. Turtles were housed in individual outdoor plastic aquaria (60 × 40 cm and 30 cm high) containing water and rocks that allowed turtles to bask out of water. The photoperiod and temperature were the same as those of the surrounding area. Turtles were fed with minced meat, earthworms and a commercial compound of turtle “pellets” three times a week. They were held in captivity and the investigator minimized contact with the animals before and during all behavioural experiments to avoid possible effects of habituation. All individuals were healthy and in good condition during the tests. Once the experiments had finished, they were returned to the exact locations of capture at the first days of August.

2.2. Reproductive state, size and body condition of females

In turtles, X-ray photographs have been effectively used to directly evaluate clutch size (Gibbons, 1982; Gibbons et al., 1982; Iverson, 1991). This technique allows reproductive data to be gathered in a non-destructive manner (Gibbons and Greene, 1979). Thus, we used direct digital X-ray photography (Direct Digital System, SEDECAL) to determine gravity state of female turtles. Turtles were X-rayed on their abdomen, where the absence or the entire clutch of eggs could be seen on a single plate (gravid: $N=7$; non-gravid: $N=13$; egg load of gravid females: mean ± 1 SE = 8.1 ± 0.6 eggs, range = 6–10).

We used a metal ruler (1 mm precision) to measure carapace length (CL) as the greatest straight-line distance from the anterior end to the posterior end of the shell (mean ± 1 SE = 190 ± 3 mm, range 168–209 mm). We used a Pesola spring scale to measure body weight (mean ± 1 SE = 952 ± 40 g, range = 680–1300 g).

2.3. Hiding behaviour

We simulated predatory attacks on individual turtles ($N=20$) in outdoor conditions always on sunny days (approximately 25 °C). For the ‘low risk’ treatment, we took one turtle from its home cage, handled it once, briefly (approx. 20 s) and gently, and then released it prone in the middle of an open field with short grass. To avoid other confounding effects that might affect risk perception of turtles (Burger and Gochfeld, 1993; Cooper, 1997; Cooper et al., 2003), the same person wearing the same clothing performed all tests following the same procedure. Turtles were used only once in each trial to avoid stress; the trials were spaced sufficiently apart (at least 1 day) so that fatigue resulting from one test did not affect subsequent tests. Before the trials, we allowed turtles to bask in their outdoor home cages for at least 2 h, which allowed them to attain and maintain an optimum body temperature within the tolerated and preferred temperature range of the species (Andreu and López-Jurado, 1998; Keller and Busack, 2001).

After the simulated attacks, the experimenter retreated and remained immobile observing with binoculars from a hidden position situated 5 m away from the turtle. After the simulated attack, and as a consequence of handling, turtles typically remained immobile and withdrawn entirely into the shell (i.e. the head, legs and tail were not visible at all or were only barely visible from above the carapace). We then measured the time that the turtle spent withdrawn into the shell from the time when we released it on the ground to the moment when its head emerged from the shell (i.e. when the eyes could be seen from above the shell; ‘appear-

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