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*Successful reproduction of the introduced slider turtle (*Trachemys scripta elegans*) in the South of France*

ANTOINE CADI[a,b]*, VIRGINIE DELMAS[c], ANNE-CAROLINE PRÉVOT- JULLIARD[c], PIERRE JOLY[a], CLAUDE PIEAU[d] and MARC GIRONDOT[c]

[a] *UMR 5023, Ecologie des Hydrosystèmes Fluviaux, CNRS et Université Claude Bernard Lyon 1, Villeurbanne, France*

[b] *Conservatoire Rhône-Alpes des Espaces Naturels, Vourles, France*

[c] *UMR 8079, Ecologie, Systématique et Evolution, CNRS et Université Paris-Sud, Orsay, France*

[d] *UMR 7592, Institut Jacques Monod, CNRS et Universités Paris 6 et 7, Paris, France*

ABSTRACT

1. Massive importation of slider turtles (*Trachemys scripta elegans*) as a pet in France over the past few decades has been followed by the release of many of these turtles into natural environments. *T. scripta elegans* is now widely distributed in France.

2. This paper reports on the successful reproduction of this species in France, with confirmed production of both sexes from nests incubated in the wild. These results indicate that the turtle *T. scripta elegans* can reproduce in the wild and that its long-term persistence is possible in France.

3. The potential impact of this invasive species in natural ecosystems warrants future study. Meanwhile, authorities are strongly encouraged to educate the public to the potential danger of exotic species introduction for local ecosystems and to capture and remove this species from wetlands in southern Europe.

KEY WORDS: introduction; invasion; reproduction; temperature-dependent sex determination; sex ratio; *Trachemys scripta elegans*

INTRODUCTION

The introduction of exotic species has contributed to the global loss of biodiversity and also to the increasing number of threatened or endangered species (Wilson, 1988). However, most introduced species do not persist (Williamson, 1996; Mooney and Cleland, 2001). Successful invasion by an introduced species involves three essential stages: (i) the introduction of organisms to a new environment, (ii) the establishment and increase in the local population, and (iii) an expansion in regional distribution, spreading out from the initial location of the successful introduced population (Shea and Chesson, 2002). In this context, firm

*Correspondence to: A. Cadi, UMR 5023 Ecologie des Hydrosystèmes Fluviaux, CNRS et Université Claude Bernard Lyon 1, 69622 Villeurbanne cedex, France. E-mail: cadi@univ-lyon1.fr

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evidence of successful reproduction by the introduced species is a key step towards understanding its possible impact on the ecosystem invaded (Herbold and Moyle, 1986).

The natural distribution of slider turtles *Trachemys scripta* includes large parts of North and Central America (Iverson, 1992; Painter and Christman, 2000). Since the 1970s, massive numbers of young slider turtles have been generated on turtle farms in the USA for the pet trade. The most commonly exported species is the red-eared slider *T. scripta elegans*, with more than 52 million individuals being produced for foreign markets between 1989 and 1997 (Telecky, 2001). As slider turtles are often sold as small hatchlings (3–4 cm carapace length), unsuspecting owners are rarely prepared to continue maintaining them in captivity when the turtles reach adulthood (up to 30 cm carapace length). Often, larger turtles are released by their owners, which has led to the introduction of many slider turtles into natural ecosystems. The release of turtles has occurred in Europe (Warwick, 1991), Africa (Newberry, 1984), South America (Girondot, pers. obs.) and Asia (Warwick, 1991; Moll, 1995; Chen and Lue, 1998). Following release, one of the main limiting factors for the successful invasion by this species is successful reproduction. Egg deposition has been observed in Spain (de Roa and Roig, 1997; Martinez-Silvestre, 1997; Bertolero and Canicio, 2000; Capalleras and Carretero, 2000), and near Paris, France (Moran, pers. comm.). However, the production of both sexes of hatchlings has never been demonstrated for introduced *T. scripta elegans*. Thus, the long-term persistence of this introduced species in an ecosystem is uncertain. Indeed, sex determination of the *Trachemys* embryos is temperature-dependent, with cooler incubation temperatures producing only males, and warmer incubation temperatures only females (Ewert *et al.*, 1994). Therefore, incubation temperature could be a limiting factor for the invasion of this species in France, if hatchlings of only one sex are produced in the nests in the wild.

The objectives of this study were to investigate the reproductive potential of *Trachemys* turtles in France, as a prerequisite of the potential long-term persistence of slider turtles in France. Specifically, answers were sought to the following four questions: (1) Is egg production of *T. scripta elegans* possible in the wild in France? (2) Are eggs laid in the wild fertilized? (3) Can natural incubation produce viable hatchlings? (4) Are both sexes produced in nests deposited in the soil? To answer these questions, reproduction of *Trachemys* was investigated in two semi-natural ponds in the south of France. Laboratory and field incubations were combined to check for fertility of different individual females, for hatching success of their eggs and sex ratio of their offspring.

METHODS

Species and study sites

The sex determination of slider turtles is temperature dependent, from all-male offspring at low incubation temperatures to all-female offspring at high incubation temperatures (pattern type called MF or TSD 1A; Ewert *et al.*, 1994). The differentiation of both sexes is possible within a range of temperatures called the transitional range of temperatures (TRT: Mrosovsky and Pieau, 1991). There is a significant relationship between sex ratio and constant incubation temperature (Figure 1). Based on this relationship, the TRT spans 2.31°C for *T. scripta elegans*, meaning that both sexes can be produced from constant incubation temperatures between 28.30 and 30.61°C. The effect of temperature on gonadal differentiation occurs during a period of embryonic development called the thermosensitive period (TSP). Both the starting date and the length of this period depend on the overall incubation temperature, although, in general, the TSP extends for approximately 2 weeks.

Turtles used in this study were reared outdoors in two ponds (10×5 m^2, maximum depth 1 m) located at Pierrelatte (in the 'Ferme aux Crocodiles' zoological facility, 4°41′47″E, 44°22′37″N; all geographic data used to WGS84 coordinates system) and Vergèze ('Centre de Récupération' facility, 4°13′12″E

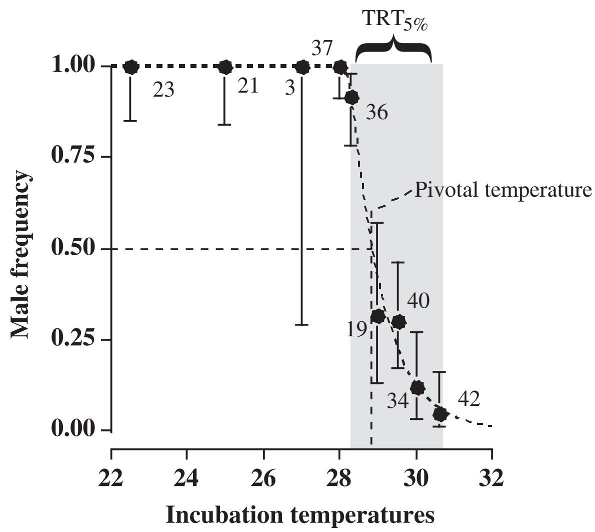

Figure 1. Best-fit curve of sex ratio versus constant incubation temperatures in *Trachemys scripta elegans*, based on the method of Godfrey *et al*. (2003). $TRT_{5\%}$ is the range of temperature that produces between 5% and 95% of males (2.31°C) and the pivotal temperature (28.91°C) is the temperature that produces 50% of each sex. Data from incubation at constant temperature came from Bull *et al*. (1982), Ewert and Nelson (1991) and Ewert *et al*. (1994). Values near each point indicate the number of incubated eggs for each temperature.

43°44′36″N), both located in southern France. Turtles were prevented from escaping by an enclosed T-shaped 50 cm high fence placed within 2 m of the edges of the ponds. The ponds were surrounded by naturally occurring short prairie grass that is common to the region. The origins of the slider turtles in these ponds include several zoological gardens, private donors and also animals captured in the wild. Each pond held approximately 150 individuals, mainly females, with the oldest captive individual being admitted in September 1997. Turtles were fed mainly a fish diet, three times a week, although various other food types were also used. Turtles hibernated in the pond during winter.

Data collection

Egg collection and experimental incubations

Artificial incubation was used to evaluate the rate of unfertilized eggs (question 2 in the Introduction). Indeed, it is impossible to discriminate between early failure in development and unfertilized eggs from an analysis of nests incubated in the soil. In 2002, 13 egg-bearing females from Pierrelatte were identified by means of abdomen palpation. To induce oviposition, these females were injected with oxytocin (5 IU in 1 mL of saline solution). A total of 75 eggs were laid 30 min to 5 h after injection, although subsequently the females accidentally destroyed six of these eggs. The remaining 69 eggs were incubated in Memmert IPP400 incubators at constant (28.5°C) or fluctuating temperatures (27 ± 3°C) in moistened vermiculite (water:vermiculite, 0.5:1). Eggs were checked every 3 days for the presence of the white spot that is evidence of embryonic development (Chan, 1989).

Monitoring of natural nests

In 2001, the first nesting turtle was observed on 25 May and the last on 12 August. The majority of females laid eggs during June. In total 13 clutches from Pierrelatte and 15 from Vergèze, all laid in June, were monitored for fertility and/or sex ratio analysis at hatching. Incubation was interrupted early on in development by opening up and inspecting all nests after 15 days of incubation except for four nests from Pierrelatte and five nests from Vergèze. In the nests opened up early, fertilized and unfertilized eggs were distinguished by the presence of a white spot on the eggshell. For the remaining nine nests, emergence of juveniles was checked daily after 50 days of incubation. Only the number of living hatchlings could be determined, owing to the difficulty in clearly distinguishing between eggs that suffered early embryonic death and those that were unfertilized at the end of incubation. The sex of the young produced from these nine natural nests was determined by dissecting out their genital system for macroscopic examination under a dissecting microscope ($40\times$). Gonads with distinguishable immature seminiferous tubules and degenerated Müllerian ducts signified males, whereas gonads without distinguishable organized tubules and wide and complete Müllerian ducts signified females (Raynaud and Pieau, 1985).

Data were obtained on daily temperature variation at 10 cm depth in the soil from 1984 to 2001 from Météo-France at two stations located close to the natural nest study sites (Nîmes station for Vergèze and Montélimar station for Pierrelatte). Temperature data were grouped to identify 10-day periods where the average maximal daily temperature was greater than 30°C.

Statistical analysis

Checks were made to determine whether access to egg fertilization is similar for all females. If some females exhibit high fertilization rates and others lower, then this could indicate insufficient males for efficient fertilization. Such a data structure induces over-dispersion of fertilization rate per female compared with the null hypothesis. Over-dispersion of the proportion of fertilized eggs per female was tested by comparing the observed variance with its null distribution based on a binomial distribution of fertilized eggs per clutch. Classical tests of variance do not take into account differences in sample size for each nest (Gabriel, 1963). Therefore, 1000 Monte Carlo simulations were used to generate the null distribution of the variance under the hypothesis that there is no difference among clutches for the probability that an egg is fertilized. The proportion of times the calculated variance for H_0 was above the observed variance is directly the α risk. Over-dispersion of the proportion of fertilized eggs for these clutches is statistically significant for α values lower than 0.05.

RESULTS

Clutch size and fertility

Clutch size was in the range 4–11 eggs for nests laid in the field in Pierrelatte, 4–15 eggs at Vergèze, and 2–11 eggs for clutches obtained from Pierrelatte females and subsequently incubated in the laboratory (Table 1). There was no significant difference in the size of natural clutches between Pierrelatte and Vergèze (Mann–Whitney U test, $U = 55.5$, $p = 0.46$).

The proportion of fertilized eggs varied from 0 to 100% and over-dispersion was significant for the three conditions ($p = 0.011$ for laboratory sample; $p < 10^{-3}$ for both natural sites). We found no significant difference in the proportions of fertilized eggs from the two field sites (0.64 and 0.66, $\varepsilon = 0.17$, $p = 0.05$). However, the proportion of fertilized eggs was significantly higher in natural clutches laid in Pierrelatte in 2001 than in clutches obtained from females after oxytocin injection in 2002 (0.33 and 0.66, $\varepsilon = 3.72$, $p = 0.001$).

Table 1. Synthesis of *Trachemys scripta elegans* eggs incubation[a]

Clutch size[b]	Unfertilized eggs	Fertilized eggs[c]	Number of hatchlings	Number of males	Number of females
Eggs from Pierrelatte incubated in the laboratory					
10 (9)	9	0	–	–	–
11 (11)	1	10	–	–	–
3 (2)	1	1	–	–	–
9 (8)	8	0	–	–	–
5 (5)	4	1	–	–	–
8 (8)	4	4	–	–	–
6 (6)	6	0	–	–	–
7 (6)	1	5	–	–	–
3 (2)	2	0	–	–	–
3 (3)	3	0	–	–	–
3 (3)	3	0	–	–	–
2 (2)	2	0	–	–	–
5 (4)	2	2	–	–	–
Eggs from Pierrelatte incubated in the field					
6	2	4	–	–	–
9	3	6	–	–	–
10	6	4	–	–	–
6	2	4	–	–	–
6	3	3	–	–	–
5	0	5	–	–	–
4	4	0	–	–	–
7	0	7	–	–	–
11	2	9	–	–	–
8	–	–	8	4	4
9	–	–	7	1	6
7	–	–	4	0	4
7	–	–	7	0	7
Eggs for Vergèze incubated in the field					
7	2	5	–	–	–
7	4	3	–	–	–
6	2	4	–	–	–
6	3	3	–	–	–
7	0	7	–	–	–
8	1	7	–	–	–
7	3	4	–	–	–
6	1	5	–	–	–
15	15	0	–	–	–
7	6	1	–	–	–
4	–	–	2	0	2
9	–	–	4	0	4
9	–	–	4	0	4
7	–	–	4	3	1
10	–	–	5	3	2

[a] A dash indicates that the information is not available for the nest.
[b] For artificial incubation, the numbers in brackets correspond to the eggs that were incubated.
[c] Fertilized eggs either had a white spot characteristic of embryonic development in the early phases of incubation, or they contained a dead but recognizable embryo or a living hatchling.

Sex ratios and temperatures

Young of both sexes were found in field nests from Pierrelatte and Vergèze (Table 1). Based on the time of clutch deposition (i.e. mid-June) and the daily temperatures recorded near to the respective sites (see Methods section), the thermosensitive period of sexual differentiation during embryonic development probably occurred within the first 2 weeks of July. The daily soil temperatures crossed the TRT nearly every day within this period (Figure 2). Analysis of the temperature profiles recorded in these places between 1984 and 2001 shows that this pattern occurred frequently (Figure 3).

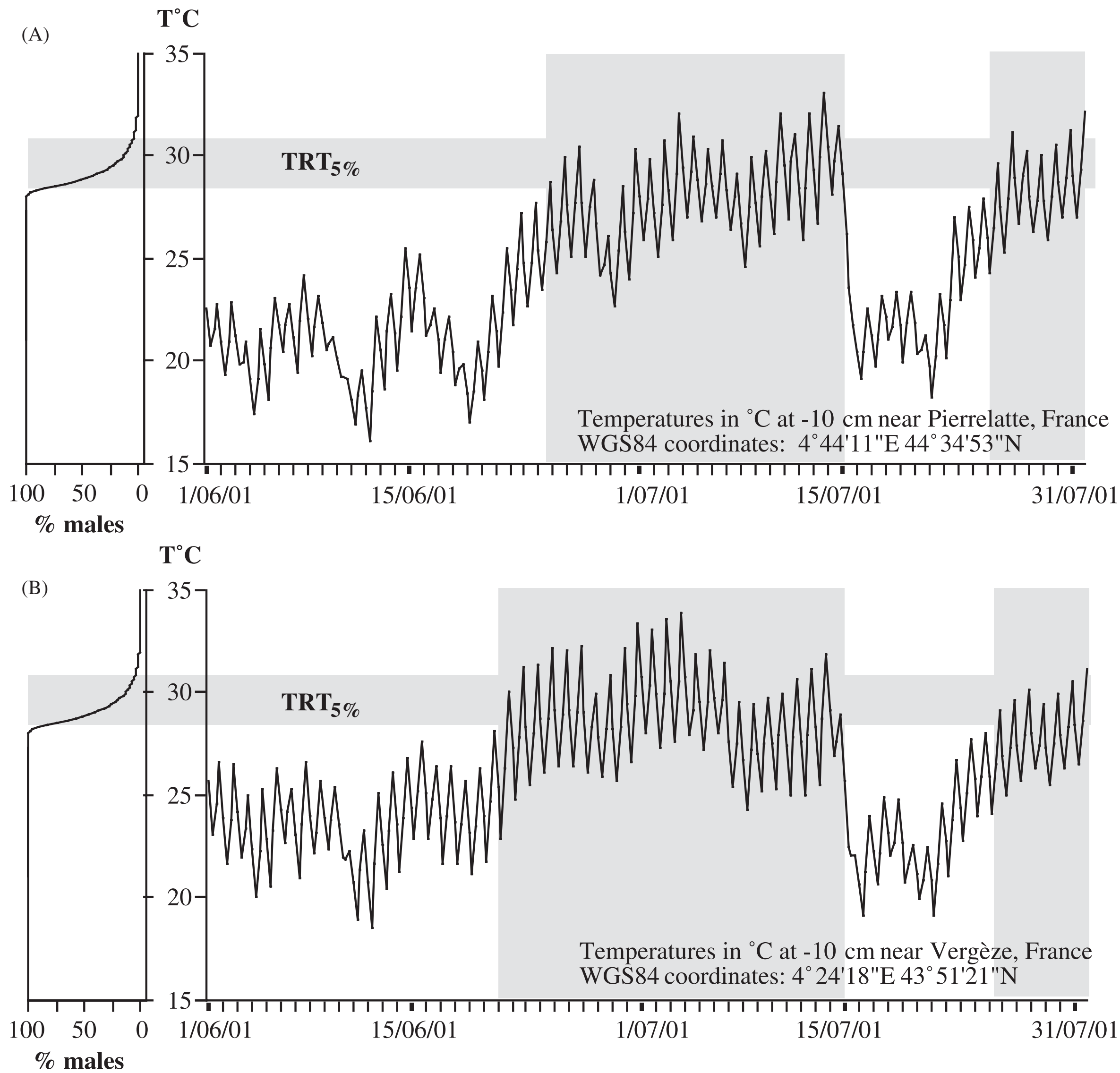

Figure 2. Soil temperatures at 10 cm depth at the two nearest meteorological stations from the Pierrelatte (A) and Vergèze (B) sites. The profile of sex ratio upon constant incubation temperature at the left of each temporal series corresponds to the best fit. The horizontal greyed region corresponds to the range of temperatures in which both sexes can be produced ($TRT_{5\%}$), and the vertical greyed bands represent those dates when daily temperatures at nest depth overlapped with the $TRT_{5\%}$.

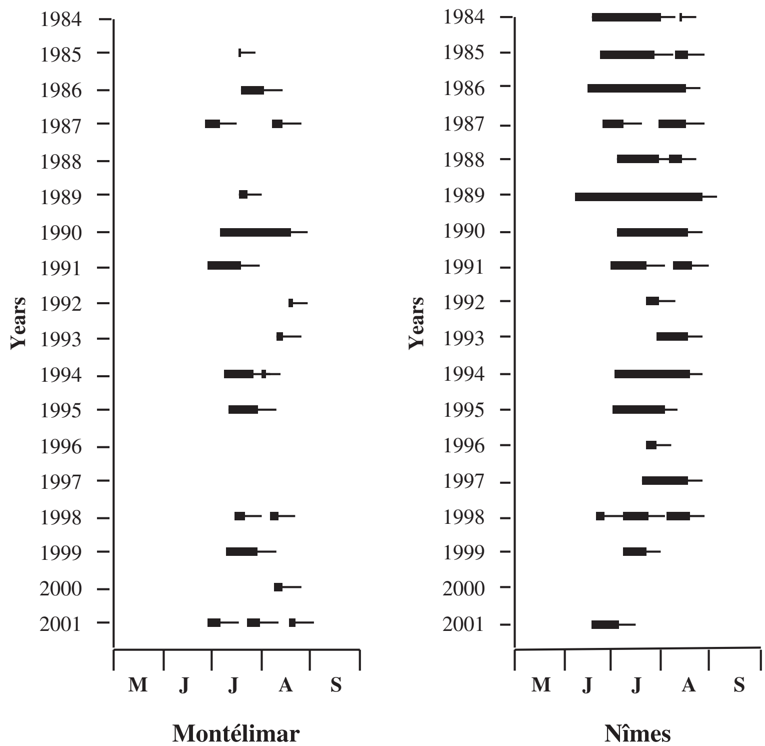

Figure 3. Periods of 10 consecutive days (approximately corresponding to the length of the thermosensitive period of embryonic development for sex determination) where the average of maximal daily temperature is higher than 30°C (feminizing conditions) at 10 cm depth in the ground at Montélimar (near Pierrelatte) and Nîmes (near Vergèze). Bold lines indicate possible beginning of the 10 feminizing days and the thin lines encompass all the putative thermosensitive period.

DISCUSSION

T. scripta elegans is now present in all parts of France (Arvy and Servan, 1996), but data related to its long-term status are lacking. In particular, there is little information on whether this species can reproduce outside its natural distribution range. This study has demonstrated that egg production and emergence occur in France, which is much further north than the previous reports from Spain (de Roa and Roig, 1997; Martinez-Silvestre, 1997; Bertolero and Canicio, 2000; Capalleras and Carretero, 2000). Eggs produced by these released females were fertilized, although there was a high proportion of unfertilized eggs in many clutches. The eggs incubated in the laboratory were more likely to be unfertilized than eggs from natural clutches. This observation may have been due to natural variation in reproductive success across years (2001 versus 2002), although it is more likely related to the sampling methods used. There is a bias towards detecting more successful natural nests because there are visible signs of emergence by the young, compared with nests that do not produce any hatchlings. Eggs incubated in the laboratory came from females that were forced to lay, hence hatchling success was likely to be more random than that from natural clutches.

The high number of unfertilized eggs could have resulted from individuals failing to find a mate. This does not appear to be related to low density (Berec *et al*., 2001), because the animals in this study were maintained in captivity at relatively high density. In contrast, the lack of available males to mate with females may be a more likely explanation. Indeed, in France, the sex ratio of adults released in the wild, as well as in artificial ponds, is strongly biased in favour of females (unpublished data). A lack of males could also explain the observed over-dispersion of the proportion of unfertilized eggs: some females probably did not have access to a male for a given year, hence they had no fertile eggs in their clutches.

This study has shown for the first time that both sexes were produced in field nests laid by slider turtles outside their natural range. Varying soil temperatures during July, when the eggs were incubating, were concordant with the production of both sexes in 2001. Moreover, soil temperatures at a depth of 10 cm during the last 18 years are generally within the temperature range that would be expected to produce both sexes. At the same time, a recent report revealed that fertilized eggs have been produced by slider turtles near Paris (north France), but without evidence of successful reproduction (Prévot-Julliard *et al.*, in press). It could be that cooler soil temperatures in the north might limit the successful reproduction of this species.

Other sightings of slider turtles in France suggest a positive correlation between turtle density and concentration of human settlements (Arvy and Servan, 1996). Slider turtles are hardy enough to survive most winters in France, although reports of dead turtles in garden ponds (Cadi, pers. obs.) imply they may be at the limit of their possible distribution as an invasive species in Europe. Nevertheless, the present observation of successful breeding by *T. scripta elegans* in southern France suggests that the potential expansion of feral populations is a real possibility. The rate of spread by this species probably depends on many unknown life-history parameters, although theoretical results have shown that colonization by invasive species can be rapid during the initial stages (Hastings, 1996).

The European Union Wildlife Trade Regulation (Council Regulation (EC) No. 338/97 9 December 1996 modified by Council Regulation (EC) No. 2307/97 18 November 1997) regulates the import of species into the European Community. *T. scripta elegans* is listed in Annex B of Council Regulation (EC) No. 2551/97 15 December 1997 and all further modifications of this annex. (This species is not listed in the CITES convention.) This classification is 'of live specimens of species for which it has been established that their introduction into the natural environment of the Community presents an ecological threat to wild species of fauna and flora indigenous to the Community'. The introduction into the Community of specimens of the species listed in Annex B shall be subject to completion of the necessary checks and the prior presentation, at the border customs office at the point of introduction, of an import permit issued by a management authority of the Member State of destination. However, sale of individuals born in the Member State is not forbidden.

Information is lacking about the impact of *T. scripta elegans* on local flora and fauna and experiments are in progress. However, as a precaution, we strongly urge two immediate actions to reduce the potential impact of this invasive species in natural ecosystems before the species becomes fully established: (1) the introduction of this (and other) exotic species should be strongly discouraged in France; and (2) we recommend the capture and removal of freshwater exotic turtles from all southern European wetlands. The first point is already covered in European legislation via the Bern Convention (19 October 1979) ratified by France on 1 August 1990 and the Habitats Directive 92/43/EEC (21 May 1992). In the former, 'each Contracting Party undertakes to strictly control the introduction of non–native species'. In the latter, 'Member States shall ensure that the deliberate introduction into the wild of any species which is not native to their territory, is regulated so as not to prejudice natural habitats within their natural range or the wild native fauna and flora and, if they consider it necessary, prohibit such introduction'. The Convention on Biological Diversity ratified by France on 1 July 1994 (which came into force on 29 September 1994) has also introduced the necessity of controlling invasive species. Article 8-H states that 'each Contracting Party shall, as far as possible and as appropriate prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species'. This has been transposed into French legislation by Article L.411-3 of the Rural Code introduced by the law No. 95-101 (2 February 1995). However, the decree that should prescribe the conditions under which Article L.411-3 showed be applied has never been published. We urge the French Authorities to introduce this decree in French legislation.

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