Does the exotic invader turtle, *Trachemys scripta elegans*, compete for food with coexisting native turtles?

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Abstract. Nowadays, established populations of exotic turtles, *Trachemys scripta elegans*, coexist with native turtles in the wild in southern Spain. We analysed the diet of this exotic species and compared it with the diet of the two native species (*Mauremys leprosa* and *Emys orbicularis*) in two ponds. The exotic turtle is an opportunistic omnivore. In one of our study ponds where exotic invasive crayfish were very abundant, adult and juvenile exotic turtles fed mainly on this prey. In the other study pond, juveniles fed mainly on animal matter and adults ate similar proportions of plants and animals. Native turtles also ingested mainly crayfish in the first study pond, but *M. leprosa* were mainly herbivorous in the second pond. We did not detect strong differences among the diets of the three species. While native species significantly differ in their diets, the exotic turtles did not differ from some groups of native ones. Exotic turtles had the widest range of food, overlapping the food spectra of different age groups of the two native species in both localities. Comparing with previous reports on native turtles diet of the same area, our results did not reveal changes in the diet which could be associated to interactions with exotic turtles, but the observed shift to a higher proportion of animals in the diet in one of the ponds were mainly due to the high abundance of exotic crayfish.

Keywords: exotic aquatic turtles, exotic crayfish, food competition.

Introduction

Red-eared sliders, Trachemys scripta elegans, were the most traded reptiles worldwide in the last century (Telecky, 2001; Reed and Gibbons, 2003). The establishment of reproductive populations has been confirmed in natural environments in several countries (Chen and Lue, 1998; Pérez-Santigosa et al., 2006; Perry et al., 2007; Ficetola, Thuiller and Padoa-Schioppa, 2009; Kikillus, Hare and Hartley, 2010). Competition for basking resources has been experimentally demonstrated to affect survival of native turtles such as Emys orbicularis (Cadi and Joly, 2003, 2004). Similarly, competition for feeding resources may be also expected to affect native turtles. The knowledge of natural history information, such as the diet, of exotic species is essential to evaluate their ability to survive in their new invaded habitats and to assess the probability of interactions or competition with native species.

The diet of T. scripta in its native range has been widely documented (Cagle, 1950; Clark and Gibbons, 1969; Parmenter, 1980; Schubauer and Parmenter, 1981; Hart, 1983; Parmenter and Avery, 1990; Dreslik, 1999). It is considered an omnivore species in which individuals may experience a characteristic ontogenetic variation from a mainly carnivorous diet in juveniles to a more herbivorous diet in adults (Clark and Gibbons, 1969; Hart, 1983; Dreslik, 1999; Bouchard and Bjorndal, 2005). However, there is scarce information on the diets of these turtles as exotic introduced species. Released animals in France were omnivorous, ingesting vegetation, invertebrates and fish (Prévot-Julliard et al., 2007).

In Spain, reproductive populations of *T. s.* elegans coexist in ponds with two native species of aquatic turtles: *Mauremys leprosa* and *Emys* orbicularis (Pérez-Santigosa et al., 2006). The diet of the native species has not been extensively studied. Vegetation was found to predominate over animal matter in the diet of *M. lep*rosa (Fritz, 2001; Keller and Busack, 2001). In contrast, *E. orbicularis* is considered to be a predominantly carnivorous species which

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also can ingest vegetation (Ottonello, Salvidio and Rosecchi, 2005; Ficetola and De Bernardi, 2006). The diets of the two native species were thoroughly assessed in Doñana National Park (the same area that includes one of our study ponds) before the introduction of the exotic turtles, when the ingestion of exotic crayfish was already detected among the animal matter ingested by both species (Keller and García-Mudarra, unpublished data). The knowledge of the diets of coexisting species is useful information to asses if similar diets result in important interactions or competition with negative consequences on some of the species. In native turtle assemblages, resource partitioning is expected to favour species coexistence in particular habitats (Vogt and Guzman, 1988). In contrast, the introduction of exotic species with similar trophic requirements may result in competition and exclusion of native species.

In this study we analysed the diet of the three turtle species in order to provide information for the evaluation on the influence of the introduction of *T. s. elegans* on native aquatic turtles. We compared the diet of exotic individuals from a feral established population with the diet of native turtles coexisting in the same ponds. This is the first study providing information on the food of exotic individuals born and grown under natural conditions in an invaded area.

Materials and methods

From April to August 2003, a removal programme of exotic turtles was carried out in two localities in southwestern Spain (El Acebuche Pond and El Portil Pond) where reproductive populations of exotic turtles had been established. In these ponds, the Mediterranean Pond turtles (M. leprosa) are abundant, while the European Pond turtles (E. orbicu*laris*) are scarce or in decline (a more detailed descriptions of these populations as well as of the study ponds can be found in Pérez-Santigosa et al., 2006, and Pérez-Santigosa, Díaz-Paniagua and Hidalgo-Vila, 2008). Most turtles were captured with submerged nets; female exotic turtles were also captured by hand when leaving the pond for nesting. Exotic turtles were removed from the ponds and then humanely killed using thiopental sodium injection (Tiobarbital, Braun Medical). Turtle digestive tracts were removed and preserved in ethanol 70%. Because they were usually

killed some days after being trapped, stomach contents were useful for diet examination only in two adult *T. s. elegans* from El Acebuche and in 13 (10 adults and 3 juveniles) *T. s. elegans* from El Portil. We also obtained faecal samples of 12 exotic turtles from El Acebuche and 5 from El Portil. For *M. leprosa*, we obtained faecal samples of 15 adults and 6 juveniles from El Acebuche and 14 adults and 5 juveniles from El Portil. For the reduced populations of *E. orbicularis*, we could obtain faecal samples from only 18 adults in El Acebuche, and in two adults from El Portil. We also included data from the stomach contents of two adult *M. leprosa* which were found drowned in a poacher's net in El Portil. The straight carapace length and body mass of all turtles were measured. All native turtles were marked and then released into the ponds.

To obtain faecal samples, we isolated each turtle for 24 hours in a tank with water. The water was then filtered and faeces were preserved in 70% ethanol. Faeces and stomach samples were washed with abundant water and filtered with a 0.2 mm sieve, and their total volume was estimated through water displacement. After separation of vegetation and animal matter in the samples, we calculated the volume of each of these two main general categories. Animal matter was inspected under the microscope for prey identification, and the volumetric content of each identified taxon was also estimated. Unidentified materials were grouped in a food category named as "Other". We have identified prey using the general categories listed in tables 1, 2 and 3. Crustaceans only included the species Procambarus clarkii, an exotic crayfish introduced in 1974 in marshes close to El Acebuche pond, where it is presently very abundant (Guttiérrez-Yurrita and Montes, 1999; Geiger et al., 2005).

In this study, we had different types of samples (faeces and stomach content), which were standardized by averaging the volumetric content of each food category. Faecal analyses are reported to be efficient to reveal plant matter while may underrepresent the importance of animal matter (Caputo and Vogt, 2008). Combination of both types of samples is recommended to provide a comprehensive picture of turtle diets (Caputo and Vogt, 2008). After testing that there were not significant differences in the content of vegetation and animal matter between stomach and faeces samples (Mann-Whitney test: P > 0.05 in all cases) in this study we grouped both types of samples in the diet results. Quantitative analyses of the diet were carried out using the frequencies of occurrence (percentages of individuals in which we found each food category) and percentage of total volume for each food category. The importance of the different food categories for each species was calculated using the index of relative importance (IRI), following Lindeman (2007).

In order to obtain a graphical representation of the general volumetric composition of the main components in the diets of turtles of different age and from different localities of the three species we performed a Correspondence Analysis (using STATISTICA v.6), in which we included only those food categories appearing with volume over 20% in the general diet of juveniles or adults of any one of the three species. The variables included in the analysis were the feeding categories: plants, crustaceans, gastropods, odonates, and an additional variable including the remaining animal food. We tested particular differences in diet compositions (applying Bray-Curtis similarity index) between localities, species and ages through ANOSIM analyses (Primer v.6, 9999 permutations, Clarke and Warwick, 2001). The ANOSIM test statistic, R, is close to one when the levels of grouping factor are different. It means all dissimilarities between levels of grouping factor are larger than any dissimilarity among samples in every level of grouping factor (Clarke and Warwick, 2001). In order to test the differences in diet composition between the two localities we performed a one-way ANOSIM test (Clarke and Warwick, 2001). As both localities differed in diet compositions, we used a two-way ANOSIM test with replication (Clarke and Warwick, 2001) using as two grouping factors: the locality, and a combination of species (M. leprosa, E. orbicularis and T. scripta) and age (adult and juveniles).

Results

The diet of Trachemys scripta elegans

Adult turtles did not have a predominant general pattern in the volumetric plant/animal composition of the diet, but El Acebuche turtles fed mainly on animal matter, while ingested similar proportions of plants and animals in El Portil (table 1). Only 37.5% of the adult turtles examined from El Acebuche contained plants, and 75.0% contained animal food, which had the highest relative importance. In El Portil, both general categories had higher occurrence than in El Acebuche.

Plant matter mainly consisted of leaves, seeds or weeds of aquatic macrophytes, and filamentous algae. The animal portion of the diet in adult turtles from El Acebuche were mainly composed of crustaceans, including only the exotic crayfish *Procambarus clarkii*, reaching the highest prey importance, and appearing in 50% of these turtles (table 1). Remains of a small bird were found in the diet of an adult female turtle. In contrast, crustaceans were not important in the diet of adult turtles from El Portil, while gastropods of the genus *Physa* were the main animal food together with heteropterans (Notonectidae and Corixidae) and odonates (larvae and adults) (table 1).

In juveniles, 85% of the diet volume was animal matter in both localities (table 1). All

juvenile turtles included animals while plants only occurred in 50% of juveniles examined from El Portil and 33.3% from El Acebuche (table 1). As in adults, in El Portil the most important animal food was gastropods, occurring in 83.3% of juvenile turtles. Odonates (adults and larvae) and crustaceans (exotic crayfish) were also important components in the diet (table 1). Juveniles from El Acebuche mainly fed on odonates, found in all examined individuals, and coleopterans and crustaceans were also important food categories. Diet of juveniles differed from adults of this locality in the lower importance of crayfish, which composed 16.5% of the animal volume, although occurred in 83.3% juveniles (table 1). In this locality, ingestion of a fish (Cyprinus carpio) was also detected in one juvenile.

The diet of Mauremys leprosa

The diet of *M. leprosa* showed wide differences between the two ponds. In El Portil, adults were mainly herbivorous while in El Acebuche turtles mainly fed on animals. In El Acebuche the high increase in animal food was due to the high proportion of the exotic crustacean, P. clarkii, reaching an average volume of 53.5% and occurring in 80% of individuals. Among other animals, coleopterans had 20% occurrence, and remains of fish were found in two individuals. In El Portil, crustaceans did not reach such high relative importance as in El Acebuche, although they were the animal food with highest volumetric proportion in the diet. In El Portil, the ingestion of odonates (mainly fed as adults) was also important. Although the volumetric proportion of dipterans (chironomid larvae) ingested was not high, they occurred in 43.7% of individuals (table 2).

Juvenile *M. leprosa* ingested similar proportions of plant and animal matter in both localities and we did not find significant differences with adult turtle diets. In El Acebuche, aquatic coleopterans (present in all individuals examined) had the highest relative importance among animal food, also including important values

| Food categories | El Portil | | | | | | El Acebuche | | | | | |
|-----------------|-------------------|------|------|----------------------|-------|------------------|-------------|------|---------------------|------|-------|------|
| | Adults $(N = 12)$ | | | Juveniles (N = 6) | | Adults $(N = 8)$ | | | Juveniles $(N = 6)$ | | | |
| | %V | %F | IRI | % V | %F | IRI | % V | %F | IRI | %V | %F | IRI |
| Plants | 59.6 | 75.0 | 44.9 | 15.0 | 50.0 | 5.0 | 26.1 | 37.5 | 10.6 | 15.0 | 33.3 | 3.2 |
| Animals | 40.4 | 91.7 | 37.2 | 85.0 | 100.0 | 56.9 | 73.9 | 75.0 | 60.1 | 85.0 | 100.0 | 54.4 |
| Heteropters | 10.8 | 50.0 | 5.4 | 4.0 | 50.0 | 1.3 | 1.6 | 12.5 | 0.2 | 5.6 | 50.0 | 1.8 |
| Odonata | 8.5 | 33.3 | 2.8 | 16.4 | 66.7 | 7.3 | 0.6 | 12.5 | 0.1 | 37.3 | 100.0 | 23.9 |
| Hymenopters | 1.7 | 16.7 | 0.3 | 1.5 | 33.3 | 0.3 | 0.9 | 25.0 | 0.3 | 1.3 | 16.7 | 0.1 |
| Dipterans | 1.7 | 33.3 | 0.6 | 1.0 | 33.3 | 0.2 | 0.6 | 12.5 | 0.1 | 6.0 | 16.7 | 0.6 |
| Coleopterans | 1.0 | 33.3 | 0.3 | 6.8 | 33.3 | 1.5 | 16.0 | 25.0 | 4.3 | 10.3 | 83.3 | 5.5 |
| Crustaceans | 3.3 | 25.0 | 0.8 | 9.3 | 50.0 | 3.1 | 41.6 | 50.0 | 22.6 | 16.5 | 83.3 | 8.8 |
| Gasteropods | 11.8 | 58.3 | 6.9 | 32.5 | 83.3 | 18.2 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| Worms | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Fish | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 16.7 | 0 |
| Others | 1.7 | 41.7 | 0.7 | 13.5 | 66.7 | 6.0 | 12.5 | 12.5 | 1.7 | 7.7 | 33.3 | 2 |

Table 1. Diet of the exotic turtle, *Trachemys scripta elegans* in two ponds of Southern Spain. %V = Average of the percentage of each category volume in all the samples; %F = frequency of occurrence; IRI = index of relative importance.

Table 2. Diet of native turtles, *Mauremys leprosa*, coexisting with exotic turtles in two ponds of Southern Spain. %V = Average of the percentage of each category volume in all the samples; %F = frequency of occurrence; IRI = index of relative importance.

| Food categories | El Portil | | | | | | El Acebuche | | | | | |
|-----------------|-------------------|--------|---------------------|------|--------------------|------|-------------|---------------------|------|------|-------|------|
| | Adults $(N = 16)$ | | Juveniles $(N = 5)$ | | Adults (N = 15) | | | Juveniles $(N = 6)$ | | | | |
| | %V | %F | IRI | % V | %F | IRI | % V | %F | IRI | % V | %F | IRI |
| Plants | 84.61 | 100.00 | 83.8 | 49.3 | 60.0 | 32.9 | 31.8 | 40.0 | 10.9 | 49.6 | 100.0 | 35.1 |
| Animals | 14.35 | 75.00 | 10.7 | 50.7 | 80.0 | 45.0 | 68.2 | 86.7 | 50.8 | 50.4 | 100.0 | 35.8 |
| Heteropters | 0.44 | 31.25 | 0.1 | 0 | 0 | 0 | 2.0 | 13.3 | 0.2 | 10.5 | 83.3 | 6.2 |
| Odonata | 2.98 | 31.25 | 0.9 | 12.0 | 40.0 | 5.3 | 0.0 | 6.7 | 0.0 | 13.4 | 66.7 | 6.3 |
| Hymenopters | 0.11 | 18.75 | 0 | 1.0 | 20.0 | 0.2 | 0.0 | 6.7 | 0.0 | 3.1 | 66.7 | 1.5 |
| Dipterans | 0.77 | 43.75 | 0.3 | 8.0 | 40.0 | 3.6 | 0.6 | 6.7 | 0.0 | 0.2 | 33.3 | 0.1 |
| Coleopterans | 1.73 | 50.00 | 0.9 | 9.0 | 40.0 | 4.0 | 4.6 | 20.0 | 0.8 | 13.3 | 100.0 | 9.4 |
| Crustaceans | 5.94 | 50.00 | 2.9 | 0 | 0 | 0 | 53.5 | 80.0 | 36.8 | 9.2 | 83.3 | 5.4 |
| Gasteropods | 0 | 0 | 0 | 0.7 | 20.0 | 0.1 | 0 | 0 | 0 | 0.3 | 16.7 | 0 |
| Worms | 1.55 | 12.50 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Fish | 0.19 | 6.25 | 0 | 0 | 0 | 0 | 6.7 | 6.7 | 0.4 | 0 | 0 | 0 |
| Others | 0.65 | 20.00 | 0.1 | 20.0 | 40.0 | 8.9 | 0.3 | 13.3 | 0 | 0.3 | 50.0 | 0.1 |

170

for odonates and heteropterans. The relative importance of crustaceans was not as high as for adults, although its frequency of occurrence was 83.3% (table 2).

The diet of Emys orbicularis

Adults of *Emys orbicularis* ingested mainly animal food in both localities with a low contribution of plants to the volumetric composition of the diet in El Acebuche (table 3). As in the other native turtle species, crustaceans (exotic crayfish) were the animal food with highest volumetric content, and were consumed by all individuals examined in El Acebuche. In this pond the other prey had low frequencies, although it is relevant to consider the presence of hairs indicating the ingestion of a mammal which could have been fed upon as carrion.

We obtained faeces from only two adult turtles from El Portil, which had only fed on animal matter, predominantly odonates (table 3).

Comparison among the diets of the three turtle species

The correspondence analysis required four dimensions to explain 100% of the total inertia, with Dimensions 1 and 2 extracting 64% of the total inertia (table 4). The graphical representation of our cases in these two dimensions distinguished predominantly herbivorous diets from those with high proportions of crustaceans and a general group including other animal matter, such as gastropods and odonates (fig. 1).

We detected significant differences between the diet compositions of turtles in the two localities, El Acebuche and El Portil (one-way ANOSIM test, Global R = 0.249, P = 0.0001). The main difference between localities is the absence of a group with predominant crustaceans in El Portil where gastropods were the main animal food.

Comparing among species and ages, we also detected significant but non-strong differences in their diet composition (two-way ANOSIM, Global R = 0.269, P = 0.0001). In pair-wise comparisons, we only did not detect significant

Table 4. Description of the four dimensions resulting in Correspondence Analyses using the main feeding categories of the diets of *Trachemys scripta elegans*, *Mauremys leprosa* and *Emys orbicularis*.

| Dimensions | Percentage of Inertia | Cumulative Percentage of Inertia |
|------------|--------------------------|-------------------------------------|
| 1 | 34.6 | 34.6 |
| 2 | 29.8 | 64.4 |
| 3 | 20.1 | 84.5 |
| 4 | 15.5 | 100 |

Table 3. Diet of native turtles, *Emys orbicularis*, coexisting with exotic turtles in two ponds of Southern Spain. %V = Average of the percentage of each category volume in all the samples; %F = frequency of occurrence; IRI = index of relative importance.

| Food categories | | El Portil | | El Acebuche Adults (N = 18) | | | |
|-----------------|-------|------------------|------|--------------------------------|-------|------|--|
| | | Adults $(N = 2)$ | | | | | |
| | %V | %F | IRI | %V | %F | IRI | |
| Plants | 0.0 | 0.0 | 0.0 | 25.0 | 33.3 | 4.8 | |
| Animals | 100.0 | 100.0 | 57.6 | 76.3 | 94.4 | 41.5 | |
| Heteropters | 7.5 | 50.0 | 2.2 | 1 | 22 | 0 | |
| Odonata | 47.5 | 100.0 | 27.3 | 0.6 | 16.7 | 0.1 | |
| Hymenopters | 2.5 | 50.0 | 1 | 0.1 | 11.1 | 0 | |
| Dipterans | 5.0 | 50.0 | 1.4 | 0 | 0 | 0 | |
| Coleopterans | 12.5 | 50.0 | 3.6 | 0.9 | 22.2 | 0.1 | |
| Crustaceans | 0 | 0 | 0 | 71.5 | 100.0 | 41.2 | |
| Gasteropods | 25.0 | 50.0 | 7 | 0 | 5.6 | 0 | |
| Worms | 0 | 0 | 0 | 0 | 0 | 0 | |
| Fish | 0 | 0 | 0 | 1 | 6 | 0 | |
| Others | 0 | 0 | 0 | 0 | 0 | 0 | |

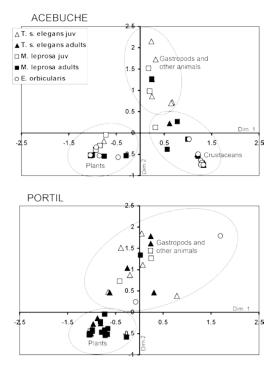


Figure 1. Representation of turtle diets in the two localities studied, El Acebuche and El Portil, grouped after a Correspondence Analyses in which the main food categories were considered.

Table 5. Pair-wise comparisons between the diet composition of the three turtle species (*Emys orbicularis, Mauremys leprosa, Trachemys scripta*) of different ages (adults and juveniles) after a two-way ANOSIM test. Spearman R and P values are shown (* is P < 0.05; ** is P < 0.01; *** is P < 0.001; n.s. is non-significant).

| Pair-wise comparisons | | Spearman R |
|-------------------------|--------------------------|------------|
| T. s. elegans adults | T. s. elegans juveniles | 0.15 n.s. |
| T. s. elegans adults | M. leprosa adults | 0.12* |
| T. s. elegans adults | M. leprosa juveniles | 0.05 n.s. |
| T. s. elegans adults | E. orbicularis adults | 0.27** T. |
| s. elegans juveniles M | 1. <i>leprosa</i> adults | 0.56*** |
| T. s. elegans juveniles | M. leprosa juveniles | 0.13 n.s. |
| T. s. elegans juveniles | E. orbicularis adults | 0.43** |
| M. leprosa adults | M. leprosa juveniles | 0.31** |
| M. leprosa adults | E. orbicularis adults | 0.29** |
| M. leprosa juveniles | E. orbicularis adults | 0.45** |

differences in some comparisons in which *T. s. elegans* were included (table 5). The highest difference was found between the diet composition of adults of *M. leprosa* and juveniles of *T. s. elegans* followed by the differences between adults of *E. orbicularis* and juveniles of *M. lep*-

rosa; and adults of *E. orbicularis* and juveniles of *T. s. elegans* (table 5).

The diets of E. orbicularis and M. leprosa adults were grouped as herbivorous and mainly feeding on crustaceans in El Acebuche, while in El Portil, most M. leprosa adults were herbivorous, and the only two E. orbicularis examined did not ingest plants. Juvenile M. leprosa were included in a group with more diverse animal food, in which there were also juveniles T. s. elegans in El Acebuche, and also adult T. s. elegans in El Portil. The abundant resource of exotic crayfish in El Acebuche grouped T. s. elegans adults in this locality with adult M. leprosa, while in El Portil exotic turtles showed a wide variation in their diets, coinciding with juveniles and adults of the two native species (fig. 1).

Discussion

Trachemys scripta elegans, as an exotic invader, can be considered an opportunistic omnivore, as reported for *Trachemys scripta* in its native areas (Cagle, 1950; Clark and Gibbons, 1969; Hart, 1983; Parmenter and Avery, 1990; Dres-lik, 1999) which favours their distribution in a wide range of habitats. In this study we have detected general differences among the two study ponds, and the opportunistic diet of *T. s. elegans* is confirmed by the variation in the general diet composition observed among individuals from both localities. It is also confirmed by the general non significant differences among juveniles and adults of exotic turtles while in the native *M. leprosa* the ontogenetic diet shift was detected.

While in one pond (El Acebuche), adults and juveniles fed mainly on animal matter (mainly feeding on exotic crayfish), in the other (El Portil) we observed the reported shift from a predominantly carnivorous diet of juveniles to an increase in plant materials in adults, which presented similar proportions of plant and animal content. As the introduced exotic crayfish were a very abundant feeding resource in El Acebuche, adult turtles increased their ingestion in detriment to the more common ingestion of plants usually reported in most adult turtles (Parmenter and Avery, 1990; Bouchard and Bjorndal, 2006). However, the carnivorous diet of juveniles was mainly composed of smaller prey, such as odonates, which probably are easier to capture for small turtles than crayfish. In El Portil, adult diet contained a similar volume of plants and animals, although most individuals contained animals. Similarly, juvenile turtles were predominantly carnivorous, and the high proportion of gastropods in the diet of both juveniles and adults probably revealed the high abundance of this resource in the pond.

We detected general differences among the diets of the three species, although they were not strong. While native species significantly differ in their diets, the exotic turtles did not differ from some groups of native ones. The predominance of crayfish was observed for adults of both native turtles in El Acebuche, as occurred with T. s. elegans. Also a predominance of plants is observed in M. leprosa in El Portil, while an increase in plant ingestion was also observed in T. s. elegans, although of lower proportion. Our main interest was to know whether the diet of native turtles would be influenced by the presence of exotic turtles in their habitats. Keller and García-Mudarra (unpublished data) described the diet of the native species in other ponds of the same area as El Acebuche and where exotic turtles were not present. They found that the volumetric composition of the diet of M. leprosa included 80.7% vegetation in adults and 60% in juveniles. In our study, we observed that adults of M. leprosa coexisting with T. s. elegans ingested a similar proportion of plants and animals in El Portil but had higher proportions of animal matter in El Acebuche; juveniles presented a similar composition of plant and animal matter in both ponds. These results do not seem to reflect a shift in the diet due to interactions with exotic turtles, but they could be due mainly to a high abundance of cravfish in El Acebuche, causing the deviation of adult diet to a higher than usual intake of animal matter.

A predominant proportion of animal matter (95%) was reported for adults and juveniles of E. orbicularis in ponds without exotic turtles in SW Spain (Keller and García-Mudarra, unpublished data). A similar predominance of animal matter in the diet was also found in our study, although with a lower proportion of animals than in the ponds without exotic turtles. However, Keller and García-Mudarra (unpublished data) reported a more diverse diet, including aquatic insects as the commonest prey, although crayfish were also abundant in their study ponds. These variations could indicate that the presence of an exotic turtle population could affect the availability of animal resources, their ingestion decreasing in quantity and diversity, although the high abundance of exotic crayfish would be able to sustain the feeding necessities of the three species, as reported for other species in the same study area (Tablado et al., 2010).

Dietary shifts as a result of competition for food in a same habitat have been observed in aquatic turtles assemblages (Berry, 1975; Vogt and Guzman, 1988), although Lindeman (2000) found that interspecific competition was of little importance among five sympatric aquatic turtle species (including T. scripta). All three species of aquatic turtles included in this study seem to be able to vary their diet as a response to the availability of feeding resources. However, our results revealed that, out of the three turtles, T. s. elegans had a wider range of food resources, overlapping with the food spectra of different age groups of the two native species in both localities, while narrower range of food is observed within age groups of the native species.

In our study period, food resources did not appear to be a constraining resource for any of the three turtle species. Plant resources did not seem to be limited, but the main characteristic of our study area (mainly in El Acebuche) is the presence of exotic crayfish, which constitute an abundant feeding resource reported to complement the diet of these and other vertebrate species (Adrian and Delibes, 1987; Geiger et al., 2005; Ottonello et al., 2005, Tablado et al., 2010). Thus, animal food did not appear to be constrained for native or exotic turtles, due to the high abundance of exotic crayfish reported during the last decades in one of the areas (Gómez-Yurrita and Montes, 1999), although native turtles and especially E. orbicularis, narrowed their animal food spectra. The introduction of exotic T. s. elegans has been reported to affect the survival of native turtles (Cadi and Joly, 2004). However, in this study, so far, we did not detect changes in the diet which could be associated to interactions or competition with exotic turtles. However, the widely opportunistic diet of T. s. elegans may be a key factor favouring the colonization of aquatic habitats in which this species is able to reproduce successfully. Moreover, we can not discard the possibility of food competition in areas with different conditions from our study sites, containing a higher number of individuals of T. s. elegans, reduced populations of native turtles, or even an impoverishment of feeding resources.

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