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Effect of Ingestion by Alligator Snapping Turtles (Macrochelys Temminckii) on Seeds of Riparian Vegetation

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EFFECT OF INGESTION BY ALLIGATOR SNAPPING TURTLES (*MACROCHELYS TEMMINCKII*) ON SEEDS OF RIPARIAN VEGETATION

A Masters Thesis
Presented to
The Graduate College of
Missouri State University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science, Biology

By
Jean Pierre Elbers
May 2010

EFFECT OF INGESTION BY ALLIGATOR SNAPPING TURTLES (*MACROCHELYS TEMMINCKII*) ON SEEDS OF RIPARIAN VEGETATION

Biology

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Master of Science

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ABSTRACT

The alligator snapping turtle (*Macrochelys temminckii*) is a large freshwater turtle that inhabits many lotic water bodies in the Southeastern United States. The species consumes primarily fish but also consumes large amounts of vegetation including seeds of common persimmon (*Diospyros virginiana*), tupelos (*Nyssa* sp.), willow oak (*Quercus phellos*), and pecan (*Carya illinoensis*). Captive specimens of *M. temminckii* were fed samples of the above-mentioned seeds to assess how the species affects ingested seeds in order to evaluate the potential role this species may play as a seed disperser. The proportion of seeds defecated intact varied with species (57−99 %), was lowest in *D. virginiana*, and highest in *N. aquatica*. Ingestion reduced the percentage of seeds that germinated in comparison to uneaten controls in all species except *Q. phellos* where ingestion increased germination percent. Germination percent also decreased the longer seeds remained inside turtles. Ingestion reduced the germination rates of *D. virginiana* and *N. aquatica* seeds but increased germination rates for seeds of *Q. phellos* in comparison to uneaten controls. Due to fungal contamination, conclusions could not be drawn regarding the effect of ingestion on germination percent or rate of *C. illinoensis* seeds. This study suggests *M. temminckii* could potentially play some role as a disperser of *Q. phellos* and *N. aquatica* but is less likely for *D. virginiana*. Information regarding post-dispersal fates of seeds ingested by *M. temminckii* and other freshwater turtles is needed to evaluate the importance of freshwater turtles as dispersers of riparian and wetland vegetation.

KEYWORDS: alligator snapping turtle, *Macrochelys temminckii,* seed dispersal, chelonochory, saurochory

This abstract is approved as to form and content

Don Moll
Chairperson, Advisory Committee
Missouri State University

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Approved:

Don Moll

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INTRODUCTION

Seed Dispersal

Reproduction in plants can proceed by means of both sexual and asexual methods, with the former resulting in genetically unique offspring and the latter with clonal offspring. In unstable and changing environments, genetically unique offspring are thought to have an advantage over clonal offspring due to likelihood that some offspring will be suited for future environmental conditions (Smith 1968; Waxman and Peck 1999); however, offspring resulting from asexual reproduction, especially ramets still connected to the parent plant, can also have higher survival in comparison to seedlings resulting from sexual reproduction (Raphael and Nobel 1986). Many plants are capable of reproducing both sexually and asexually with biotic and abiotic factors determining the allocation of resources to each reproductive mode (Ronsheim and Bever 2000). During times when sufficient resources have been acquired, a given plant may invest resources into sexual reproduction eventually culminating with the production of seeds. Although most plants produce seeds through sexual processes, some seeds are produced asexually through the process of agamospermy (Fenner and Thompson 2005). Seeds created through agamospermy lack the genetic differentiation common in seeds produced by sexual processes; however, seeds produced by both modes of reproduction share superior dispersal capabilities in comparison to other propagules produced during asexual reproduction, which is one argument for the persistence of the seed production in mostly-clonal species (Eriksson 1992).

Another important characteristic of seeds is their ability to become dormant, i.e., to postpone germination until conditions are the most favorable for survival (Copeland and McDonald 2001; Fenner and Thompson 2005). Dormancy prevents a seed from germinating even when all of the components required for germination are present and must be broken for germination to proceed. Although there is no universally accepted classification system for seed dormancy, one conventional system delineates dormancy into three general types: physical, morphological, and physiological (Fenner and Thompson 2005). In physical dormancy, the seed coat is generally impermeable to water (Rolston 1978) and gas exchange (Villiers and Wareing 1964) and can mechanically restrict the growing embryo (Barnett 1976). When the seed coat is responsible for dormancy regulation, dormancy can only be broken when the integrity of the seed coat is compromised either mechanically (Townsend and McGinnies 1972) or chemically (Wang et al. 2007) in a process called scarification. Morphological dormancy describes seeds that are immature even after detaching from the parent (Ives 1923). With physiological dormancy, seeds may contain excess germination inhibitors which prevent seeds from germinating (Bell and Amen 1970). One important and ecologically relevant means of breaking physiological dormancy is stratification, which involves exposing seeds to low temperatures under moist conditions for a prolonged period, which reduces levels of germination inhibiting compounds (Bewley and Black 1994).

Dispersal of seeds allows for the spatial displacement of progeny from parents. Howe and Smallwood (1982) suggest three hypotheses for evolution of seed dispersal based on a review of the available literature. The Escape Hypothesis suggests that dispersal away from the parent is advantageous because it allows progeny to avoid already established predators, pathogens, and herbivores at the home site and reduces the likelihood of competition between parents and progeny and among siblings (Janzen 1970; Connell 1971). The Colonization Hypothesis suggests that dispersal is advantageous because it increases the likelihood that some of the progeny become established in changing environments (*cf.*, Platt 1976). The Directed Dispersal Hypothesis contends dispersal is advantageous if progeny require specific environments for successful establishment and dispersal processes direct progeny to areas suitable for the germination and establishment (*cf.*, Handel 1978).

Many plants have evolved unique adaptations to facilitate the dispersal of their offspring. Seeds can be dispersed through physical forces such as wind (anemochory) and water (hydrochory). Anemochorous seeds possess forms that maximize surface area and increase air resistance such as plumes and samaras and are widespread in forests of the nearctic and less so in neotropical forests (Fenner 1985). Hydrochorous seeds possess structures that aid in buoyancy; however, some anemochorus seeds can also float (Edwards et al. 1994).

In contrast to seed dispersal by the physical forces previously mentioned, seed dispersal can also occur through biotic means. Some plants are capable of dispersing their own seeds in a process called autochory. The seeds are generally contained in structures on the plant that effectively explode, launching the seed a short distance away (Stamp and Lucas 1983). Animals are also prominent dispersers of seeds (zoochory). Mutualisms exist between some species of ants and plants (myrmecochory) in which the plant produces seeds with a structure called an elaiosome, which contain an oil reward for the ant. Ants gather seeds, remove the elaiosome, reap the reward within, and deposit the seeds in generally favorable places for establishment (Culver and Beattie 1978). Plants have also developed adaptations in seeds or fruits containing seeds to assist transportation while attached to the outside of an animal's body (epizoochory or exozoochory), or contained within the digestive system of an animal (endozoochory). Birds and mammals are the most notable of the vertebrate groups implicated in epizoochorous seed dispersal (Sorensen 1986); however, Burgin and Renshaw (2008) noted that a species of aquatic turtle may also be a disperser of seeds that become entangled on the algae attached to the turtle's shell.

With endozoochory, seeds are ingested by an animal, passed through the digestive tract, and finally defecated. Depending on digestive processes and animal movement patterns, seeds may exit the host and germinate away from the location of ingestion. The effectiveness of the seed disperser is determined by the quantity, consisting of the number of visits and number of seeds dispersed per visit, and the quality of seed dispersal, consisting of the quality of treatment, which is how ingestion affects seeds, and deposition, which is what happens to seeds after leaving the disperser (Schupp 1993). Although endozoochory occurs in many different types of animals, it is best-studied in the vertebrates, especially in birds and mammals (reviewed in Snow 1981; Howe 1986; Traveset 1998; Fenner and Thompson 2005). Within the vertebrates, other taxonomic groups in which the potential for seed dispersal has been noted include the reptiles such as snakes (Engel 1997) and lizards (Valido and Olesen 2007), amphibians (da Silva and Caramaschi 1989), and fishes (reviewed in Correa et al. 2007).

Seed dispersal by reptiles (saurochory) commonly involves seeds that are low to the ground, colorful, and aromatic (van der Pijl 1982). One type of saurochory involves the dispersal of seeds by turtles and tortoises (chelonochory: Stone 2002). Chelonians generally do not reduce food items in size once inside of the mouth, i.e., they do not chew food before swallowing, and this behavior reduces the likelihood of initial physical damage to ingested seeds when compared to mammals, which frequently chew foods before swallowing, and birds, which mechanically process food in the gizzard (Schwenk and Rubega 2005). This method of seed dispersal may be an important means of dispersal for terrestrial and aquatic plants because the diets of many chelonians include a variety of seeds and fruits (Ernst and Barbour 1989; Akani et al. 2001; Loehr 2002; Ford and Moll 2004; Moll and Moll 2004; El Mouden et al. 2006; Stone and Moll 2009 and references within). Although several studies have investigated seed dispersal by terrestrial turtles and tortoises (Cobo and Andreu 1988; Stone 2002; Varela and Bucher 2002; Carlson et al. 2003; Liu et al. 2004; Strong and Fragoso 2006; Gibbs et al. 2008; Guzman and Stevenson 2008; Moolna 2008; Jerozolimski et al. 2009 and references within), less is known about seed dispersal by freshwater turtles, which also ingest a diverse array of seeds and fruits and may serve as important dispersers of wetland and riparian plants (Moll and Jansen 1995; Kimmons 2003; Calviño-Cancela et al. 2007).

The Alligator Snapping Turtle

The alligator snapping turtle, *Macrochelys temminckii*, is North America’s largest freshwater turtle (Ernst and Lovich 2009) obtaining a maximum straight-line carapace length of up to 80 cm and a mass of 113 kg (Pritchard 1989). This species ranges from northern Illinois south along the floodplains of the Mississippi River then west to eastern Oklahoma (Riedle et al. 2005) and Texas. It is restricted to river drainages of the Gulf of

Mexico in the Southeastern United States, excluding the Florida peninsula (Ernst and Lovich 2009). Typical habitats for *M. temminckii* include permanent waterways such as rivers (Ewert and Jackson 1994), oxbows (Dundee et al. 1989), bayous (Harrel et al. 1996), creeks (Trauth et al. 1998; Riedle et al. 2006), and sloughs and canals (Boundy and Kennedy 2006). Individuals are almost entirely aquatic and seldom leave water except during rare bouts of basking (Ewert 1976; Shelby and Jensen 2002; Farr et al. 2005; Selman et al. 2009; Thomas 2009), when terrestrial refuges (e.g., beaver dens) are cooler than the adjacent water (Riedle et al. 2006; Howey and Dinkelacker 2007), or when females lay their eggs (Pritchard 1989).

This turtle is unique in possessing a vermiforme tongue that it manipulates to lure prey, consisting primarily of fish, into its guillotine-like jaws (Allen and Neill 1950; Drummond and Gordon 1979). In addition, *M. temminckii* is thought to actively forage for food (Carr 1952; Pritchard 1989; Iverson 2005) as evidenced by the diversity of its prey, including aquatic salamanders, snakes, other turtles including other *M. temminckii*, fish, freshwater mussels, snails, wood ducks (*Aix sponsa*), unidentified passerine birds, and mammals, vegetation such as palmetto berries (*Sabal* sp.), common persimmons (*Diospyros virginiana*), tupelo fruit (*Nyssa* sp.), pecans (*Carya illinoensis*), and acorns from various oaks [water oak (*Quercus nigra*), overcup oak (*Q. lyrata*), and willow oak (*Q. phellos*)], and non-living materials such as rocks, fish hooks, wood, cardboard, and vinyl gloves (personal observation) that have been found in the intestines and stomachs of wild and commercially processed *M. temminckii* (Uley Bass in Pritchard 1989; Sloan et al. 1996; Elsey 2006). Sloan et al. (1996) found acorns in 28 of 65 *M. temminckii* stomachs examined from Louisiana, Arkansas, and Mississippi, concluded that acorns were the most abundant food item by mass and volume, and noted little attention had been given to investigating the turtle's role as a seed disperser for riparian and wetland plant species. Don Winteron (in Pritchard 1989) described a large *M. temminckii* collected from the Suwannee River (Madison County, Florida) that defecated many undigested acorns. Additionally, Uley Bass of Chipley, Florida described *M. temminckii* found in Lake Seminole containing intestines filled with whole tupelo fruit (in Pritchard 1989).

Study Objectives

The purpose of this study is to assess the effect of ingestion for *D. virginiana*, *N. aquatica*, *Q. phellos*, and *C. illinoensis* seeds consumed by *M. temminckii* by documenting the percentage of undamaged seeds voided in the feces, comparing cumulative germination of ingested and uneaten seeds (germination percent), and comparing how quickly ingested seeds germinate in relation to uneaten seeds (germination rate). Considering turtles seldom chew food, and the gut is probably gentler than that of a bird or mammal, I predicted that *M. temminckii* would have neutral effect on the germination rate and percent and void most ingested seeds undamaged.

MATERIALS AND METHODS

Seed Acquisition and Storage

Nyssa aquatica, *Q. phellos*, and *C. illinoensis* seeds were purchased from Sheffield's Seed Co., Inc. (Locke, NY, USA), and *D. virginiana* seeds were purchased from Louisiana Forest Seed Co., Inc. (Lecompte, LA, USA) (Table 1). All seeds were stored in sealed polyethylene bags before feeding trials at temperatures recommended by the suppliers (3−6 °C for *Q. phellos*, *D. virginiana,* and *C. illinoensis* and -9−-6 °C for *N. aquatica*).

Table 1. Seed lot information.

Species	Source	Lot No.	Year Collected
D. virginiana	Tennessee	NA	2008
N. aquatica	Louisiana	080090	2008
Q. phellos	Arkansas	080301	2008
C. illinoensis	Missouri	070348	2007

Feeding Trials

Each turtle was housed separately to facilitate data collection. Seeds were pressed into 27-mL gelatin cubes (water, ground commercial turtle food, carrots, collard greens, and gelatin) and offered to turtles with tongs. During feeding, each turtle was offered the same amount of food with an equal number of seeds. After feeding, the remaining amount of food and seeds was noted. Feeding trials were completed when all seeds of a species had been fed to the turtles (Table 2). Between trials, the turtles were offered gelatin cubes ad libitum except for the *D. virginiana* feeding trail, when each turtle was offered two gelatin cubes daily for 30 days then offered gelatin cubes ad libitum. Prior approval for this project was obtained from the Missouri State University Institutional Animal Care and Use Committee (9-Oct-2008; approval #2008-BB).

Table 2. Feeding trial information.

Species	Duration No. Days	No. Seeds per Gelatin Piece	No. Gelatin Pieces Offered[1]
D. virginiana	8	4	4
N. aquatica	7	2	12
Q. phellos	8	1	24
C. illinoensis	9	1[2]	1−28[3]

[1] Offered to each turtle once a day during the duration of a given feeding trial.
[2] Gelatin pieces for all other trials were 1/2 cubes. Whole cubes with the middle removed were used in *C. illinoensis* feeding trials.
[3] Because the turtles' appetites were unpredictable during this feeding trial, they were offered up to 28 gelatin pieces (mean ± SD = 8.6 ± 9.89) when eager to accept food.

The first feeding trial was for *D. virginiana*, and as these seeds appeared in the feces, they were washed, blotted dry, and placed into polyethylene bags and refrigerated at 3−6 °C. Once most the *D. virginiana* seeds had been collected from turtle feces, feeding was halted for one week to ensure the turtles would consume seeds for the next feeding trial for *N. aquatica*. This first eaten group of seeds for *D. virginiana* (voided early seeds) along with 400 uneaten seeds was then shipped to the USDA Forest Service National Seed Laboratory (Dry Branch, GA, USA) for germination tests (Table 3). After the completion of the feeding trials for *N. aquatica*, voided early seeds and uneaten seeds for *N. aquatica* along with additional *D. virginiana* seeds collected after the first shipment (voided late seeds) were shipped for germination tests. This process was repeated for *Q. phellos*, and voided late seeds for *N. aquatica* were also shipped along with voided early and uneaten *Q. phellos* seeds. Eaten and uneaten *C. illinoensis* seeds and voided late seeds of *Q. phellos* were the final shipment. All species had an uneaten, voided early, and voided late treatment for germination tests except *C. illinoensis*.

Table 3. Germination test specifications. Seeds were germinated at alternating temperatures of 20 °C for 16 hr and 30 °C for 8 hr.

Species	No. Days Prechilled	Temperature of Prechill (°C)	Germination Medium	No. Days for Germination Test
D. virginiana	60	5	Metro-Mix 300[1]	49
N. aquatica[2]	30	2	Kimpak[3]	35
Q. phellos	NA[4]	NA	Metro-Mix 300	35
C. illinoensis[2]	63	2	Kimpak	28

[1] Metro-Mix 300 Growing Medium (Sun Gro Horticulture, Vancouver, British Columbia).
[2] Following Association of Official Seed Analysts Rules for Testing Seeds (AOSA 2008).
[3] Kimpak (= Versa-Pak, NPS Corporation, Green Bay, WI, USA).
[4] Instead of prechilling, 1/3 of the cup scar was cut off, and the pericarp was removed.

Statistical Analysis

During germination tests, seeds for each treatment were separated into 1−4 replicates depending on sample size, and tested in separate germination containers. Every 7 days, the number of germinated seeds was noted and removed from each germination container. This process was repeated until the completion of the germination tests (Table 3).

All statistical analyses were performed using the statistical analysis package Minitab 15 (Minitab Inc 2007). Germination percent (based on the cumulative number of seeds that germinated in each germination container) and germination rate (based on the number of additional seeds that germinated every 7 days in each germination container) were analyzed independently. Replicates of germination percent were compared using chi square analyses of two-way contingency tables (Zar 1996), and replicates of the germination rate were compared using two-way ANOVAs.

No differences in replicates were detected for germination rate, so replicates were pooled for each treatment. Significant differences in replicates were detected for germination percent in uneaten and voided early *N. aquatica* and voided early *D. virginiana* and *Q. phellos* treatments. After pooling the appropriate germination percent replicates, each species possessed an unequal number of replicates for each treatment (e.g., *N. aquatica* had 4, 3, and 1 replicates for uneaten, voided early, and voided late treatments respectively). This unbalanced design prohibited analyses to account for replicate heterogeneity, and germination percent replicates were therefore pooled for each treatment.

Germination rate was then analyzed for each species with a one-way ANOVA. Pair-wise comparisons of each treatment level were used to determine if significant differences were detected in the mean time for seeds to germinate and to infer the effect of ingestion on germination rate. A one-way ANOVA was used with germination percent for each species to determine the effect of ingestion on germination percent. Tukey's multiple comparison tests with a Type-I family error rate of 0.05 were used to make pair-wise comparisons between levels when statistical tests indicated significant main effects.

RESULTS

Feeding Trial Summary

Five *M. temminckii* were offered seeds for each feeding trial (Table 4). All turtles consumed *D. virginiana* seeds. Only turtles 1, 2, 3, and 5 consumed *N. aquatica* and *Q. phellos* seeds, and only turtles 2, 3, and 5 consumed seeds of *C. illinoensis* (Table 5).

Table 4. Description of *M. temminckii* before starting feeding trials.

Turtle[1]	Gender	SCL (cm)[2]	Mass (kg)
1	F	36.0	10.80
2	M	49.8	28.21
3	F	41.3	16.42
4	F	36.2	11.61
5	F	38.8	15.60

[1] Values refer to turtle identity.
[2] SCL indicates the mid-line straight carapace length.

Whether seeds exited turtles damaged or undamaged, not broken or cracked, varied between species. Seeds of *D. virginiana* had the highest proportion of damaged seeds followed by *C. illinoensis*, *Q. phellos*, and *N. aquatica* (Table 6). Because feeding trials lasted between 7–9 days (Table 2), and it was not possible to determine the day during the feeding trials a given seed had been fed to a turtle, only the minimum and maximum gut retention times are reportable. The maximum duration that seeds remained inside of turtles was shortest in *Q. phellos*, followed by *N. aquatica*, and longest in *D.*

virginiana, and the first *D. virginiana* seeds exited turtles much later in comparison to the other species (Table 6).

Both eaten and uneaten *C. illinoensis* seeds were covered in fungus not long after prechilling ended and germination tests began. In all, 4 out of 400 uneaten seeds and 0 out of 55 eaten seeds germinated; thus, these data were excluded in further analysis.

Table 5. Seed consumption by *M. temminckii.* Values represent the total number of a given seed eaten by each turtle.

Turtle	*D. virginiana*	*N. aquatica*	*Q. phellos*	*C. illinoensis*
1	45	118	41	0
2	135	110	83	21
3	138	84	91	34
4	44	0	0	0
5	132	96	79	19
Total	494	408	294	74

Effect of Ingestion on Germination Percent

There was a significant effect of ingestion the proportion of *D. virginiana* seeds that successfully germinated ($F = 31.96$, $df = 2$, $P < 0.001$). Uneaten seeds of *D. virginiana* had a significantly higher percentage of seeds germinate compared to seeds ingested by turtles (both comparisons, $P < 0.0001$), and seeds voided early had a significantly higher percentage germinate than seeds voided late ($P = 0.0074$; Fig. 1a; Table 7).

A significant effect of ingestion was also detected in the percent of *N. aquatica* seeds that successfully germinated ($F = 17.46$, $df = 2$, $P < 0.001$). Uneaten *N. aquatica* seeds had a significantly higher proportion germinate in comparison to seeds ingested by turtles ($P = 0.0099$ for seeds voided early, $P < 0.0001$ for seeds voided late). In addition, seeds that spent less time inside of turtles had a significantly higher percentage germinate than seeds that remained in turtles longer ($P = 0.0003$; Fig. 1b; Table 7).

Table 6. Condition of defecated seeds and gut retention times.

Species	Condition		Gut Retention Time (days)[1]	
	Undamaged[2]	Damaged[3]	Minimum	Maximum
D. virginiana	282	212	8–16	86–94
N. aquatica	407	1	1–6	64–71
Q. phellos	230	64	1–6	43–50[4]
C. illinoensis	55	19	1–9	14–22[4]

[1] Values are ranges because seeds were fed over a period of 7–9 days depending on species (*cf.*, Table 2); seeds could not be separated by the day each was fed to a turtle.
[2] Physically intact (i.e., not broken or cracked).
[3] Broken, cracked, or presumably digested.
[4] Because the turtles had to be returned to their owner, it is possible more seeds would have been voided, lengthening the maximum gut retention time and potentially altering the proportion of undamaged to damaged seeds.

There was also evidence for a significant effect of ingestion on *Q. phellos* seed germination percent ($F = 12.04$, $df = 2$, $P < 0.001$). Interestingly, *Q. phellos* seeds ingested by turtles had significantly higher percentage germinate than uneaten seeds when seeds did not remain inside of the turtles for long ($P < 0.0001$), but uneaten seeds were equivalent in germination percent when compared to seeds that remained longer inside of turtles ($P < 0.5132$). Additionally, the amount of time that seeds spent inside of turtles produced significant differences. Seeds that spent less time in turtles had higher germination percent ($P = 0.0006$; Fig. 1c; Table 7).

Table 7. Germination percent and time (mean ± SE) for seeds.

Species	Treatment	Germination Percent	Germination Time (days)
D. virginiana			
	Uneaten	38.00 ± 2.43a[1]	23.40 ± 0.45a
	Voided Early	18.35 ± 3.09b	27.76 ± 1.72b
	Voided Late	1.14 ± 1.14c	35.00[2]
N. aquatica			
	Uneaten	57.25 ± 2.48a	19.84 ± 0.49a
	Voided Early	46.33 ± 2.88b	22.16 ± 0.78b
	Voided Late	20.59 ± 4.94c	16.50 ± 0.93ab
Q. phellos			
	Uneaten	38.00 ± 2.43a	16.21 ± 0.49a
	Voided Early	58.28 ± 3.87b	12.01 ± 0.57b
	Voided Late	30.36 ± 6.20a	11.53 ± 0.84b

[1] Values with the same letter in each column are not significantly different ($P \geq 0.05$).

[2] Due to insufficient sample size (n=1), a measurement of sample variability could not be calculated, and multiple comparison tests of germination time data between the voided late treatment and the other treatments could not be conducted.

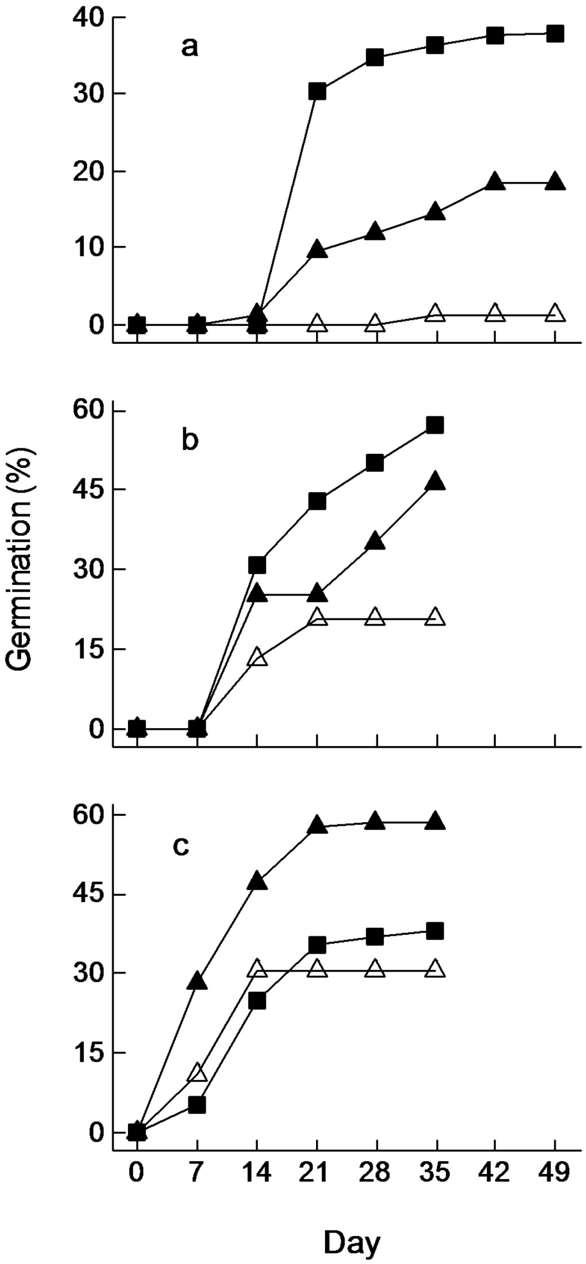

Figure 1. Cumulative germination for (a) *D. virginiana*, (b) *N. aquatica*, and (c) *Q. phellos* seeds that were uneaten (filled sqaures) and ingested by turtles then defecated in two groups: the first group (voided early seeds, filled triangles) and the last group (voided late seeds, open triangles).

Effect of Ingestion on Germination Rate

A significant effect of treatment was detected for the mean germination time (mean time for seeds to germinate) of *D. virginiana* seeds ($F = 7.43$, $df = 2$, $P = 0.001$). Uneaten seeds germinated significantly faster than seeds voided early ($P = 0.0021$). Germination time of seeds voided late could not be compared to uneaten or seeds voided early due to an insufficient sample size in the voided late treatment (Fig. 1a; Table 7).

For *N. aquatica* seeds there was an effect of treatment for mean germination time ($F = 5.47$, $df = 2$, $P = 0.005$). Mean germination times were not significantly different for voided late and uneaten seeds ($P = 0.2587$) but were different for uneaten and seeds voided early ($P = 0.0196$) and both ingested groups ($P = 0.0320$; Fig. 1b; Table 7).

There was a significant treatment effect detected in mean germination time of *Q. phellos* seeds ($F = 17.86$, $df = 2$, $P < 0.001$). Uneaten seeds had a longer germination time than those that were eaten (both eaten groups, $P \leq 0.0042$), and the time spent inside of the gastrointestinal tract had no effect on germination time ($P = 0.9459$; Fig. 1c; Table 7).

DISCUSSION

Effect of Ingestion

One major factor in considering the quality of seed dispersal by a disperser is the quality of treatment which is how a disperser affects ingested seeds and can be assessed by determining whether seeds are voided intact or damaged and whether germination percent or rate is altered (Schupp 1993). A high proportion of *D. virginiana* seeds were damaged during ingestion compared to the other tested species, suggesting *M. temminckii* affects the physical state of ingested *D. virginiana* seeds more than *N. aquatica, Q. phellos,* and *C. illinoensis* seeds.

Chelonians have been shown to differentially damage seeds of different plant species (Cobo and Andreu 1988; Kimmons 2003; Strong 2005; Jerozolimski et al. 2009). Krefting and Roe (1949) also reported differences in the proportion of seeds damaged as a result of ingestion by ring-necked pheasants (*Phasianus colchicus torquatus*) and bobwhite quail (*Colinus virginianus*) and noted three seed species that were either completely digested by pheasants, quail, or both bird species. Utilizing captive neotropical birds, Murray (1988) demonstrated that quality dispersers for three neotropical plants consisted of bird species that not only consumed large amounts of fruits and seeds but also voided every seed intact in comparison to lower quality disperser species, which did not eat as many fruits, discarded the majority of the seeds, and did not void many of the ingested seeds intact.

The gut retention times for seeds ingested by *M. temminckii* were very long in comparison to values listed in the literature for birds (Murphy et al. 1993) and bats

(Shilton et al. 1999), and similar to those mentioned for large mammals and herbivorous reptiles. Rick and Bowman (1961) noted gut retention times of 12–20 days in juvenile captive Galápagos tortoises (*Chelonoidis porteri*). Janzen (1981) noticed that horses fed guanacaste tree (*Enterolobium cyclocarpum*) seeds continued to void them even after 70 days. More so, the gut retention times in the present study could have been much longer considering *M. temminckii* were fed ad libitum after each feeding trial, except during the first 30 days after the *D. virginiana* feeding trial, which is probably why *D. virginiana* seeds had such a long retention time in comparison to the other species (Bjorndal 1987).

Ingestion by *M. temminckii* altered the germination percent of species tested. Studies testing the effect of ingestion by chelonians (Carlson et al. 2003; Liu et al. 2004; Calviño-Cancela et al. 2007) and other vertebrates (reviewed in Traveset 1998) have noted similar results. Seed ingestion by *M. temminckii* also reduced the proportion of seeds that successfully germinated over time because germination percent for groups of seeds that remained longer inside turtles was lower than those spending less time inside turtles. Rick and Bowman (1961) noted decreased germination percent the longer seeds of Galápagos tomatoes (*Lycopersicon cheesmanii* var. *minor*) remained inside two juvenile specimens of *C. porteri*. Murray et al. (1994) found short periods of ingestion by black-faced solitaire birds (*Myadestes melanops*) increased germination percent in some seeds, but longer periods actually caused germination percent to decrease back to levels similar to uneaten seeds. In this study, ingestion increased the proportion of *Q. phellos* seeds that germinated; however, if seeds remained too long inside turtles, then germination percent was equivalent to uneaten seeds. Because a second uneaten group was not tested along with ingested seeds voided late for any species, it is only appropriate to compare the germination percents and rates of the voided late seeds to the other ingested seeds and not the uneaten seeds. For example, although *Q. phellos* is a member of the red oak group in which some species' seeds can be stored for up to 3 years without much loss in viability, its seeds in particular do not store well (Bonner 1973).

Ingestion increased the germination rate of *Q. phellos* seeds but delayed germination of *D. virginiana* and *N. aquatica* seeds voided early. In a review of the literature regarding the effects of ingestion on seed germination characteristics, Traveset (1998) noted differences in germination rates and percent as a result of variation within a species of disperser or seed and also unique combinations of particular plant species and dispersers. Lieberman and Lieberman (1986), in a large study of 52 seed and animal combinations, found only ten combinations involving three seed species in which ingestion altered germination rate.

I do not know what caused the fungal growth in both eaten and uneaten *C. illinoensis* seeds. Prior to separating seeds out to eaten and uneaten treatments, a representative sample of the *C. illinoensis* seeds underwent a tetrazolium test to determine whether there was a large enough proportion of seeds capable of germinating in the sample to justify using the remaining seeds in the study. Tetrazolium tests stain seed tissues essential for development and emergence, and appropriate staining signifies a viable seed capable of producing normal seedlings (Leist et al. 2003). Tetrazolium test results indicated a viability of 60 % for the submitted sample of *C. illinoensis* seeds, which justified the usage of the remaining *C. illinoensis* seeds in the study. Bonner (1976) noted reduced germination percent in *C. illinoensis* as a result of moist, long-term storage of seeds compared to seeds stored under drier conditions. The seed lot used in the current study was already 2 years old, and although Bonner did not implicate fungal growth as a cause of mortality, it is possible that the seeds used in the current study may have been stored under excessively moist conditions that encouraged fungal growth.

Potential Post-Dispersal Fate

Information regarding the quality of deposition or post-dispersal fate, which is what happens to seeds after leaving the disperser, for *M. temminckii* and many other freshwater turtles is lacking. Schupp (1993) defined the quality of deposition as movement and deposition patterns of the seed disperser. Data are not available for deposition patterns, but I can speculate how *M. temminckii* may disseminate seeds to growing sites by comparing movement patterns of *M. temminckii* along with ecological requirements for germination and establishment of *D. virginiana*, *N.* aquatica, *Q. phellos*, and *C. illinoensis*.

Macrochelys temminckii move extensively throughout their aquatic environments but are primarily associated with specific “core” sites offering cover (Sloan and Taylor 1987; Shipman 1993; Harrel et al. 1996; Trauth et al. 1998; Riedle et al. 2006; Shipman and Riedle 2008; Howey and Dinkelacker 2009). Sloan and Taylor (1987) and Harrel et al. (1996) noted that radio-tracked adult and subadult *M. temminckii* in a northeastern Louisiana bayou were found almost exclusively in the flooded baldcypress (*Taxodium distichum*) forest associated with structures such as logs, stumps, branches, and buttonbush (*Cephalanthus occidentalis*). Mean home range length for *M. temminckii* was 513 m in northeastern Louisiana (Harrel et al. 1996), 778 m in eastern Oklahoma (Riedle et al. 2006), and 1794 m in southeastern Missouri (Shipman and Riedle 2008).

In order for successful establishment to occur, seeds dispersed by *M. temminckii* must survive, germinate, and grow to some stable state, which will depend primarily on characteristics of the post-dispersal habitat patch for a given seed. *Diospyros virginiana*, *N.* aquatica, *Q. phellos*, and *C. illinoensis* generally occur within riparian wetlands surrounding rivers or streams that experience seasonal patterns of water levels which can differ locally due to factors such as terrain and proximity to the water source (Mitsch and Gosselink 2007). Many tree seeds cannot germinate underwater (Burns and Honkala 1990). Seeds of *Q. phellos* are still viable after inundation lasting 8 weeks (Larsen 1963), and *N. aquatica* seeds remain viable for at least 14 months of continuous immersion (Applequist 1959). Seeds ingested by *M. temminckii* would have to be dispersed to specific microsites with a long enough drawdown period for survival, germination, and establishment. Seedlings of *N. aquatica* can tolerate inundation for several months depending on the consistency and depth of the water (Kennedy 1970). *Quercus phellos* seedlings can tolerate saturated soils for at least 60 days by going dormant (Hosner and Boyce 1962). *Carya illinoensis* seedlings can tolerate continuous water levels of 60 cm for 4 weeks with greater than 50 % survivorship (Loucks and Keen 1973), but the seedlings of *D. virginiana* die after prolonged submergence or flooding during the growing season (Burns and Honkala 1990). Seeds ingested and voided by *M. temminckii* are negatively buoyant but commonly float in the turtles' feces (personal observation), which could enable seeds to move via hydrochory to potential growing sites. The given diet offered to *M. temminckii* may have contributed to its floating feces, and I do not know the general buoyancy of feces for wild *M. temminckii*.

Synopsis

Considering these results on the effect of ingestion for ingested seeds, it seems *M. temminckii* may play a role as a disperser of *Q. phellos* and *N. aquatica* but is less likely to be an effective disperser for *D. virginiana* because of the large proportion of damaged seeds that result from ingestion and subsequent defecation. Unfortunately, I cannot comment on the role *M. temminckii* may play as a disperser of *C. illinoensis* due to fungal contamination of both eaten and uneaten seeds. Regrettably, information on what happens to seeds after ingestion and defecation from *M. temminckii* is lacking to complete the overall assessment of the effectiveness of this disperser. Information regarding the post-dispersal fates of seeds ingested by *M. temminckii* and other freshwater turtles is needed in the evaluation of the importance of freshwater turtles as dispersers of riparian vegetation.

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