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ORIGINAL ARTICLE

José Martín · Iván Marcos · Pilar López

When to come out from your own shell: risk-sensitive hiding decisions in terrapins

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Abstract Animals should optimize the decision of when to come out from a refuge after a predator's unsuccessful attack because hiding may be costly. Many prey run to hide in refuges in their habitat, whereas others are sessile and take refuge in a protective structure surrounding their body. An intermediate situation is when animals, such as turtles, have morphological structures that provide some partial protection, but they are also able to escape actively to safer refuges. This might complicate hiding decisions predicted by the theory of optimal-refuge use. We studied antipredatory tactics of Spanish terrapins (*Mauremys leprosa*) in response to simulated predatory attacks with different characteristics (i.e. combinations of several risk factors) and under different conditions (i.e. proximity to safe refuges), which should contribute to overall risk-level estimation. We specifically examined how risk level affected time spent withdrawn into the shell and time until turtles switched to an active escape tactic. The results showed that turtles were able to adjust their hiding behavior by assessing the risk of emerging before the predator had left the area. However, increasing hiding time may also increase the risk that the predator was able to injure or kill the turtle. Thus, the possibility of switching the antipredatory tactic to an alternative active escape to safer refuges (i.e. water) also influenced hiding times.

Keywords Hiding behavior · Refuge use · Predation risk · *Mauremys leprosa* · Turtles

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J. Martín (✉) · I. Marcos · P. López
Departamento de Ecología Evolutiva,
Museo Nacional de Ciencias Naturales, CSIC,
José Gutiérrez Abascal 2, 28006 Madrid, Spain
e-mail: Jose.Martin@mncn.csic.es
Fax: +34-91-5645078

Introduction

Many prey respond to predator presence by using refuges (Cooper 1998; Sih et al. 1992). However, refuge use may have some costs (Dill and Fraser 1997; Martín and López 1999; Sih 1997), and some refuges may be readily available, but not be entirely effective for eluding predators (Martín and López 2000). For these reasons, animals should optimize the decision of when to come out from a refuge after a predator's unsuccessful attack, either by balancing antipredator demands with costs of refuge use (Dill and Fraser 1997; Sih 1992, 1997) or, when refuges are only partially safe, by assessing risk level accurately to decide when to switch to alternative antipredatory tactics if the predator persists in the attack (Martín and López 2003).

Many animals run to hide in refuges such as rock crevices or thick vegetation where predators cannot access them, but they are also able to escape by fleeing without hiding, to choose the refuge type, and to change between refuges after persistent attacks (Cooper 1998; Martín and López 1999, 2003). In contrast, many other species are relatively sessile and can only take refuge in a protective structure surrounding their body, such as polychaete tubeworms, caddis-fly larvae, mollusks, or barnacles (Dill and Fraser 1997; Dill and Gillett 1991; Johansson and Englund 1995). These species are not able to switch to an effective active escape tactic, and their hiding decisions depend just on costs of hiding and on assessing the probability that the predator is waiting outside before re-emerging (Hugie 2003; Sih 1992). An intermediate situation is when animals have morphological or protective structures that provide some partial protection, but they are also able to escape actively to safer refuges in their habitat (Edmunds 1974; Endler 1986). This is a particular situation that occurs in animals such as hermit crabs, hedgehogs, pangolins, porcupines, armadillos, some fishes, and turtles (Doncaster 1993; Ernst and Barbour 1989; McLean and Godin 1989; Mima et al. 2003; Scarratt and Godin 1992; Sweitzer and Berger 1992), and which could complicate escape and hiding decisions predicted by the theory of optimal refuge use (Hugie 2003; Martín and López 1999; Sih 1992, 1997; Ydenberg and Dill 1986). However, the factors that modulate refuge use in these animals remain little explored (Mima et al. 2003).

Turtles are characterized by having a shell that evolved as a structural defensive adaptation against predators in a semiaquatic ancestor, and which might have facilitated a slow-moving and sustained searching foraging tactic (Ernst and Barbour 1989; Greene 1988). Turtles typically move away to safe refuges if a threat is perceived at a distance. However, because turtles move relatively slowly, predators can often approach closely or capture them. Then, turtles respond to predators by withdrawing the limbs, tail, and the head into the shell. In some species, there are even shell-closing mechanisms that form a tightly closed box around the head and legs. The shell is, however, not always an entirely safe refuge, as some predators are sometimes able to break the shell with their jaws (e.g., crocodiles or wildboars), or to access the soft exposed parts of the turtle's body with the beak (e.g., raptors or storks). Thus, some turtles have other alternative defensive mechanisms, such as discharging strong-smelling fluids from the cloaca. Also, turtles will always try to escape to safe refuges such as water or thick vegetation before the predator approaches or after attempting to deter the attack of a close predator by withdrawing into the shell (see review in Greene 1988).

Increasing time spent withdrawn into the shell might finally persuade a predator to leave the turtle (Hugie 2003), but it might also increase the probability that the predator is able to break the shell or, at least, injure the soft parts of the turtle (see Mima et al. 2003 for a similar situation in hermit crabs). Additionally, time spent in the shell may be costly in terms of loss of time available for other activities. Thus, the decision of when to come out from the shell and initiate active escape should be influenced by the risk level posed by the predator, and also by the probability of reaching a safe refuge before the predator could capture the turtle and reach the exposed parts of its body. This would require turtles to assess risk level accurately and flexibly employ different antipredatory tactics as risks change. At various stages of predator-prey encounters, prey must select among several potential defenses (Endler 1986; Lima and Dill 1990), and decide when to switch from one defense to another. However, this hypothesis remains little explored in relation to refuge use or hiding decisions (Mima et al. 2003), and is specially untested in animals such as turtles, which use their own morphological defensive structures as a refuge. Moreover, in spite of the conspicuous antipredatory behavior of turtles, only anecdotal observations refer to this behavior (see reviews in Ernst and Barbour 1989; Greene 1988).

In this paper, we experimentally tested the factors that determine the hiding decisions of Spanish terrapins (*Mauremys leprosa*) under variable conditions that may affect their risk perception. We simulated predatory attacks with different characteristics (i.e., combinations of several risk factors) and under different conditions (i.e., proximity to safe refuges), which should contribute to overall risk-level estimation. We specifically examined how risk level affected time spent withdrawn into the shell and time until turtles switched to an active escape tactic.

Methods

Species and study site

The Spanish or Mediterranean terrapin (*M. leprosa*) is a semiaquatic medium-sized turtle widespread in the south and central Iberian Peninsula and northwestern Africa (Andreu and López-Jurado 1998; Busack and Ernst 1980; Keller and Busack 2001). These turtles are predominantly aquatic, but they need to come to land for basking and for egg-laying, where they are potential prey of birds and mammals (Martín and López 1990). For this reason, during basking bouts, turtles are very wary, being extremely alert and vigilant, and diving quickly into the water at the least disturbance. However, because turtles are relatively slow-moving, predators may often be able to capture them before they reach water safely, or even to extract them from shallow water (e.g., during summer drought). Then, turtles typically withdraw into their shell, but they will not pass up the opportunity to escape to a safer refuge (i.e., deep water) if the predator releases them temporarily.

During May 2003, we used funnel traps to capture turtles (carapace length, mean+SE=152+5 mm) in several ponds and small tributary streams of the Guadiana river. These freshwater habitats, which are located inside dehesa-oak woodlands at Olivenza and Alconchel (Badajoz Province, southwestern Spain), held a substantial population of terrapins. In this area, we have recorded the presence of a relatively large number of potential predators of this turtle: birds, such as white storks (*Ciconia ciconia*), grey herons (*Ardea cinerea*), Egyptian vultures (*Neophron percnopterus*), or black kites (*Milvus migrans*), and mammals such as wild boars (*Sus scrofa*), foxes (*Vulpes vulpes*), or otters (*Lutra lutra*) (Andreu and López-Jurado 1998; Keller and Busack 2001; Martín and López 1990).

Turtles were individually housed at "El Ventorrillo" Field Station near Navacerrada (Madrid province, central Spain), in outdoor terraria (80×50 cm) containing water and stones that allowed turtles to bask out of the water. They were fed bits of minced lamb, earthworms, and slugs three times weekly. The photoperiod and temperature were those of the surrounding region. Turtles were held in captivity at least 2 weeks before testing, to allow acclimation to captivity conditions. However, to avoid habituation to human presence, we checked terraria, changed water, and provided food after sunset or before sunrise, when turtles were less active. During other times, we did not stay close to the terraria, but observed terraria with binoculars from a hidden vantage point to monitor turtles' behavior. We also avoided handling turtles except when necessary for the experiments. Prior to experiments, turtles always tried to escape quickly when we approached the terraria and hid immediately in their shell when we tried to touch them. This was similar to their behavior in the field after the first capture. Thus, we were confident that turtles had not habituated to humans during the trials, and that they reacted to simulated attacks as if we were predators. All the turtles looked healthy during the trials. We did not observe behavioral or physiological changes from possible stress of experiments; at the end of the experiment, all had maintained or increased their original body mass, and they were returned to their exact capture sites.

Hiding behavior

We simulated predatory attacks toward individual turtles in outdoor circular enclosures (150 cm diameter) filled with either a sand substrate (“land” treatment) or with 2-cm-deep clean water (“water” treatment). Thus, we simulated two microhabitat conditions, where the turtle was attacked on land far from a water body, or at the shallow water edge, presumably close to safer deep-water areas. This was justified because, in the habitat of these turtles, most ponds and streams have shores with shallow water that gradually increase in water depth towards the centre of the water body. Tests were performed, on land and in water, under two different levels of predation risk (i.e., threat of attack), and under two conditions of persistence of the predator after the attack. To simulate the two levels of risk, we took one turtle from its home cage, and either handled it once, briefly and gently, and then released it in the middle of the experimental enclosure (“low” predation-risk level), or we handled it for a few seconds, took it to the enclosure, and continued simulating the attack by handling and tapping the turtle’s shell with the hand five times for 20 s before releasing the turtle (“high” predation-risk level). Thereafter, and without further handling, the experimenter simulated either a persistent waiting predator, by remaining immobile at a point close to the enclosure (less than 1 m) (“close” treatment), or a simulated predator that had left the area, by retreating to a hidden position at a distance of 5–7 m (“far” treatment). To avoid other confounding effects that may affect risk perception of turtles (Burger and Gochfeld 1993; Cooper 1997), the same person wearing the same clothing performed all tests in a similar way.

Each individual turtle (*N*=16) was tested in all of the eight possible combinations of treatments, and order of presentation of treatments was randomized. Turtles were used only once in each trial to avoid stress; the trials were spaced sufficiently (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 optimal body temperature within the activity and preferred temperature range of the species (Andreu and López-Jurado 1998; Keller and Busack 2001).

Experiments were recorded from above on videotape (Hi-8 format, 40 ms per frame) using a video-camera aligned perpendicularly to the enclosure. Timing and characteristics of turtles’ hiding behavior were measured by a frame by frame analysis of the videotapes. 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 or were only barely visible from above the carapace). We then recorded the time that the turtle spent withdrawn into the shell, from when we released it in the enclosure until the head emerged from the shell (i.e., when the eyes could be seen from above the shell; “appearance time”), and the time from appearance until the turtle emerged entirely from the shell and initiated walking (“waiting time”). We chose these two hiding times because when the turtle was completely withdrawn into the shell, it had no visual information on the predator or the surrounding habitat until the “appearance time”. Thereafter, “waiting time” represented the time that the turtle could spend visually evaluating the situation, until it decided when to switch to active escape.

Hiding behavior when the turtle was turned over onto its carapace by the predator

In this experiment, we followed the same procedure and treatments as above, but turtles (*N*=16) were released in the enclosures placed onto their carapace with the plastron upside. We, thus, simulated a predator that had turned over the turtle to prevent it from escaping and, thus, attack it more easily. This is a higher risk situation because in this position a turtle could not walk but, before escaping, it had to extend its legs and neck entirely outside of the shell, and use them to turn itself back to its normal position (personal observation). We recorded “appearance time” (i.e., when the head emerged from the carapace and the eyes could be seen from above) and “waiting time” from then until the turtle initiated walking after having emerged from its shell and turned to its normal position. We considered just this latter time because turtles typically initiated walking immediately after having turned over, and this was done immediately after having extended the legs and neck. Thus, these partial times were not independent and would yield similar results.

Effects of repeated attacks

In this experiment, we simulated repeated successive attacks each time the turtle switched from hiding in the shell to active escape. Prey may consider that successive attacks represent an increase in the risk of predation because each new attack may indicate that the predator persists in capturing that particular prey (Cooper 1998; Martín and López 2001). In each test, we took one turtle from its home cage, handled it once, briefly, and then released it in the middle of the experimental enclosure, where there was one of two types of substrate (land vs water). The experimenter always remained close to the enclosure, and immediately after the turtle emerged from the shell and started walking, he simulated another predatory attack by handling the turtle again in the same way as in the first attack. We simulated a total of five successive attacks with the same procedure. Each individual turtle (*N*=25) was tested on different days in the two types of substrate in a randomized sequence. These turtles were different individuals than those used in the first experiments, and were captured later at the same field sites.

Data analyses

Previous analyses showed no differences between sexes in hiding behavior and, thus, we considered males and females together. We used three-way repeated measures analyses of variance (ANOVAs) to test for differences in appearance or waiting times of the same individuals in each condition of substrate (land vs water), predation risk (low vs high), and predator persistence (close vs far) (all within-subjects factors). Similarly, we used two-way repeated measures ANOVA to test for differences in appearance or waiting times in each condition of substrate (land vs water), and between successive repeated attacks (all within-subjects factors). Data were log-transformed to ensure normality (Shapiro-Wilk’s test). Tests of homogeneity of variances (Levene’s test) showed that variances were not significantly heterogeneous after transformation (Sokal and Rohlf 1995).

Results

Hiding behavior

Appearance times of turtles were significantly longer on land than in water (three-way repeated measures ANOVA: $F_{1,15}$=13.84, *P*=0.002), and significantly longer when the risk level was high ($F_{1,15}$=11.14, *P*=0.004), but they were not significantly dependent on predator persistence ($F_{1,15}$=2.35, *P*=0.15). However, the interaction between substrate type and risk level was significant ($F_{1,15}$=19.61, *P*=0.0005) (Fig. 1a). Risk level strongly affected appearance times when turtles were on land, but not in the water. Other interactions were not significant (*P*>0.20 in all cases).

Waiting times were significantly longer on land than in water (three-way repeated measures ANOVA: $F_{1,15}$= 19.75, *P*=0.0005), and significantly longer when the predator was close to the turtle after the attack ($F_{1,15}$= 14.83, *P*=0.0016), but they were not significantly dependent on risk level ($F_{1,15}$=0.40, *P*=0.54) (Fig. 1b). However, the interactions between substrate type and

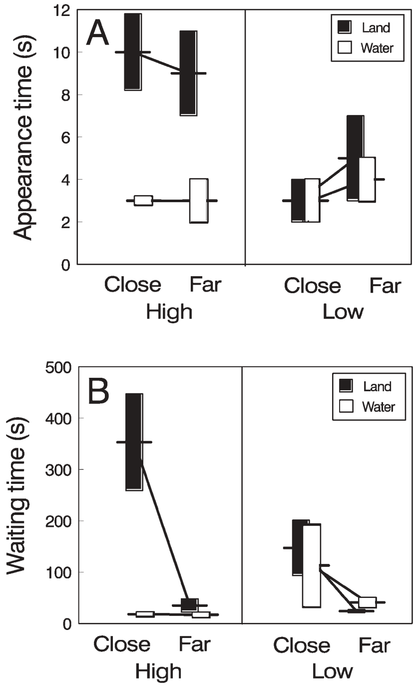

Fig. 1 Mean (+SE) **a** appearance and **b** waiting time that turtles spent withdrawn in the shell after suffering a simulated attack by an experimenter with two different risk levels (“low” vs “high”), in two different substrates (“land” vs “water”) and when, thereafter, the experimenter either remained close to the turtle (“close”) or retreated to a far hidden position (“far”).

predator persistence ($F_{1,15}=18.48$, $P=0.0006$) and between substrate type and risk level ($F_{1,15}=15.73$, $P=0.001$) were significant. Waiting times were particularly long when turtles were on land and predators remained nearby. Other interactions were non-significant ($P>0.25$ in all cases).

Hiding behavior when the turtle was turned over onto its carapace by the predator

Turtles appeared significantly sooner from the shell when they were in water (three-way repeated measures ANOVA: $F_{1,15}=39.48$, $P<0.0001$), but there were no significant differences dependent on risk level ($F_{1,15}=0.06$, $P=0.81$) or predator persistence ($F_{1,15}=0.69$, $P=0.42$) (Fig. 2a). None of the interactions were significant ($P>0.30$ in all cases).

Waiting times were significantly longer on land than in water (three-way repeated measures ANOVA: $F_{1,15}=34.08$, $P<0.0001$), and when the predator was close to the turtle after the attack ($F_{1,15}=43.87$, $P<0.0001$), but were not significantly dependent on risk level ($F_{1,15}=1.09$, $P=0.31$) (Fig. 2b). However, the interaction between substrate type and predator persistence was significant ($F_{1,15}=17.10$, $P<0.001$). Predator persistence strongly affected waiting times when turtles were on land, but not in the water. Other interactions were not significant ($P>0.20$ in all cases).

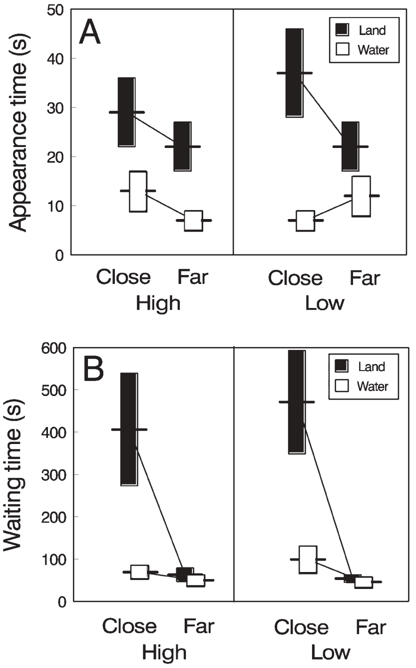

Fig. 2 Mean (+SE) **a** appearance and **b** waiting time that turtles spent withdrawn in the shell after suffering a simulated attack by an experimenter that had turned it over onto its carapace, with two different risk levels (“low” vs “high”), in two different substrates (“land” vs “water”) and when, thereafter, the experimenter either remained close to the turtle (“close”) or retreated to a far hidden position (“far”).

Effects of repeated attacks

Successive appearance times were not significantly different (two-way repeated measures ANOVA: $F_{4,96}=1.47$, $P=0.22$), and, on average, did not differ significantly depending on substrate ($F_{1,24}=3.63$, $P=0.07$), but the interaction between repeated attacks and substrate was significant ($F_{4,96}=4.31$, $P=0.003$). There was little difference between successive appearance times in water, whereas on land the first appearance time was shorter than subsequent times (Fig. 3a).

Successive waiting times were significantly different (two-way repeated measures ANOVA: $F_{4,96}=16.60$, $P<0.0001$) and, on average, significantly longer on land ($F_{1,24}=15.21$, $P<0.001$), and the interaction between repeated attacks and substrate was significant ($F_{4,96}=14.71$, $P<0.0001$). Successive waiting times differed little in water, whereas on land the first time was longer than subsequent waiting times (Fig. 3b).

Discussion

The results show that turtles are able to adjust their hiding behavior by assessing the level of predation risk. Turtles seem to adjust time spent withdrawn into the shell in a similar way as other relatively sessile animals adjust hiding times inside their defensive structures (e.g. Dill and Fraser 1997; Dill and Gillett 1991; Johansson and

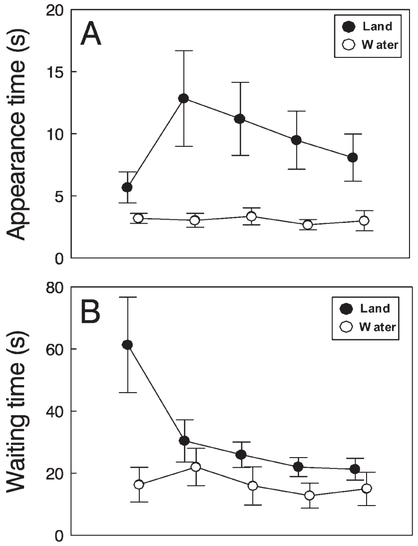

Fig. 3 Mean (+SE) of successive **a** appearance and **b** waiting times that turtles spent withdrawn in the shell after suffering repeated simulated attacks by an experimenter each time the turtle switched from hiding to active escape on two different substrates ("land" vs "water").

Englund 1995), and also as mobile animals adjust the use of refuges in their habitat (Cooper 1998; Martín and López 1999). Thus, as predicted by theoretical models, hiding times were partly dependent on risk of emerging before the predator had left the area (Hugie 2003; Sih 1992). However, our experiments show that the possibility, or the need, of switching their antipredatory tactic to an alternative active escape to safer refuges also influences hiding times of turtles.

Appearance times from the shell were longer when risk level, as indicated by the predator's behavior during the attack, was higher. By increasing time spent withdrawn in the shell, turtles may expect the predator to depart (Hugie 2003; Martín and López 1999; Sih 1992). However, increasing hiding time may have costs (e.g., loss of time available for other activities, and possibly risk of overheating if ambient temperature is too high) (Sih 1997), and it may also increase the risk that the predator is able to injure or kill the turtle by breaking the shell, or by accessing the partially exposed soft parts of the body. Thus, turtles may face a trade-off when deciding hiding times. In contrast to sessile animals, turtles have the option of escaping to safer refuges, and the likelihood of success of this alternative tactic seemed to influence hiding times. Thus, appearance times were dependent on predator risk level when turtles were on land (i.e., far from refuges), but not in water, when the chances of a successful escape to deep water may be higher than the expectation that the predator would be deterred by the shell protection. Alternatively, higher thermal costs of cold water when compared to land temperatures (Martín and López 1999), and the potential presence of other predator types in water might explain the observed differences. This is, however, unlikely, as field observations indicate that turtles at the water shore quickly escape into deep water, where these potential costs should be higher, and not outside of water as expected if they were avoiding these costs.

Appearance from the shell was not dependent on predator persistence, very likely because, when a turtle was withdrawn into its shell, it could not visually monitor the presence of the predator outside. This was favored in our experiment because the simulated predator remained immobile and silent, and did not handle the turtle after the attack. It remains possible that hiding turtles could have information on real predators' persistence through tactile, vibrational, or hearing cues, if predators are moving or making noise nearby, and that this may affect appearance times too. In any case, once the turtle had its eyes outside the shell, it could acquire more visual information on the predator. Thus, waiting times were affected by predator persistence. However, similar to the effect of risk level, this additional factor was important only when the turtle was on land, and there were no alternatives to hiding in the shell, but it did not seem important when there was a possibility of escaping to a safer water refuge. Even if the predator is close, it might be safer to try to flee to deep water, when this seems likely, than waiting longer in the shell.

Turning the turtles onto their carapace clearly increased their risk perception because in this position turtles were prevented from fleeing, and required a risky "maneuver" to return to their normal position. Thus, in response to this higher risk, turtles increased appearance times (i.e., pooling all trials, average appearance times when turned over were 4 times longer than in the normal position). However, there were no differences between initial risk levels, probably because risk level when a turtle is turned over is already much higher than the simulated risk levels when they were handled. Then, turtles would respond to this greater risk factor, rather than to differences in handling. As in the previous experiment, predator persistence was not considered, or could not be assessed, but substrate type did influence appearance times. Also, waiting times were longer than in the normal position (about 1.7 times longer on average) in response to the higher risk level. Waiting times were influenced by predator persistence, but this depended on substrate, which again supported the theory that the presence of water offered the possibility of switching the antipredatory tactic.

The effects of repeated attacks on hiding behavior also highlight the differences between turtles and other animals with respect to refuge use. Each new attack may increase prey perception of risk, either because an individual predator persists in capturing that particular prey, or because the density of different individual predators in the area has increased (Cooper 1998). Thus, other prey species increase the duration of successive hiding times, because the probability of a new attack in the immediate future is high, and they should wait longer until the predator leaves the area (Cooper 1998; Martín and López 2001; Polo et al. 2004). However, for turtles, a persistent predator may indicate that it is confident, or is more motivated, in trying to break the turtle's defenses, because otherwise it should have left after the turtle had withdrawn into the shell the first time.

Also, the probability that a persistent predator was actually effective, irrespective of its motivation, may increase with time. However, in response to this increase in risk, turtles did not increase successive hiding times as other animals do. In contrast, and depending on substrate, turtles either maintained constant successive hiding times in water, or even tended to decrease successive hiding times on land. In turtles, repeated attacks may increase perception that the shell per se is becoming less effective in deterring the predator after each successive attack. Thus, turtles should change their tactic and try to escape sooner, because remaining hidden for longer only increases the risk of being killed.

The variation in responses observed in turtles would be similar to the observed differences between fish species with different defensive morphological armour, with less-protected species starting to flee earlier (McLean and Godin 1989). Also, refuge duration and time to switch to fleeing in hermit crabs depends on vulnerability of the shell used as refuge (Mima et al. 2003). Therefore, the decision of when to switch from passive defense to active escape may adjust to the expected by the optimal escape theory (Ydenberg and Dill 1986), because when risk increased, turtles and hermit crabs initiated active escape earlier. Alternatively, it remains possible that turtles habituated to the simulated attack during the trial, and because the danger might not be considered serious enough after an increasing number of unsuccessful repeated attacks, they decided not to prolong hiding times and actively escape. The trade-offs with potential costs of hiding, such as the loss of opportunities for foraging or thermoregulation constraints, should also be examined to ascertain the applicability of optimal-escape and refuge-use theories to a wider range of prey species.

In conclusion, the antipredator decisions of *Mauremys leprosa* turtles were influenced by the risk of predation posed by the predator, by their perception that the shell was effective in deterring the predator, and by the likelihood of success of alternate tactics. Turtles were able to flexibly employ different antipredatory tactics as risks changed, switching from passive defense to active escape when risk increased, but also when the availability of safer refuges in the habitat (i.e. water) increased. However, the results must be confirmed on free-living animals before a generalization of the conclusions is possible.

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