Interference competition between native Iberian turtles and the exotic *Trachemys scripta*

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The red-eared slider, *Trachemys scripta elegans*, is a worldwide invasive species, currently introduced in most freshwater habitats as a consequence of the exotic pet trade. In the Iberian Peninsula, this American turtle is competing and displacing the Iberian turtles, *Emys orbicularis* and *Mauremys leprosa*. Recent studies have pointed out to diverse competitive advantages of sliders over Iberian terrapins. For instance, native turtles avoid chemical cues from *T. scripta*, which is more aggressive and dominant in direct competition for food and basking places. This avoidance behaviour displayed by Iberian terrapins might serve as a spacing mechanism to avoid unfavourable competitive interactions with the introduced species. Sliders also benefit from morphological and thermoregulatory advantages: they are more spherical, thus presenting a less surface to volume ratio and a greater thermal inertia that facilitates heat retention. On the other hand, introduced turtles show a more accurate assessment of predatory risk in altered habitats, and are more efficient predators of local prey than native species. These inter-specific asymmetries could contribute jointly to the greater competitive ability of introduced *T. scripta*, thus facilitating the expansion of this alien species in detriment of native populations of Iberian terrapins.

Key words: biological invasions; chemical communication; competition; Iberian turtles; morphology; thermal biology.

Interferencias competitivas entre los galápagos nativos ibéricos y el galápago exótico Trachemys scripta. El galápago de Florida, Trachemys scripta elegans, es una especie invasora a nivel mundial, introducida en la mayor parte de los ecosistemas acuáticos como consecuencia del comercio masivo de mascotas. En la Península Ibérica, este galápago americano compite y desplaza a los galápagos ibéricos, Emys orbicularis y Mauremys leprosa. Estudios recientes han puesto de manifiesto la existencia de diversas ventajas competitivas del galápago de Florida sobre los galápagos nativos ibéricos. Por ejemplo, los galápagos nativos evitan ocupar espacios donde detectan secreciones químicas de los galápagos exóticos, quienes se muestran más agresivos y dominantes en la competencia directa por la comida y los recursos de asoleamiento. Este comportamiento aversivo podría ser utilizado por las especies nativas para evitar las interacciones competitivas desfavorables con la especie invasora. Los galápagos de Florida se benefician también de ventajas morfológicas y termorreguladoras: presentan una forma más esférica y por tanto una menor relación superficie-volumen y una mayor inercia térmica que facilita la retención de calor. Por otra parte, los galápagos exóticos muestran un mejor ajuste del riesgo de depredación en hábitats alterados y poseen ventajas en la captura de presas nativas. Estas asimetrías inter-específicas podrían contribuir conjuntamente a una mayor habilidad competitiva del galápago de Florida, facilitando la expansión de esta especie invasora en detrimento de las poblaciones nativas de galápagos ibéricos.

Key words: biología térmica; competencia; comunicación química; galápagos ibéricos; invasiones biológicas; morfología.

The introduction of alien species outside their natural distribution ranges represents, after habitat destruction, the second greatest threat to biodiversity (WILCOVE *et al.*, 1998; GUREVITCH & PADILLA, 2004). Introduced species have caused severe alterations in terrestrial and aquatic ecosystems, altering energy flows and displacing native organisms from their ecological niches (HERBOLD & MOYLE, 1986; WILLIAMSON, 1996; MOONEY & HOBBS, 2000; LOCKWOOD *et al.*, 2007). Competition for resources is one of the most habitual ways alien species may impact native populations (SHIGESADA & KAWASAKI, 1997; LOCKWOOD *et al.*, 2007).

The red-eared slider (Trachemys scripta elegans Wied, 1839) is a chelonian belonging to the family Emydidae. Native from Southeast USA and Northeast Mexico, the species has become worldwide, introduced especially in Mediterranean countries, as a result of the massive exotic pet trade occurred during the last decades (LUISELLI et al., 1997; CHEN & LUE, 1998; PLEGUEZUELOS, 2002). Trachemys scripta is a semiaquatic turtle, generalist and ubiquitous, with a great adaptive capacity (GIBBONS, 1990). In the Iberian Peninsula, a large number of young red-eared sliders have been imported from the USA and released in the natural environment, causing a great expansion of the species. Many populations have become naturalized in marshes and wetlands of the littoral, as well as in dispersed points inland (PLEGUEZUELOS, 2002). These populations may cause important impacts on the ecosystems and eventually the displacement of native fauna (DA SILVA & BLASCO, 1995; PLEGUEZUELOS, 2002; VILÀ et al., 2008; LINDSAY et al., 2013).

Field observations have pointed out the existence of competitive interactions between *T. scripta* and the two species of Iberian turtles,

the European pond turtle, *Emys orbicularis*, and the Spanish terrapin, *Mauremys leprosa*. These two native species have suffered a considerable recession of their populations and a reduction of their distribution ranges (Figs. 1a,b) during the last decades, both being currently considered as endangered (TORTOISE & FRESHWATER TURTLE SPECIALIST GROUP, 1996; VAN DIJK *et al.*, 2004). Habitat destruction and human pressure are major factors responsible for this decline, but competition with exotic introduced turtles might be worsening the state of the remaining populations (Fig. 1c).

Competition for food, basking places or nesting sites is likely to occur (CRUCITTI et al., 1990; CADI & JOLY, 2003, 2004), since both introduced sliders and native terrapins overlap in diet and feeding areas, devote a high percentage of their time budget to bask and coincide in the timing of reproductive seasons (GIBBONS, 1990; Andreu & López-Jurado, 1998; Keller & 2001: PLEGUEZUELOS, BUSACK, 2002). Transmission of pathogens between introduced turtles and native ones is another interaction likely occurring in syntopic populations (HIDALGO-VILA et al., 2009; VERNEAU et al., 2011). Potential advantages of T. scripta over native Iberian turtles might be a larger adult body size, a more diverse diet, a higher fecundity and a greater tolerance to pollution and human presence (PLEGUEZUELOS, 2002). Also, the origin of T. scripta in environments with saturated fauna where a great number of competitive turtle species coexist, compared to the few competitors of Iberian turtles, might endow the introduced species with competitive advantages in Mediterranean habitats.

Here we review some biological, ecological and behavioural aspects of introduced sliders and Iberian turtles, especially focu-

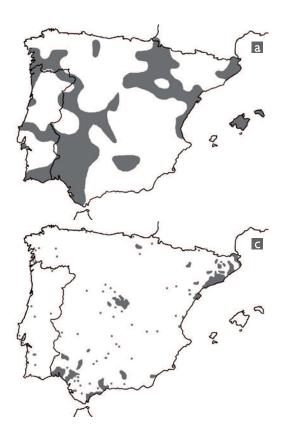




Figure 1: Distribution range of (a) *Emys orbicularis*, (b) *Mauremys leprosa*, and (c) the exotic *Trachemys scripta*, in the Iberian Peninsula (adapted from ANDREU & LÓPEZ-JURADO, 1998; PLEGUEZUELOS, 2002; LOUREIRO *et al.*, 2008).

sing on T. scripta and M. leprosa, which may contribute to explain competitive interactions between freshwater turtle species. We firstly examine the effect of direct competition with T. scripta on three key factors affecting the ecology and behaviour of M. leprosa: use of space, feeding efficiency and basking efficiency. Subsequently, we compare the specific morphology and thermal biology of the native and invasive species, which might have consequences for the outcome of competition. Finally, we examine other potential advantages that antipredatory behaviour (i.e. inter-specific differences in risk assessment) and predator efficiency (i.e. the inability of prey to recognise introduced predators) might confer to invasive turtle species.

DIRECT COMPETITION

Chemical Avoidance

Experiments studying direct competition between native and introduced turtles have demonstrated that different functions and activities of native terrapins are limited in presence of red-eared sliders. Moreover, semiochemicals (chemical substances conveying a signal for communication between organisms) seem to play an important role in inter-specific competition between native and exotic turtles. In an experiment comparing the use by *M. leprosa* and *T. scripta* of pools with clean water and pools with water containing chemical cues from conspecific or heterospecific turtles, *M. leprosa* preferred

water with chemical stimuli from conspecifics and avoided water with chemical cues from T. scripta, whereas T. scripta neither avoided nor preferred water pools with chemical cues from native M. leprosa (POLO-CAVIA et al., 2009a; Fig. 2). This suggests that *M. leprosa* is able to discriminate water-borne cues from introduced T. scripta and modify their use of space to avoid the costs of potential encounters with T. scripta. If scents of T. scripta result aversive for native turtles, dispersal would be a logical consequence in natural environments. On the other hand, the lack of chemosensory responses by T. scripta towards chemical cues of native terrapins -due to its inability to detect heterospecific cues, or simply to that, although detected, these cues do not represent a threat for them-, might further favour the expansion of the invasive species.

Feeding Competition

Alteration in space use by *M. leprosa* in presence of T. scripta seems to respond to the negative effects of direct competition with the invasive species for limited resources. The two species are likely to compete for feeding areas in nature, given that both native and introduced turtles mainly consume animal matter, though they also feed on plants (Keller & BUSACK, 2001; PLEGUEZUELOS, 2002). Trachemys scripta individuals are aggressive omnivores with high preferences for a carnivorous diet (PARMENTER, 1980; GIBBONS, 1990), capable of threatening or biting other individuals during competitive activities such as feeding (ARVY & SERVAN, 1998; LINDEMAN, 1999). Given that the access to resources is

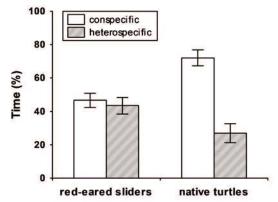


Figure 2: Percent time (mean \pm SE) that exotic red-eared sliders and native turtles spent in experimental ponds with water-borne chemical cues from conspecifics (open rectangles) and heterospecifics (barred rectangles). Native turtles prefer water with cues from conspecifics and avoid water with cues from introduced turtles (adapted from POLO-CAVIA *et al.*, 2009a).

constrained by dominant individuals when competition between foragers is asymmetrical (HOLMGREN, 1995; MOODY & HOUSTON, 1995; SPENCER *et al.*, 1995), a higher level of aggressiveness displayed by introduced sliders during feeding might lead *M. leprosa* to the displacement from areas with more profitable feeding resources.

Recent findings indicate that feeding competition between native *M. leprosa* and introduced *T. scripta* follows an asymmetrical pattern (POLO-CAVIA *et al.*, 2011). Food ingestion of *M. leprosa* and *T. scripta* were compared in the laboratory under situations of intra- and inter-specific competition, analysing the frequency of aggressive interactions between individual turtles of similar size, and observing that, when the two turtle species were forced to forage together, the access of *M. leprosa* to feeding resources was severely restricted by *T. scripta*, which ingested a greater percentage of the

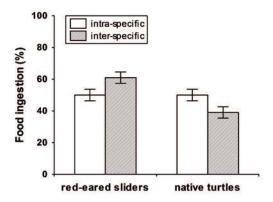


Figure 3: Percentage of food (mean \pm SE) ingested by exotic red-eared sliders and native turtles under situations of intra- (open rectangles) and interspecific (barred rectangles) feeding competition. When native and introduced turtles are forced to forage together the exotic species restrict the access of native turtles to food resources (adapted from POLO-CAVIA *et al.*, 2011).

supplied food (POLO-CAVIA et al., 2011; Fig. 3). As expected, aggressions occurred more frequently between heterospecific individuals and were more frequently inflicted by introduced T. scripta than by native M. leprosa. This high percentage of aggressions directed from T. scripta to M. leprosa suggests that the former is a more aggressive species and dominant over the latter. Furthermore, the percentage of food ingested by M. leprosa under inter-specific competition correlated positively with the level of suffered aggressiveness, thus indicating that daring M. leprosa which incurred in active competition for food were harshly punished by aggressive sliders, whereas shier individuals that displayed a subordinate role were less attacked (POLO-CAVIA et al., 2011). These findings suggest the existence for *M. leprosa* of a trade-off between feeding efficiency and costs of aggressive competition with T. scripta.

Basking Competition

Competition for basking sites is another important matter concerning direct competition between freshwater turtle species. Aerial basking serves to activate metabolism by attaining optimal body temperatures that maximize the efficiency of physiological processes (JACKSON, 1971; KEPENIS & MCMANUS, 1974; CRAWFORD et al., 1983; HAMMOND et al., 1988; BEN-EZRA et al., 2008; DUBOIS et al., 2008), favours dermal synthesis of vitamin D (PRITCHARD & GREENHOOD, 1968; AVERY, 1982), and allows conditioning of the skin and the shell (CAGLE, 1950; NEILL & ALLEN, 1954; BOYER, 1965). Thus, both native terrapins and T. scripta spend a large amount of their diel activity basking (MEEK, 1983; GIBBONS, 1990; ANDREU & LÓPEZ-JURADO, 1998). However, appropriate basking sites such as logs and stones emerging in deep water are limited, and therefore, T. scripta may monopolize optimal basking resources, displacing native terrapins to less preferred sites, and ultimately causing deficiencies in their basking behaviour and thermoregulation (DíAZ-PANIAGUA et al., 2002; CADI & JOLY, 2003; POLO-CAVIA et al., 2010a). In a long-term competition experiment, native M. leprosa subjected to inter-specific competition with T. scripta reduced basking activity, basked for shorter periods than sliders, and avoided sharing platforms with exotic turtles (POLO-CAVIA et al., 2010a; Fig. 4). Likewise, CADI & JOLY (2003) reported that native E. orbicularis sharing experimental ponds with T. scripta were reluctant to climb onto solaria that were already occupied by T. scripta, shifting instead to basking places of lower quality. Also, field observations of the western pond turtle, Emys

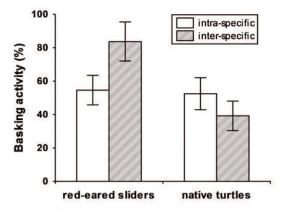


Figure 4: Percent time (mean \pm SE) that exotic redeared sliders and native turtles spent basking under intra-specific (open rectangles) and inter-specific competition (barred rectangles). When native and introduced turtles compete for basking sites native turtles significantly reduce the time devoted to bask (adapted from POLO-CAVIA *et al.*, 2010a).

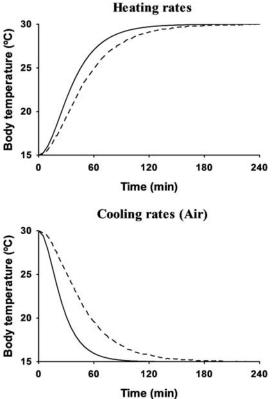
marmorata, sharing basking sites with *T. scripta* indicate that introduced sliders are much more selective in habitat use than native terrapins (LAMBERT *et al.*, 2013). This avoidance and subordinate behaviour and the consequent detriment in basking activity might lead native turtles to a loss in the efficiency of their physiological functions associated with ineffective thermoregulation, thus favouring the expansion of the invasive species.

MORPHOLOGICAL AND THERMAL Advantages of Exotic Sliders

Body shape has been established as a critical factor in the ability of organisms to thermoregulate (BOGERT, 1949; GOULD, 1966). Hence, morphological differences between native and exotic turtles, resulting from adaptation to different original habitats, might also confer thermoregulatory advantages to introduced sliders in the new environments

in which they are introduced, in detriment of native terrapins. Compared to M. leprosa, T. scripta turtles present a more rounded shell shape that confers them a low surface-tovolume ratio and a greater thermal inertia (POLO-CAVIA et al., 2009b; Fig. 5), thus facilitating heat retention and favouring the efficiency of physiological functions such as aquatic foraging or digestion (HUEY & SLATKIN, 1976; DUNHAM et al., 1989). In temperate zones, mechanisms for conserving body heat could have selective advantages in aquatic turtles, since individuals that have achieved high body temperatures through aerial basking may suddenly be exposed to very cool conditions when entering the water (BARTHOLOMEW, 1982). Consequently, slight differences in thermal inertia between species might favour introduced T. scripta in Mediterranean habitats. For instance, in the Iberian Peninsula, T. scripta specimens have been observed to be active at lower water temperatures than native terrapins, and therefore, they can start earlier their annual cycle (ACEITUNO, 2001). Such adaptation is consistent with the higher thermal inertia of T. scripta observed in the laboratory. In contrast, the more flattened shell shape and lower thermal buffering of M. leprosa compared to T. scripta may entail a difficulty for retention of body heat that, with the presence of a new competitor species interfering in their basking activity, might result in the achievement of suboptimal body temperatures, subsequently causing reduced locomotor activity and food intake, or altered digestive function (POLO-CAVIA et al., 2009b).

In particular, a reduced body temperature negatively influences righting performance of turtles. Turtles may result overturned acci-



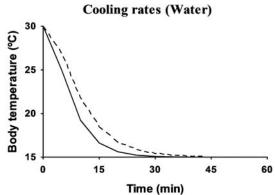


Figure 5: Inter-specific differences in thermal exchange rates between exotic red-eared sliders (solid lines) and native turtles (dotted lines), following exposure to step changes of ambient temperature in air and water (adapted from POLO-CAVIA *et al.*, 2009b).

dentally while climbing to basking sites, during male fights, or as consequence of predatory attacks (CORTI & ZUFFI, 2003; STANCHER et al., 2006). In these cases, righting behaviour is critical to survival, since turtles in an upside-down position may suffer increased predation exposure, changes in body temperature and dehydration, as well as experience difficulties to breathe (FINKLER, 1999; STEYERMARK & SPOTILA, 2001; MARTÍN et al., 2005). At suboptimal temperatures, both native and exotic terrapins were found to increase the time needed to turn themselves over (POLO-CAVIA et al., 2012a). Consequently, turtles that attain and maintain optimal body temperatures will increase their survival possibilities. Thus, the high thermal inertia of T. scripta is also advantageous insofar as it favours the performance and reduces the risks of exposure to potential predators and overheating while overturning (CARR 1952; WYNEKEN *et al.*, 2008; POLO-CAVIA *et al.*, 2009b). Also, the domed shape of the shell facilitates mechanical righting in *T. scripta*, which needs shorter times on average to turn right-side up than *M. leprosa* (DOMOKOS & VÁRKONYI, 2008; POLO-CAVIA *et al.*, 2012a).

Experiments comparing bioenergetics of *M. leprosa* and *T. scripta* also revealed that the two turtle species differ in thermal requirements (POLO-CAVIA *et al.*, 2012b). Thus, the upper set point body temperature (i.e. the body temperature at which turtles cease basking and dip into the water; KINGSBURY, 1993, 1999; TOSINI & AVERY,

1994; BEN-EZRA et al., 2008; DUBOIS et al., 2008; POLO-CAVIA et al., 2012b) is 5°C higher on average in M. leprosa compared to T. scripta. This suggests that native M. leprosa, more flattened and with higher surfaceto-volume ratio than T. scripta, might compensate their greater tendency to loss body heat by attaining higher optimal temperatures during basking. Also, individuals with higher surface-to-volume ratios have been observed to bask until attaining higher set point body temperatures, suggesting a close relation between specific thermal requirements and carapace morphology of each species. On the other hand, in response to starvation, the two turtle species similarly reduce their set point temperatures, which points out to the existence of an adaptive energy saving mechanism during periods of low food availability (POLO-CAVIA et al., 2012b). As a result, interferences of T. scripta on feeding and basking behaviour of native terrapins might ultimately cause a reduction in their metabolic rates and a general depression of their physiological functions (PARMENTER, 1981; SIEVERT et al., 1988; GIANOPULOS & ROWE, 1999). Such negative effects may explain the loss of weight and decreased survival rates found in E. orbicularis after long term competition with T. scripta (CADI & JOLY, 2004).

PREDATORY RISK IN ALTERED HABITATS

When a predator approaches, turtles typically flee to safe refuges such as deep water or dense vegetation (LÓPEZ *et al.*, 2005). However, if the predator gets close enough, turtles tend to withdraw inside the shell with the legs, tail and head hidden

(GREENE, 1988; HUGIE, 2003). Then, the decision of when to emerge is accurately adjusted basing on risk factors such as the perceived predation threat, the persistence of the predator or the probability of reaching a safer refuge, vs. the costs of remaining within the shell (i.e. overheating risk, interruption of basking, loss of foraging or mating opportunities, etc.) (SIH et al., 1998; MARTÍN et al., 2005; POLO-CAVIA et al., 2008). In these cases, the high thermal inertia of T. scripta protects turtles from desiccation (CARR, 1952; WYNEKEN et al., 2008; POLO-CAVIA et al., 2009b) and its spherical shell shape reduces the risk of successful predatory attacks, as it hampers the capture by snapping jaws or avian predators (PRITCHARD, 1979; JANZEN et al., 2000). In contrast, M. leprosa hidden within the shell are more prone than T. scripta to overheating or predation due to their more flattened shape. Thus, as expected, M. leprosa escapes quickly to the water when facing a terrestrial threat while T. scripta tends to remain for longer in land, hidden inside the shell (POLO-CAVIA et al., 2008). These inter-specific differences in response to predation risk between native and introduced turtles may result advantageous for the introduced species in altered habitats where human pressure has considerably reduced the risk of predation by natural predator species. In such environments, where T. scripta is mainly introduced, the costs derived from interruption of basking and repeated unnecessary flees to water due to human disturbance (DILL & FRASER, 1997; SIH, 1997; MARTÍN & LÓPEZ, 1999) might suppose a disadvantage for native turtles when competing with introduced sliders.

INTERACTIONS WITH TADPOLE PREY

Human alteration of ecosystems may cause disruption of the antipredatory behaviour of native turtles, but may also affect their predatory efficiency by means of introducing a competitor species that fed on the same prey and benefit from an evolutionary release. Antipredatory responses of prey are expected to be adaptive in the specific habitats in which they evolved, but however, prey may not be innately equipped to cope with suddenly introduced predators with which they have not shared a long evolutionary past (SCHLAEPFER et al., 2002, 2005). For this reason, native prey are generally unable to detect or adequately respond to the hunting tactics of novel predators, which do not experience some of the difficulties of finding prey that keep working for native predators (LAWLER et al., 1999; KIESECKER et al., 2001; BABER & BABBITT, 2003). This is the case of tadpoles of several Iberian anuran species, which are common prey of both native and introduced turtles. These tadpoles have been observed to innately respond to predator chemical cues from the two Iberian turtles, E. orbicularis and M. leprosa, but contrarily, tadpoles are not able to recognise exotic predatory turtles of the genera Trachemys or Graptemys (POLO-CAVIA et al., 2010b). Consequently, exotic turtles may easily capture larval amphibian prey outcompeting native Iberian turtles. The advantage of an evolutionary release may explain the paradox of why invasive species sometimes prosper better in their new habitats than native adapted species (BLOSSEY & NÖTZOLD, 1995; SHEA & CHESSON, 2002; Allendorf & Lundquist, 2003).

Synthesis and Future Research

The studies to date analysing interference competition between native Iberian turtles and T. scripta suggest a greater competitive ability of the exotic T. scripta in vying for resources. In direct competition, native turtles seem to rely on water-borne chemical cues to discriminate between conspecifics and heterospecifics, thus avoiding potential costly interactions with exotic turtles, deserting resources or displacing to less preferred areas (POLO-CAVIA et al., 2009a). Thus, the higher aggressiveness and dominance of sliders in competition for food or basking sites may lead native terrapins to a detriment in their nutritional state and thermoregulatory behaviour (POLO-CAVIA et al., 2010a, 2011). On the other hand, species-specific traits such as a more spherical shell shape and a greater thermal buffering may confer additional competitive advantages to exotic *T. scripta* in comparison to turtles native to the new habitats where they are introduced. Hence, the high thermal inertia of T. scripta facilitates heat retention and favours physical and physiological performances (POLO-CAVIA et al., 2009b, 2012a). Also, a greater thermal buffering reduces overheating and dehydration risks in situations in which turtles have lost the behavioural control of their body temperature (e.g. if they result overturned or suffer a predatory attack) (CARR, 1952; WYNEKEN et al., 2008).

Inter-specific differences in risk perception between introduced *T. scripta* and native Iberian turtles may also benefit the former in anthropogenically disturbed environments in which they are mainly introduced. In these habitats, where terrestrial predators are reduced and human presence carries little risk of actual predation, T. scripta could avoid unnecessary flees to water and subsequently basking interruptions by remaining hidden in the shell (POLO-CAVIA et al., 2008). These findings emphasise the importance of further studies linking habitat conservation with invasion success. Likewise, comprehension of adaptive evolutionary responses of native and introduced species is essential in understanding competition processes, given that alien introduced species create new ecological contexts in which adaptive responses of native organisms may loss functionality (CALLAWAY & ASCHEHOUG, 2000; SHEA & CHESSON, 2002). Hence, the inability of amphibian tadpoles to innately recognise chemical cues from exotic predatory turtles may represent a further competitive advantage for introduced turtles over native ones in the Iberian Peninsula (POLO-CAVIA et al., 2010b). However, the magnitude and impact of this evolutionary release on native populations of Iberian turtles remains uncertain, as amphibian prey might acquire learned recognition of novel competitive predators and enhance survival (MIRZA & CHIVERS, 2000; GAZDEWICH & CHIVERS, 2002; POLO-CAVIA & GOMEZ-MESTRE, 2014).

Native organisms have been observed to alter morphology and/or behaviour as a result of their interactions with exotic species (REZNICK & ENDLER 1982; MAGURRAN, 1989; SINGER *et al.*, 1993; CARROLL *et al.*, 1997, 1998). Thus, under favourable circumstances, native species may induce or evolve mechanisms to cope with invasions and maintain their populations (MEYERS & BULL, 2002). However, despite the existing cases of induced plasticity and rapid evolution in response to sudden environmental changes (ASHLEY *et al.*, 2003; RICE & EMERY, 2003; STOCKWELL *et al.*, 2003; SHINE, 2012), the evolutionary processes are hardly ever incorporated into conservation plans (SCHLAEPFER *et al.*, 2005). The studies reviewed here evidence the necessity of managing biological invasions basing on evolutionary dynamics, behaviour and plasticity of native species, with the purpose of guaranteeing the conservation goal of long-term persistence (ASHLEY *et al.*, 2003; STOCKWELL *et al.*, 2003; SHINE, 2012).

In conclusion, the existing asymmetries in morphology, ecology and behavioural responses of native Iberian turtles and introduced redeared sliders, resulting from adaptation to their respective natural habitats, seem to be jointly responsible for the greater competitive ability of exotic T. scripta. These inter-specific differences might favour the displacement of native turtles to suboptimal resources and facilitate the expansion of introduced sliders in their new habitats. Future investigations comparing native populations of Iberian turtles in coexistence and free from introduced turtle competitors will help to evaluate the ability of native terrapins to resist the invasion in a long-term scenario (WILLIAMSON, 1996; JOLY, 2000), enabling the design of management strategies that support native populations long enough to allow them to adapt to the new challenges posed by invasive turtle species (ASHLEY et al., 2003; SCHLAEPFER et al., 2005; SHINE, 2012).

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References

- ACEITUNO, J. (2001). La Población del Galápago de Florida (Trachemys scripta elegans) en la Desembocadura del Río Cofio-Embalse de San Juan (Madrid). Unpublished report, Asociación Herpetológica Española, Madrid, Spain.
- ALLENDORF, F.W. & LUNDQUIST, L.L. (2003). Introduction: population biology, evolution, and control of invasive species. *Conservation Biology* 17: 24-30.
- ANDREU, A.C. & LÓPEZ-JURADO, L.F. (1998). *Mauremys leprosa* (Schweigger, 1812), *In*A. Salvador (coord.) *Reptiles*. Series: Fauna Ibérica, Vol. 10 (M.A. Ramos, ed.). Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, Spain, pp. 103-108.
- ARVY, C. & SERVAN, J. (1998). Imminent competition between *Trachemys scripta* and *Emys orbicularis* in France. *Mertensiella* 10: 33-40.
- Ashley, M.V.; WILLSON, M.F.; PERGAMS, O.R.W.; O'DOWD, D.J.; GENDE, S.M. & BROWN, J.S. (2003). Evolutionarily enlightened management. *Biological Conservation* 111: 115-123.
- AVERY, R.A. (1982). Field studies of body temperatures and thermoregulation, In C. Gans & F.H. Pough (eds.) Biology of the Reptilia, Volume 12, Physiology C, Physiological Ecology. Academic Press, New York, NY, USA, pp. 93-166.

- BABER, M.J. & BABBITT, K.J. (2003). The relative impacts of native and introduced predatory fish on a temporary wetland tadpole assemblage. *Oecologia* 136: 289-295.
- BARTHOLOMEW, G.A. (1982). Physiological control of body temperature, *In* C. Gans & F.H. Pough (eds.) *Biology of the Reptilia, Volume 12, Physiology C, Physiological Ecology.* Academic Press, New York, NY, USA, pp. 167-212.
- BEN-EZRA, E.; BULTÉ, G. & BLOUIN-DEMERS, G. (2008). Are locomotor performances coadapted to preferred basking temperature in the Northern Map Turtle (*Graptemys geographica*)? Journal of Herpetology 42: 322-331.
- BLOSSEY, B. & NÖTZOLD, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology* 83: 887-889.
- BOGERT, C.M. (1949). Thermoregulation in reptiles, a factor in evolution. *Evolution* 3: 195-211.
- BOYER, D.R. (1965). Ecology of the basking habit in turtles. *Ecology* 46: 99-118.
- CADI, A. & JOLY, P. (2003). Competition for basking places between the endangered European pond turtle (*Emys orbicularis* galloitalica) and the introduced red-eared slider (*Trachemys scripta elegans*). Canadian Journal of Zoology 81: 1392-1398.
- CADI, A. & JOLY, P. (2004). Impact of the introduction of the red-eared slider (*Trachemys scripta elegans*) on survival rates of the European pond turtle (*Emys* orbicularis). Biodiversity and Conservation 13: 2511-2518.
- CAGLE, F.R. (1950). The life history of the slider turtle, *Pseudemys scripta troostii* (Hoolbrook). *Ecological Monographs* 20: 31-54.

- CALLAWAY, R.M. & ASCHEHOUG, E.T. (2000). Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290: 521-523.
- CARR, A.F. (1952). Handbook of Turtles. The Turtles of the United States, Canada, and Baja California. Cornell University Press, Ithaca, NY, USA.
- CARROLL, S.P.; DINGLE, H. & KLASSEN, S.P. (1997). Genetic differentiation of fitnessassociated traits among rapidly evolving populations of the soapberry bug. *Evolution* 51: 1182-1188.
- CARROLL, S.P.; KLASSEN, S.P. & DINGLE, H. (1998). Rapidly evolving adaptations to host ecology and nutrition in the soapberry bug. *Evolutionary Ecology* 12: 955-968.
- CHEN, T.-H. & LUE, K.-Y. (1998). Ecological notes on feral populations of *Trachemys scripta elegans* in northern Taiwan. *Chelonian Conservation and Biology* 3: 87-90.
- CORTI. C. & ZUFFI, M.A.L. (2003). Aspects of population ecology of *Testudo hermanni hermanni* from Asinara Island, NW Sardinia (Italy, Western Mediterranean Sea): preliminary data. *Amphibia-Reptilia* 24: 441-447.
- CRAWFORD, K.M.; SPOTILA, J.R. & STANDORA, E.A. (1983). Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. *Ecology* 64: 989-999.
- CRUCITTI, P.; CAMPESER, A. & MALORI, M. (1990). Populazioni sintopiche di *Emys* orbicularis e Mauremys caspica nella Tracia, Grecia Orientale (Reptilia, Testudines: Emydidae). Bollettino del Museo Regionale di Scienze Naturali di Torino 8: 187-196.

- DA SILVA, E. & BLASCO, M. (1995) *Trachemys* scripta elegans in Southwestern Spain. *Herpetological Review* 26: 133-134.
- DÍAZ-PANIAGUA, C.; MARCO, A.; ANDREU, A.C.; SÁNCHEZ, C.; PEÑA, L.; ACOSTA, M. & MOLINA, I. (2002). Trachemys scripta *en Doñana*. Unpublished report, Asociación Herpetológica Española, Sevilla, Spain.
- DILL, L.M. & FRASER, A.H.G. (1997). The worm re-turns: hiding behavior of a tubedwelling marine polychaete, *Serpula vermicularis. Behavioural Ecology* 8: 186-193.
- DOMOKOS, G. & VÁRKONYI, P.L. (2008). Geometry and self-righting of turtles. *Proceedings of the Royal Society B* 275: 11-17.
- DUBOIS, Y.; BLOUIN-DEMERS, G. & THOMAS, D. (2008). Temperature selection in wood turtles (*Glyptemys insculpta*) and its implications for energetics. *Ecoscience* 15: 398-406.
- DUNHAM, A.E.; GRANT, B.W. & OVERALL, K.L. (1989). Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiological Zoology* 62: 335-355.
- FINKLER, M.S. (1999). Influence of water availability during incubation on hatchling size, body composition, desiccation tolerance, and terrestrial locomotor performance in the snapping turtle *Chelydra serpentina*. *Physiological and Biochemical Zoology* 72: 714-722.
- GAZDEWICH, K.J. & CHIVERS, D.P. (2002). Acquired predator recognition by fathead minnows: influence of habitat characteristics on survival. *Journal of Chemical Ecology* 28: 439-445.
- GIANOPULOS, K.D. & ROWE, J.W. (1999). Effects of short-term water temperature variation on food consumption in painted turtles

(Chrysemys picta marginata). Chelonian Conservation and Biology 3: 504-507.

- GIBBONS, W.J. (1990). The slider turtle, IN W.J. Gibbons (ed.) *Life History and Ecology of the Slider Turtle*. Smithsonian Institution Press, Washington, DC, USA, pp. 3-18.
- GOULD, S.J. (1966). Allometry and size in ontogeny and phylogeny. *Biological Reviews* 41: 587-640.
- GREENE, H.W. (1988). Antipredator mechanisms in reptiles, In C. Gans & R.B. Huey (eds.) Biology of the Reptilia, Volume 16, Ecology B, Defense and Life History. Academic Press, New York, NY, USA, pp. 1-152.
- GUREVITCH, J. & PADILLA, D.K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* 19: 470-474.
- HAMMOND, K.A.; SPOTILA, J.R. & STANDORA, E.A. (1988). Basking behavior of the turtle *Pseudemys scripta*: Effects of digestive state, acclimation temperature, sex and season. *Physiological Zoology* 61: 69-77.
- HERBOLD, B. & MOYLE, P.B. (1986). Introduced species and vacant niches. *The American Naturalist* 128: 751-760.
- HIDALGO-VILA, J.; DÍAZ-PANIAGUA, C.;
 RIBAS, A.; FLORENCIO, M.; PÉREZ-SANTIGOSA, N. & CASANOVA, J.C. (2009). Helminth communities of the exotic introduced turtle, *Trachemys scripta elegans* in southwestern Spain: Transmission from native turtles. *Research in Veterinary Science* 86: 463-465.
- HOLMGREN, N. (1995). The ideal free distribution of unequal competitors: predictions from a behaviour-based functional response. *Journal of Animal Ecology* 64: 197-212.
- HUEY, R.B. & SLATKIN, M. (1976). Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology* 51: 363-384.

- HUGIE, D.M. (2003). The waiting game: a "battle of waits" between predator and prey. *Behavioural Ecology* 14: 807-817.
- JACKSON, D.C. (1971). The effect of temperature on ventilation in the turtle, *Pseudemys scripta elegans. Respiration Physiology* 12: 131-140.
- JANZEN, F.J.; TUCKER, J.K. & PAUKSTIS, G.L. (2000). Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. *Journal of Evolutionary Biology* 13: 947-954.
- JOLY, P. (2000). Invasions biologiques: état de l'art et perspectives. *Revue d'Ecologie (La Terre et la Vie)* Suppl. 7: 21-35.
- KELLER, C. & BUSACK, S.D. (2001). *Mauremys leprosa* (Schweigger, 1812) – Maurische Bachschildkröte, In U. Fritz (ed.) *Handbuch der Reptilien und Amphibien Europas, Band 3/IIIA, Schildkröten (Testudines) I.* Aula-Verlag, Wiesbaden, Germany, pp. 57-88.
- KEPENIS, V. & MCMANUS, J.J. (1974). Bioenergetics of young painted turtles, *Chrysemys picta. Comparative Biochemistry* and Physiology A 48: 309-317.
- KIESECKER, J.M.; BLAUSTEIN, A.R. & MILLER, C.L. (2001). Potential mechanisms underlying the displacement of native red-legged frogs by introduced bullfrogs. *Ecology* 82: 1964-1970.
- KINGSBURY, B.A. (1993). Thermoregulatory set points of the eurythermic lizard *Elgaria multicarinata. Journal of Herpetology* 27: 241-247.
- KINGSBURY, B.A. (1999). An experimental design for examining thermoregulatory set points in ectothermic animals. *The American Biology Teacher* 61: 448-452.

- LAMBERT, M.R.; NIELSEN, S.N.; WRIGHT, A.N.; THOMSON, R.C. & SHAFFER, H.B. (2013). Habitat features determine the basking distribution of introduced Red-Eared Sliders and native Western Pond Turtles. *Chelonian Conservation and Biology* 12: 192-199.
- LAWLER, S.P.; DRITZ, D.; STRANGE, T. & HOLYOAK, M. (1999). Effects of introduced mosquitofish and bullfrogs on the threatened California red-legged frog. *Conservation Biology* 13: 613-622.
- LINDEMAN, P.V. (1999). Aggressive interactions during basking among four species of emydid turtles. *Journal of Herpetology* 33: 214-219.
- LINDSAY, M.K.; ZHANG, Y.; FORSTNER, M.R.J. & HAHN, D. (2013). Effects of the freshwater turtle *Trachemys scripta elegans* on ecosystem functioning: an approach in experimental ponds. *Amphibia-Reptilia* 34: 75-84.
- LOCKWOOD, J.L.; HOOPES, M.F. & MARCHETTI, M.P. (2007). *Invasion Ecology*. Blackwell Publishing, Oxford, UK.
- LÓPEZ, P.; MARCOS, I. & MARTÍN, J. (2005). Effects of habitat-related visibility on escape decisions of the Spanish terrapin *Mauremys leprosa. Amphibia-Reptilia* 26: 557-561.
- LOUREIRO, A.; FERRAND DE ALMEIDA, N.; CARRETERO, M.A. & PAULO, O.S. (2008) *Atlas dos Anfíbios e Répteis de Portugal.* Instituto da Conservação da Natureza e da Biodiversidade, Lisboa, Portugal.
- LUISELLI, L.; CAPULA, M.; CAPIZZI, D.; FILIPPI, E.; TRUJILLO, J.V. & ANIBALDI, C. (1997).
 Problems for conservation of pond turtles (*Emys orbicularis*) in central Italy: is the introduced red-eared turtle (*Trachemys scripta*) a serious threat? *Chelonian Conservation and Biology* 2: 417-419.

- MAGURRAN, A.E. (1989). Acquired recognition of predator odour in the European minnow (*Phoxinus phoxinus*). *Ethology* 82: 216-223.
- MARTÍN, J. & LÓPEZ, P. (1999). An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. *Oikos* 84: 499-505.
- MARTÍN, J.; MARCOS, I. & LÓPEZ, P. (2005). When to come out from your own shell: risk-sensitive hiding decisions in terrapins. *Behavioural Ecology and Sociobiology* 57: 405-411.
- MEEK, R. (1983). Body temperatures of a desert population of the stripe-necked terrapin, *Mauremys caspica*. *British Journal of Herpetology* 6: 335-337.
- MEYERS, L.A. & BULL, J.J. (2002). Fighting change with change: adaptive variation in an uncertain world. *Trends in Ecology and Evolution* 17: 551-557.
- MIRZA, R.S. & CHIVERS, D.P. (2000). Predatorrecognition training enhances survival of brook trout: evidence from laboratory and field-enclosure studies. *Canadian Journal of Zoology* 78: 2198-2208.
- MOODY, A.L. & HOUSTON, A.I. (1995). Interference and the ideal free distribution. *Animal Behaviour* 49: 1065-1072.
- MOONEY, H.A. & HOBBS, R.J. (2000). *Invasive Species in a Changing World*. Island Press, Washington, DC, USA.
- NEILL, W.T. & ALLEN, E.R. (1954). Algae on turtles: some additional considerations. *Ecology* 35: 581-584.
- PARMENTER, R.R. (1980). Effects of food availability and water temperature on the feeding ecology of pond sliders (*Chrysemys* s. scripta). Copeia 1980: 503-514.
- PARMENTER, R.R. (1981). Digestive turnover rates in freshwater turtles: the influence of

temperature and body size. *Comparative Biochemistry and Physiology A* 70: 235-238.

- PLEGUEZUELOS, J.M. (2002). Las especies introducidas de anfibios y reptiles, In J.M. Pleguezuelos, R. Márquez & M. Lizana (eds.) Atlas y Libro Rojo de los Anfibios y Reptiles de España. Asociación Herpetológica Española-Ministerio de Medio Ambiente, Madrid, Spain, pp. 501-532.
- POLO-CAVIA, N. & GOMEZ-MESTRE, I. (2014). Learned recognition of introduced predators determines survival of tadpole prey. *Functional Ecology* 28: 432-439.
- POLO-CAVIA, N.; LÓPEZ, P. & MARTÍN, J. (2008). Interspecific differences in responses to predation risk may confer competitive advantages to invasive freshwater turtle species. *Ethology* 114: 115-123.
- POLO-CAVIA, N.; LÓPEZ, P. & MARTÍN, J. (2009a). Interspecific differences in chemosensory responses of freshwater turtles: consequences for competition between native and invasive species. *Biological Invasions* 11: 431-440.
- POLO-CAVIA, N.; LÓPEZ, P. & MARTÍN, J. (2009b). Interspecific differences in heat exchange rates may affect competition between introduced and native freshwater turtles. *Biological Invasions* 11: 1755-1765.
- POLO-CAVIA, N.; LÓPEZ, P. & MARTÍN, J. (2010a). Competitive interactions during basking between native and invasive freshwater turtle species. *Biological Invasions* 12: 2141-2152.
- POLO-CAVIA, N.; GONZALO, A.; LÓPEZ, P. & MARTÍN, J. (2010b). Predator recognition of native but not invasive turtle predators by naïve anuran tadpoles. *Animal Behaviour* 80: 461-466.

- POLO-CAVIA, N.; LÓPEZ, P. & MARTÍN, J. (2011). Aggressive interactions during feeding between native and invasive freshwater turtles. *Biological Invasions* 13: 1387-1396.
- POLO-CAVIA, N.; LÓPEZ, P. & MARTÍN, J. (2012a). Effects of body temperature on righting performance of native and invasive freshwater turtles: consequences for competition. *Physiology and Behaviour* 108: 28-33.
- POLO-CAVIA, N.; LÓPEZ, P. & MARTÍN, J. (2012b). Feeding status and basking requirements of freshwater turtles in an invasion context. *Physiology and Behaviour* 105: 1208-1213.
- PRITCHARD, P.C.H. (1979). *Encyclopedia of Turtles*. TFH Publications, Neptune, NJ, USA.
- PRITCHARD, P.C.H. & GREENHOOD, W.F. (1968). The sun and the turtle. *International Turtle and Tortoise Society Journal* 2: 20-25.
- REZNICK, D. & ENDLER, J.A. (1982). The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* 36: 160-177.
- RICE, K.J. & EMERY, N.C. (2003). Managing microevolution: restoration in the face of global change. *Frontiers in Ecology and the Environment* 1: 469-478.
- SCHLAEPFER, M.A.; RUNGE, M.C. & SHERMAN, P.W. (2002). Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17: 474-480.
- SCHLAEPFER, M.A.; SHERMAN, P.W.; BLOSSEY, B. & RUNGE, M.C. (2005). Introduced species as evolutionary traps. *Ecology Letters* 8: 241-246.
- SHEA, K. & CHESSON, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17: 170-176.

- SHIGESADA, N. & KAWASAKI, K. (1997). Biological invasions: Theory and practice. Oxford University Press, Oxford, UK.
- SHINE, R. (2012). Invasive species as drivers of evolutionary change: cane toads in tropical Australia. *Evolutionary Applications* 5: 107-116.
- SIEVERT, L.M.; SIEVERT, G.A. & CUPP, P.V., JR. (1988). Metabolic rate of feeding and fasting juvenile midland painted turtles, *Chrysemys picta marginata. Comparative Biochemistry and Physiology* A 90: 157-159.
- SIH, A. (1997). To hide or not to hide? Refuge use in a fluctuating environment. *Trends in Ecology and Evolution* 12: 375-376.
- SIH, A.; ENGLUND, G. & WOOSTER, D. (1998). Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* 13: 350-355.
- SINGER, M.C.; THOMAS, C.D. & PARMESAN, C. (1993). Rapid human-induced evolution of insect-host associations. *Nature* 366: 681-683.
- SPENCER, H.G.; KENNEDY, M. & GRAY, R.D. (1995). Patch choice with competitive asymmetries and perceptual limits: the importance of history. *Animal Behaviour* 50: 497-508.
- STANCHER, G.; CLARA, E.; REGOLIN, L. & VALLORTIGARA, G. (2006). Lateralized righting behaviour in the tortoise (*Testudo hermanni*). *Behavioural Brain Research* 173: 315-319.
- STEYERMARK, A.C. & SPOTILA, J.R. (2001). Body temperature and maternal identity affect snapping turtle (*Chelydra serpentina*) righting response. *Copeia* 2001: 1050-1057.
- STOCKWELL, C.A.; HENDRY, A.P. & KINNISON, M.T. (2003). Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* 18: 94-101.

- TORTOISE & FRESHWATER TURTLE SPECIALIST GROUP (1996). *Emys orbicularis, In The IUCN Red List of Threatened Species. Version* 2014.3. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland. Available at: http://www.iucnredlist.org/details/7717/0. Retrieved on 01/08/2015.
- TOSINI, G. & AVERY, R. (1994). Diel variation in thermoregulatory set points of the lizard *Podarcis muralis. Amphibia-Reptilia* 15: 93-96.
- VAN DIJK, P.P.; MATEO MIRAS, J.A.; CHEYLAN, M.; JOGER, U.; SÁ-SOUSA, P. & PÉREZ-MELLADO, V. (2004). *Mauremys leprosa, In The IUCN Red List of Threatened Species. Version 2014.3.* International Union for Conservation of Nature and Natural Resources, Gland, Switzerland. Available at: http://www.iucnredlist.org/details/158468/ 1. Retrieved on 01/08/2015.
- VERNEAU, O.; PALACIOS, C.; PLATT, T.; ALDAY, M.; BILLARD, E.; ALLIENNE, J.-F.; BASSO, C. & DU PREEZ, L.H. (2011). Invasive species threat: parasite phylogenetics reveals patterns and processes of host-switching between non-native and native freshwater turtles. *Parasitology* 138: 1778-1792.
- VILÀ, M.; VALLADARES, F.; TRAVESET, A.; SANTAMARÍA, L. & CASTRO, P. (2008). *Invasiones Biológicas*. Consejo Superior de Investigaciones Científicas, Madrid, Spain.
- WILCOVE, D.S.; ROTHSTEIN, D.; DUBOW, J.; PHILLIPS, A. & LOSOS, E. (1998). Quantifying threats to imperilled species in the United States. *BioScience* 48: 607-615.
- WILLIAMSON, M. (1996). *Biological Invasions*. Chapman and Hall, London, UK.
- WYNEKEN, J.; GODFREY, M.H.; BELS, V. (2008). *Biology of Turtles*. CRC Press, Boca Raton, FL, USA.