

European pond turtles (*Emys orbicularis*) as alternative dispersers of “water-dispersed” waterlily (*Nymphaea alba*)¹

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Abstract: *Nymphaea alba* (white waterlily) is an aquatic plant adapted to dispersal by water. This study assesses the potential of *Emys orbicularis* (European pond turtle) to disperse seeds undamaged and to contribute to dispersal between isolated water bodies, which cannot be achieved by the standard hydrochorous mode of dispersal. We investigated the effect of seed passage through the turtles' digestive tract on seed viability and germination over a 2-y period. The effect of gut passage differed between seeds germinated in light and in darkness. In light, gut passage delayed germination, both within the first year and between years, but total germination at the end of the study did not differ from that of control seeds. In darkness, gut passage delayed germination within the first year, but accelerated it in the long term, and total germination was higher than that for control seeds. *Emys orbicularis* can be regarded as a legitimate disperser of *Nymphaea alba*. The turtles move between different water bodies and can disperse seeds when they do so, which is essential for the colonization or re-colonization of isolated water bodies.

Keywords: *Emys orbicularis*, germination percentage, germination rate, hydrochory, non-standard dispersal, *Nymphaea alba*, plant–animal interactions, saurochory, viability.

Résumé : *Nymphaea alba* (nénuphar blanc) est une plante aquatique adaptée à une dissémination des graines par l'eau. Cette étude s'intéresse au potentiel de *Emys orbicularis* (cistude d'Europe) pour la dissémination des graines de ce nénuphar sans les endommager et à son potentiel de contribuer à la dispersion entre des plans d'eau isolés, ce qui ne peut être effectué par le mode standard de dispersion, l'hydrochorie. Nous avons étudié l'effet du passage des graines dans le tube digestif de la tortue sur la viabilité et la germination des graines sur une période de deux ans. L'effet du passage dans le tube digestif différait entre les graines germant à la lumière et à la noirceur. À la lumière, le passage dans le tube digestif retardait la germination la première année et entre les années, cependant, la germination totale mesurée à la fin de l'étude ne différait pas de celle des graines contrôles. À la noirceur, le passage dans le tube digestif retardait la germination au cours de la première année mais l'accélérait à long terme ce qui fait que la germination totale était plus grande que pour les graines contrôles. *Emys orbicularis* peut donc être considéré comme un agent de dispersion potentiel de *Nymphaea alba*. De plus, en se déplaçant entre différents plans d'eau, la cistude d'Europe peut y disperser les graines du nénuphar blanc ce qui est essentiel à la colonisation ou la recolonisation de plans d'eau isolés.

Mots-clés : dispersion non standard, *Emys orbicularis*, interactions plante-animal, hydrochorie, *Nymphaea alba*, pourcentage de germination, taux de germination, saurochorie, viabilité.

Nomenclature: Castroviejo *et al.*, 1986–1997; Blanco & González, 1992.

Introduction

Movement is an essential aspect of plant life, and seeds are usually the critical mobile stage. Selective pressures imposed on diaspore design by the need for movement have led to the evolution of many adaptations that enhance dispersal (Ridley, 1930, van der Pijl, 1982), such as fleshy, nutritious pulp that attracts frugivores and fibrous pulp and other structures that enhance seed buoyancy and hence dispersal by water. *Nymphaea alba* (white waterlily) is an aquatic plant with seeds that have an aril filled with gas, making them buoyant. This is considered an adaptation for dispersal by water (hydrochory; Smits, van Ruremonde &

van der Velde, 1989). Many aquatic plants have buoyant propagules. However, water dispersal is often directional (downstream) and within a single water body. Dispersal among isolated water bodies has important consequences for the distribution and metapopulation dynamics of species and, therefore, in their regional persistence. Some authors have suggested that alternative agents of dispersal must play a role in the transport of these species over the long distances separating different bodies of water to secure species survival and to explain the large geographic ranges of many species (Sculthorpe, 1967; **van der Pijl, 1972**). For *N. alba*, dispersal between water bodies would require the intervention of animals because seed morphology renders dispersal by wind highly improbable. Waterbirds are known to be important agents of dispersal of aquatic plants, carrying seeds attached to their bodies (exozoochory) or within their digestive tracts (endozoochory) (Ridley, 1930;

Not in Literature cited. Should be 1982?

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Charalambidou & Santamaría, 2002; Clausen *et al.*, 2002; Figuerola & Green, 2002). However, *N. alba* seeds are globular and smooth, making adhesion unlikely (Smits, van Ruremonde & van der Velde, 1989). In addition, a study conducted with *Anas platyrhynchos* (mallard), *Fulica atra* (coot), and *Cyprinus carpio* (common carp) in captivity showed that gut passage destroyed all ingested seeds, which led Smits, van Ruremonde, and van der Velde (1989) to regard endozoochory as unlikely. *Nymphaea alba* also reproduces asexually, and rhizomes sometimes become detached, but their dispersal by waterfowl is improbable considering the seeds' large size (Smits, van Ruremonde & van der Velde, 1989).

Here we assess the potential of *Emys orbicularis* (European pond turtle) to disperse seeds of *N. alba*. Seed dispersal by reptiles (sauchochory) has received little attention when compared to dispersal by birds or mammals. Most reptiles are considered carnivorous and, therefore, are unlikely to play any role in seed dispersal. However, some reptiles usually regarded as carnivores (such as *E. orbicularis*) may occasionally eat plant material or shift to a predominantly herbivorous diet in certain conditions, which makes them potential agents of seed dispersal. Thus, for instance, seed dispersal by lizards (Godínez-Álvarez, 2004), frogs (Fialho, 1990), snakes (Engel, 1997), and crocodiles (Casas-Andreu & Barrios-Quiroz, 2003) has been documented. There have also been some studies on seed dispersal by turtles (Liu, Platt & Borg, 2004; Strong & Fragoso, 2006; and references therein), but most dealt with dispersal by herbivorous terrestrial turtles of fleshy-fruited plants (but see Liu, Platt & Borg, 2004), and no study to our knowledge has focused on dispersal of aquatic plants. There is only one study dealing with a predominantly aquatic turtle, *Rhinoclemmys funerea*, but that species feeds on terrestrial vegetation and disperses seeds of terrestrial plants (Moll & Jansen, 1995).

Emys orbicularis is an opportunistic feeder that relies mainly on animal material, but some studies have revealed a significant portion of plant matter in its diet (Ficetola & De Bernardi, 2006). In our study area, its diet is small fish, amphibians, crustaceans, mollusks, and other invertebrates. However, when available (summer and autumn), the seeds of *N. alba* become a predominant item in turtle feces.

In this study we assessed whether *E. orbicularis* is a legitimate disperser of *N. alba* by studying the effect of gut passage on seed viability and germination over 2 y, analyzing both total seed germination and germination speed.

Methods

We conducted the study in Gándaras de Budiño (north-west Spain, 42° 10' N, 8° 37' W), in a system of natural and artificial ponds, as part of a broader study on the status of *E. orbicularis* in the area that involved the capture of individuals throughout their annual period of activity (Cordero Rivera & Ayres Fernández, 2004). We kept captured individuals in boxes for at least 1 night and retrieved their feces. During summer and early autumn (when *N. alba* fruits are available), all turtles captured ($n = 10$) contained seeds of *N. alba*. We collected defecated seeds and counted damaged and apparently undamaged seeds. Ten feces from

10 different adult individuals were used in this study. We obtained control seeds from the plants by bagging flowers after anthesis with a thin < 1-mm cloth mesh to prevent seed escape after ripeness and a thicker 1-cm plastic mesh to prevent fruit consumption by vertebrates. We bagged the fruits (ovoid fleshy capsules 3–4 cm in diameter and 4–5 cm long) in early September and collected 15 mature fruits after 20 d. Fruits contained 392 ± 70.7 (mean \pm SE, $n = 15$) seeds. As *N. alba* reproduces vegetatively, it is difficult to determine whether the fruits belong to the same or different individuals. Since the seeds in individual turtle feces probably come from different fruits, we mixed all seeds collected from plants and performed germination tests with random subsamples (control replicates). We removed the arils, since they open naturally after some days, releasing the seeds, and all seeds from turtle feces were without arils.

The seeds of *N. alba* (ellipsoids, 2–3 mm) are recalcitrant (*i.e.*, they do not survive dry storage; Guppy 1897; Smits, van Ruremonde & van der Velde, 1989; Hay *et al.*, 2000); and storage in water at cold temperature is recommended (Hay *et al.*, 2000). In natural conditions, they have innate dormancy that prevents germination in autumn. In autumn and winter they experience cold temperatures in the water, and they germinate when temperature increases, in spring and summer. The seeds require a chilling period to overcome innate dormancy (Smits, van Avesaath & van der Velde, 1990). In accordance with these requirements, all seeds were stored in closed containers in tap water and in darkness. Storage was initially at room temperature (*ca* 20 °C). Later, in November, the seeds were moved to a refrigerator, where they were stored for 5 months at 6 °C.

We initiated the germination test on 30 April 2004. We placed seeds in closed 50-mL transparent plastic containers with tap water at room temperature (18–26 °C) under 2 treatments, 1) light and 2) darkness, to simulate conditions of a) clear and shallow waters and b) turbid or deep waters, under leaf canopy, or buried in mud. We used 10 replicates with 50 seeds each for each treatment (ingested and control seeds in light and darkness). We monitored germination weekly, and seeds were considered germinated when the radicle or coleoptile was visible. Germination occurred in the first 7 weeks and was monitored for 4 weeks more, but no new germinants were recorded after that. We then moved all the containers outdoors and monitored germination in July of the following year, when we recorded new germinations, and again in mid August, when we did not observe new germinations. We tested the seeds that remained ungerminated for viability with a tetrazolium test (Anonymous, 1985): seeds were cut open and incubated in the dark in a 2% solution of 2,3,5-triphenol-tetrazolium chloride in phosphate buffer for 24 h at 40 °C.

DATA ANALYSIS

We analyzed the effects of seed passage through turtles on the germination patterns in the first year and after 2 y of observation, analyzing the effects on both germination speed and total germination.

We tested the effects on germination speed with a failure-time analysis to properly handle right-censored

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data (*i.e.*, seeds that remained ungerminated but that were viable). Since the treatments seemed to change the likelihood of germination in the periods of high hazard rather than change the timing of these periods (Figure 1), we used a Cox proportional hazard regression model (Fox, 2000) using S-plus 6.0 (Mathsoft, 1999). We added to the model the effect of treatments (turtle seed passage *versus* control and light *versus* darkness) as main effects and their interaction, and the effect of individual turtles or different control groups as a random effect. We estimated the ties using the “exact method”. Since the interaction between treatments was significant, we analyzed the effect of turtles in light and darkness separately.

We tested the effects on total germination and viability using generalized linear models with binomial error distribution and logit link function, utilizing the EXTRABINOMIAL procedure when data were overdispersed (Williams, 1982), using GenStat, 7th edition. As binomial denominator, we used the total number of seeds for the analyses of viability and the number of viable seeds at the end of the germination trial for the analysis of final germination, thus isolating the effect on germination from that on viability.

To avoid pseudoreplication, we used the feces (each from 1 individual) as replicates rather than the individual seeds.

Results

We captured 10 turtles during summer and early autumn (when *N. alba* fruits are available), and all had seeds of *N. alba* (775 ± 149.8 seeds/fecal sample, mean \pm SE, $n = 10$). Most seeds were apparently intact ($91.1 \pm 3.0\%$, $n = 10$), and all had the aril removed.

Seed germination occurred in both the first and second years of observation. The effect of gut passage on germination speed and on total germination differed between seeds germinating in light and darkness, and this was true for both years ($P < 0.0001$ in all cases). Thus, the effect of ingestion was analyzed in light and darkness separately.

Within the first year, gut passage slowed down germination (relative to the control) in both light and darkness,

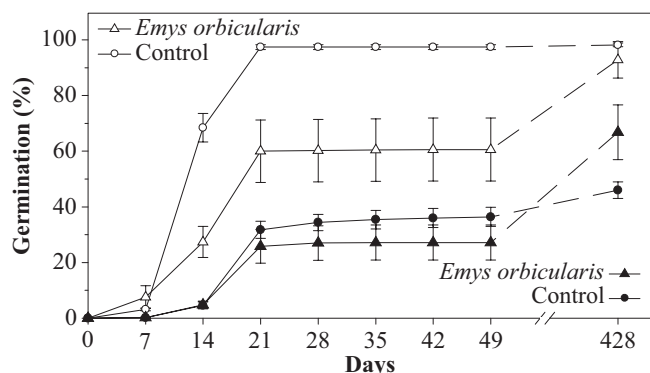


FIGURE 1. Cumulative germination (percentage) of *Nymphaea alba* seeds after passage through the digestive tract of *Emys orbicularis* and of control seeds, under light (open symbols) and dark (closed symbols) conditions. Data are mean \pm SE. Note the break in the X axis.

but more so in light (light: $\chi^2 = 111.9$, $df = 1$, $P < 0.001$, $\beta = -0.40$; darkness: $\chi^2 = 6.2$, $df = 1$, $P = 0.013$, $\beta = -0.14$) (Figure 1). Total germination was lower for ingested seeds in light (40% lower; $\chi^2 = 19.1$, $df = 1$, $P < 0.001$), but in darkness it was not significantly different from controls ($\chi^2 = 1.5$, $df = 1$, $P = 0.217$) (Figures 1 and 2). Germination was higher in light both for ingested and control seeds (Figures 1 and 2).

Between years, the effect of gut passage on germination speed was significant in both light and darkness (light: $\chi^2 = 38.3$, $df = 1$, $P < 0.001$; darkness: $\chi^2 = 14.5$, $df = 1$, $P < 0.001$) but of opposite sign: gut passage slowed down germination in light ($\beta = -0.23$) but accelerated it in darkness ($\beta = 0.16$). Total germination after 2 y was not significantly different between control and ingested seeds in light ($\chi^2 = 2.3$, $df = 1$, $P < 0.129$), but it was significantly higher for ingested seeds in darkness ($67.2\% \pm 9.8$ for ingested seeds *versus* $46.1\% \pm 3.0$ for control seeds, $n = 10$, $\chi^2 = 3.9$, $df = 1$, $P = 0.049$) (Figures 1 and 2).

At the end of the germination trial, viability was the same for ingested and control seeds ($99.1\% \pm 0.4$, $n = 10$, light and dark treatments together) but was slightly higher for seeds in the dark ($99.5 \pm 0.2\%$ in darkness *versus* $98.7 \pm 0.4\%$ in light, $n = 10$: $\chi^2 = 3.2$, $df = 1$, $P = 0.054$, ingested and control seeds together).

The overall effect of gut passage on seed viability (pooling seeds visibly damaged and not used in the germination trial and those revealed as not viable at the end of the germination trial) was significant ($\chi^2 = 24.03$, $df = 1$, $P < 0.001$): gut passage reduced viability by 8.6% ($90.5\% \pm 2.0$ for ingested *versus* $99.1\% \pm 0.4$, $n = 10$ for control seeds) (Figure 2).

Some seeds did not germinate despite being viable. This percentage was higher in the dark, where it was higher for control ($53.8\% \pm 2.9$) than for ingested seeds ($32.4\% \pm 9.6$) ($\chi^2 = 3.89$, $df = 1$, $P = 0.049$). In the light, only a small fraction of viable seeds did not germinate ($< 6\%$), and the differences between ingested and control seeds were not significant ($\chi^2 = 2.3$, $df = 1$, $P = 0.129$) (Figure 2).

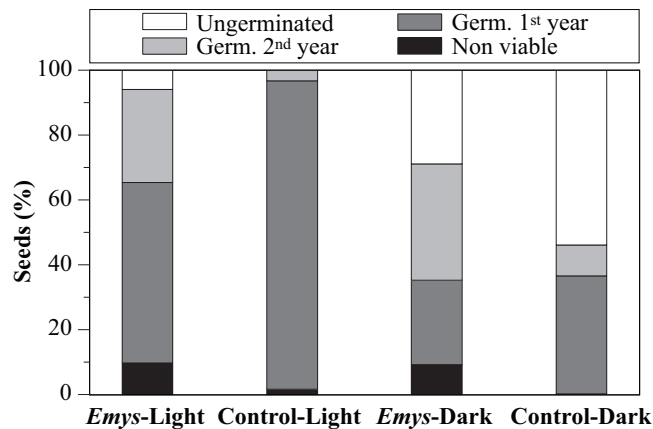


FIGURE 2. Mean percentage of seeds non-viable (black), germinated during the first year (dark grey), during the second year (light grey), and ungerminated but viable (open) for seeds recovered from feces of *Emys orbicularis* and for control seeds, in both light and darkness.

Discussion

EFFECTS OF SEED PASSAGE THROUGH TURTLES ON GERMINATION

Gut passage reduced seed germination in the first year, but after 2 y, germination of ingested seeds was higher in the dark and not significantly different from that of control seeds in the light. However, a portion of seeds remained ungerminated despite being viable, and these had the potential to germinate later, as the occurrence of more germination in the second year suggests. For this reason, the more relevant conclusions are that gut passage caused some mortality (8.6% on average), that it delayed germination in the first year, and that, between years, it delayed germination in the light but accelerated it in the dark.

Some studies have revealed that the effects of gut passage on germination can be inconsistent, depending on the conditions under which the trials were conducted, with differences between laboratory, greenhouse, and natural conditions (e.g., Traveset, Riera & Mas, 2001; Figueroa & Castro, 2002; Rodríguez-Pérez, Riera & Traveset, 2005; Robertson *et al.*, 2006). Our results show differences between light and darkness, suggesting the importance of environmental conditions in the microhabitat of seed deposition (e.g., shallow, clear waters *versus* deep, turbid waters) for seed germination (see also Calviño-Cancela, 2004). These conditions can even modify the seed response to gut passage (interaction between ingestion treatment and germination conditions, this study).

Studies on the effect of animals on germination typically have been conducted on plants adapted for dispersal by vertebrates (endozoochore), for which we expect natural selection to have produced seeds that can tolerate gut passage with little seed damage and no negative effects on germination. However, these positive effects are far from universal, even for endozoochore (reviews in Traveset, 1998; Traveset & Verdú, 2002). Birds, bats, and non-flying mammals have, in general, a positive effect on germination, whereas reptiles have had no significant effect in the few studies that have been conducted with reptiles (Traveset & Verdú, 2002). Gut passage usually accelerates germination (Traveset, 1998), but usually by only a few days or, rarely, some weeks (Traveset & Verdú, 2002), although this may be just a consequence of the length of the studies, since, in many of them, ungerminated seeds were still viable or were not tested for viability at the end of the study, and the effects observed in the short term could differ from those in the long term. For instance, in our study, at the end of the first year there was a negative effect of gut passage on germination in the dark, but after 2 y the overall effect of gut passage was positive.

The effect of gut passage on germination speed occurred both within one season and between 2 consecutive seasons. Since the consequences of emergence time for plant fitness are context dependent (Verdú & Traveset, 2005 and references therein), it is difficult to determine the final effect of the delay in germination caused by turtles. In any case, gut passage increased the variability in the germination response (Figure 1), which may, in itself, be beneficial, spreading the risk of seedling mortality in adverse conditions over longer periods, thus increasing the probability of

success for some of them (Venable & Brown, 1988; Izhaki & Safriel, 1990; Mathias & Kisdi, 2001). Regarding patterns between years, the delay in germination in the light may have negative consequences overall since seeds remain exposed to mortality hazards for longer periods (e.g., predators or pathogens). On the other hand, the presence of a seed bank could favour plant persistence during adverse periods. However, *N. alba* is a perennial plant that can compensate for the effect of adverse episodes with seed production. Hence, the presence of a seed bank would only be crucial under conditions that killed the vegetative parts or prevented seed production while allowing seed survival. Since the seeds do not survive dry conditions, the seed bank would not ensure plant persistence during drought periods.

DISPERSAL BETWEEN DIFFERENT BODIES OF WATER

Emys orbicularis is a legitimate disperser of *N. alba* seeds, acting as a non-standard agent, for which the plant apparently lacks any adaptations (Higgins, Nathan & Cain, 2003; Calviño-Cancela *et al.*, 2006, although see below). This conclusion contrasts with the results of Smits, van Ruremonde, and van der Velde (1989). They found that all seeds were destroyed by *Anas platyrhynchos*, *Fulica atra*, and *Cyprinus carpio*, in contrast with the 9% mortality caused by turtles in this study. *Anas platyrhynchos* and *F. atra* are herbivores that can grind their food effectively in their gizzards (Barnes & Thomas, 1987), which may explain the damage caused to *N. alba* seeds. *Cyprinus carpio* is omnivorous and feeds frequently on plant material, with seeds being common in its diet (e.g., Crivelli, 1981; Chapman & Fernando, 1994). It has powerful pharyngeal jaws and processes hard materials such as seeds very efficiently (Sibbing, 1982). In contrast, the milder treatment by *E. orbicularis* in this study may be a consequence of differences in its digestive tract related to its mainly carnivorous diet (Bannikow, 1951), as animal tissues are more easily digested. Also, Smits, van Ruremonde, and van der Velde (1989) used captive animals in their study, and the type and quantity of food and grit together with the seeds in the digestive tract differ from those in wild animals, which may have resulted in higher seed mortality. Therefore, we should not discard the possibility of other animals dispersing *N. alba* seeds undamaged.

Our study area is a system of natural and artificial ponds created by clay mining, and *N. alba* has been progressively colonizing the isolated, newly created ponds. *Emys orbicularis* have home ranges that can exceed 10 ha (Cadi *et al.*, 2004). They conduct most of their activity in the water, but they do make overland movements, mainly for nesting and dispersal between ponds (Cordero Rivera & Ayres Fernández, 2004). Overland movements of hundreds of metres or even kilometres have been reported (Servan, 1988; Rovero & Chelazzi, 1996; Kotenko, 2000; Cadi *et al.*, 2004). These movements are known to be fast and direct (Naulleau, 1991; Lebboroni & Chelazzi, 2000), increasing the chance of seeds being dropped in the water and not on land. In the study area, one individual captured in one pond was recaptured the following day in another pond 54 m away and in another one 224 m away 1 d later. Since turtles can retain seeds of *N. alba* for more than 2 d (C. Ayres Fernández, pers. observ.) and can move between

ponds hundreds of metres away during that time, they are likely to move *N. alba* seeds between different water bodies. This sort of dispersal is essential for *N. alba* to colonize new areas or re-colonize those areas in which it has become extinct (e.g., after periods of drought), as such requires moving over land and cannot be achieved through the standard dispersal mode of this species (water).

The fact that *N. alba* seeds can be effectively dispersed by 2 different mechanisms (zoochory and hydrochory) could favour an evolutionary change driven by this plant–animal interaction, as has occurred with some conifers dispersed by wind and seed-caching animals (Vander Wall, 1992; Vander Wall *et al.*, 2006). These systems can provide insight into the evolution of new dispersal modes (Vander Wall & Longland, 2004): if the new dispersal mode (animal) is more effective than the original mode, this could favour the evolution of traits that attract or reward the animal and enhance seed survival during gut passage, and we could expect a transition from one form of dispersal to another. Alternatively, we could expect the evolution of a dual strategy, with traits that enhance dispersal by animals and thus increase the chances of dispersal between water bodies and that enhance buoyancy, favouring dispersal within a water body.

Both the fruit and the seeds of *N. alba* seem to be attractive not only to turtles but also to waterbirds and fishes, as suggested by Ridley (1930). The fruits are succulent capsules, green to greenish yellow or reddish, filled with seeds (ca 400) embedded in a fleshy tissue. The seeds are surrounded by an aril that encloses air, making them buoyant, which has been interpreted as an adaptation for water dispersal. However, this aril could also act as a food reward for animals, like the fleshy pulps and arils in endozoochorous species. The aril is transparent, but the seeds inside the capsules are bright reddish. Thus, although this species has been regarded as hydrochorous, some of its traits may enhance seed intake by animals and could be adaptations for dispersal by animals, driven by coevolutionary interactions.

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