

Survival of the exotic Chinese mystery snail (*Cipangopaludina chinensis malleata*) during air exposure and implications for overland dispersal by boats

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Received: 13 September 2010 / Accepted: 19 November 2010 / Published online: 6 December 2010
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Abstract The exotic Chinese mystery snail (*Cipangopaludina chinensis malleata*) has invaded lakes and rivers across North America and is particularly widespread in northern Wisconsin. Although deliberate introductions and aquarium releases have likely been important, recreational boats may speed the spread of this snail into lakes. Prior research indicated boater access to be a significant predictor of invasion by *C. chinensis* and other invasive species in Wisconsin. To mimic the process of boater transport between lakes, I examined the tolerance of juvenile *C. chinensis* to air exposure in a series of field and laboratory experiments. Field experiments under mesic conditions indicated that this snail can survive exposure to air for at least 4 weeks. Larger juveniles were more resistant than smaller juveniles, an effect that was also observed in the laboratory during short-term (3–14 days) experiments. Tolerance of small juveniles to air exposure appeared to be unaffected by temperature, but was affected by humidity, with higher survival at 64% than 34% relative humidity (RH). Results from the current study suggest that *C. chinensis* is highly resistant to air exposure and

could be readily transported by boats moving between lakes, particularly in cool mesic environments. Since juvenile *C. chinensis* are common around the roots of emergent macrophytes, hitchhiking with boats should be particularly common with boats or trailers infested with aquatic plants.

Keywords *Bellamya* · Desiccation · Dispersal · Invasive species · Recreational boats · Tolerance to air exposure

Introduction

Biological invasions are a pervasive threat to the diversity and function of freshwater ecosystems worldwide (Kolar & Lodge, 2000). Because established invaders are generally difficult or impossible to eradicate (Simberloff, 2003), understanding the causes of introductions is important. Most recent introductions of exotic species are linked to the actions of humans (Mills et al., 1993), through various transport mechanisms (Carlton, 1993; Havel & Shurin, 2004; Padilla & Williams, 2004). Invasive molluscs provide good examples of this link to humans. Molluscs are generally poor dispersers into inland waters, at least on a coarse geographic scale (Dillon, 2000). Nevertheless, following long-distance transport, dreissenid mussels and *Corbicula* readily invaded North America (Strayer, 1999). Some freshwater snails are also invasive. Tracking agencies list

Guest editors: H.J. Dumont, J.E. Havel, R. Gulati & P. Spaak /
A Passion for Plankton: a tribute to the life of Stanley Dodson

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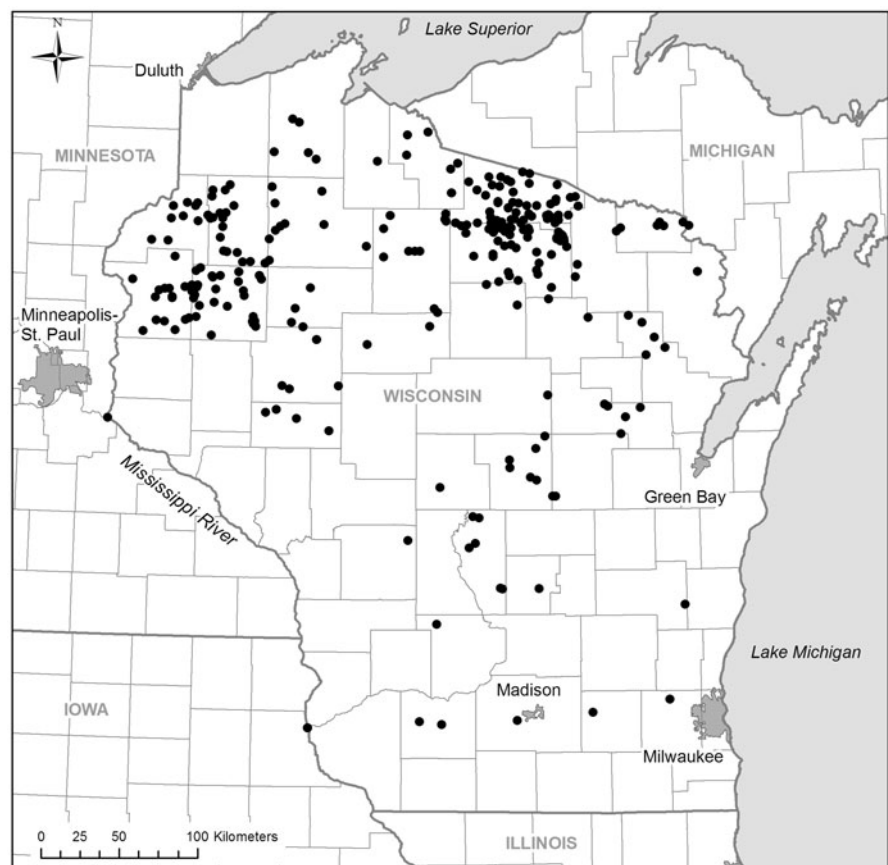
88 species of nonindigenous snails, including 24 species invading the freshwaters of the United States (USGS, 2010).

The most widespread of these exotic snails is the Chinese mystery snail (*Cipangopaludina chinensis malleata* Gray 1863). This species has also been called *Bellamya chinensis* (Smith, 2000). Since the nomenclature is still uncertain, for this article, I use the name in most common usage (Turgeon et al., 1998). Like other viviparids, *C. chinensis* is a live bearer and continuously releases small numbers of fully formed embryos over its 5-year life span (Stanczykowska et al., 1971; M. Lenhardt and J. Havel, unpublished data). This snail invaded North America following its introduction for Asian food markets in San Francisco (Wood, 1992) and dispersal elsewhere in California (Clench & Fuller, 1965). *C. chinensis* has since spread throughout North America, being reported in 34 states and 2 Canadian provinces (USGS, 2010). The species first appeared

in Wisconsin in the 1950s (Teskey, 1954) and has since become prevalent in the northern part of the state (Solomon et al., 2009; J. Havel, unpublished data). As of 2009, the Chinese mystery snail had been reported from 260 lakes and rivers in Wisconsin (Fig. 1). This species is of concern because of its occasional high abundance (Karayatev et al., 2009; Solomon et al., 2009; J. Havel, personal observation), potential for competition with native snails (Johnson et al., 2009), and its role as an intermediate host for human intestinal parasites (Michelson, 1970).

Humans can introduce exotic snails by a variety of mechanisms. They may be stocked for food (Wood, 1992) or released from aquaria and aquaculture facilities (Padilla & Williams, 2004). Numerous tropical species have been linked to aquarium releases (reviewed in USGS (2010)). As a case in point, the Chinese mystery snail is available through numerous web sites, which sell the species as a grazer of algae in aquaria and water gardens (Clark, 2009). Recreational

Fig. 1 Distribution of lakes containing Chinese mystery snails in Wisconsin USA. Data through 2009 were compiled by Wisconsin Department of Natural Resources and the map was prepared by Patrick Womble



boaters may also transmit invasive snails, such as has been demonstrated for aquatic macrophytes (Johnston et al., 1985), zebra mussels (Johnson & Carlton, 1996), and zooplankton (Havel & Stelzleni-Schwent, 2000). Consistent with boater transport are survey data that show the presence of boat landings to increase the chance of detecting invasive species (including snails) in Wisconsin lakes (Johnson et al., 2008; Solomon et al., 2009). Despite intensive educational campaigns targeted at boaters, recent surveys show that large numbers of boats and trailers continue to carry attached macrophytes (15% of 50,039 boats surveyed, http://www.uwsp.edu/cnr/uwexlakes/cbcw/CBCWbehaviortrends_2009.pdf).

Boats may carry invertebrates that are entangled in these macrophytes.

This study was designed to simulate conditions for overland dispersal of *C. chinensis* by boats. To determine their tolerance of drying, I exposed *C. chinensis* juveniles to air under different environmental conditions. I was interested in determining: (1) how long these juveniles can survive air exposure out of water, (2) how temperature affects tolerance to air exposure, (3) how humidity affects tolerance to air exposure, and (4) how snail size affects tolerance to air exposure.

Methods

Experiments testing the tolerance of *C. chinensis* to air exposure were conducted both outdoors at Trout Lake Station (University of Wisconsin, Vilas County, WI, 46.00°N, 89.75°) during August 2009 and June–July 2010 and in the laboratory (Missouri State University) during January–April 2010.

A total of 680 juvenile snails were used in the experiments. Snails for field experiments were collected from West Plum Lake (Vilas County, Wisconsin). Because *C. chinensis* is much less common in Missouri, experimental subjects for the Missouri laboratory experiments were offspring from snails cultured in the laboratory. Brood mothers for laboratory experiments (exps. 2–5) were collected from Swope Park Lagoon (Kansas City, Missouri). Snails were maintained in 38-l aquaria with bubbling air, and a maximum of 20 adults per aquarium. Water for Missouri cultures came from well water (34 mg Ca l⁻¹). Water was exchanged once every week.

Snails were fed flake fish food ad libitum every 1–2 days. Offspring were kept in the brood aquaria until tested. For each experiment, snails were isolated from the field or the brood aquarium, measured with digital calipers (± 0.01 mm), and randomly allocated to treatments. To avoid selecting dead snails, I only used snails that were clearly adhered to the holding chambers. Shell length was measured from the tip of the apex to the posterior edge of the aperture (Brown, 2001). The smallest size classes of Chinese mystery snail used in experiments (6–8 mm) were <1 week old, whereas the largest (25 mm) correspond to snails near the end of their first year of growth (Stanczykowska, 1971).

The general procedure for each air-tolerance experiment was to expose snails to drying conditions and then reintroduce them to water and later count the number of survivors for that endpoint. During air exposure, snails typically pulled back into their shells with the operculum shut. Following rehydration, snails took some time to show activity. Snails were observed at 2 and 24 h after rehydration and classified as alive if they showed activity at either post-hydration time. Observable activities that indicated viability included extending the antennae and showing probing movements, extending the foot and showing mobility along the bottom of the container, and showing responsiveness to the touch of a probe, typically by quickly withdrawing into the shell. A snail showing only an extended foot could not be classified as alive, since upon death, relaxation of the columellar muscle causes the foot to extend. Because snails had to be rehydrated to test viability, separate batches of snails were tested for each time endpoint. Testing viability by gently prying the operculum (Darby et al., 2008) was impractical because the shells of smaller size classes were too fragile (personal observation).

Field experiments were designed to estimate time to death of snails under conditions mimicking macrophytes caught on boats. During air exposure, snails were held in mesh bags (3-mm diameter openings), with 20 snails individually held in separate bags. For experiments with multiple size classes, one snail of each size class was placed into each bag. Bags were suspended in the air under shade of a mixed hardwood forest (average mid-day light level in July = $62 \mu\text{mol m}^{-2} \text{s}^{-1}$). Conditions of the three field experiments are shown in Table 1. Local climate data were provided by the US National Weather

Table 1 Conditions and summary results of field experiments on the effects of air exposure in Chinese mystery snails

Experiment	Start date	Environmental conditions ^a			Survivorship (%) by time endpoint (days)			
		Temp. (°C)	RH (%)	SL (mm)	7	14	21	28
1	7 Aug 2009	17 (4, 31)	73 (–)	25.4 (19, 31)	100	95	–	–
6	3 Jun 2010	17 (2, 30)	75 (28–100)	6.9 (6, 9)	5	10	–	–
				19.1 (15, 23)	95	95	–	–
				25.1 (23, 29)	100	100	–	–
7	17 Jun 2010	21 (8, 30)	73 (33–100)	25.6 (22, 31)	–	90	95	75

Ranges are shown in parentheses. In experiment 1, 100% survival was observed at 1, 2, 3 days endpoints. Different batches of 20 snails were used for each size class and time endpoint

Temp air temperature, RH relative humidity, SL shell length; –, no data

^a Temperature and humidity data for Rhinelander, Wisconsin, from National Weather Service climate data web site (www.weather.gov/climate)

Service (www.weather.gov/climate/), using data for Rhinelander, Wisconsin (ca. 40 km from Trout Lake Station). August 2009 was generally moderate in temperature (17°C, range 4–31°C) and humid (71% relative humidity, RH), with measurable rainfall on 16 days. June and July 2010 were similarly mesic (18.7°C, range 2–30°C, 75% RH).

Laboratory experiments tested the effects of different environmental factors on survivorship to air exposure (Table 2). The first lab experiment (exp. 2) was conducted at ambient room conditions with indirect cool fluorescent lighting. Conditions in the lab were generally warmer and less humid than in

outdoor experiments and lab-reared snails were considerably smaller than those used in the outdoor experiments. Subsequent laboratory experiments (exps. 3–5) examined the effects of temperature, humidity, and snail size on survivorship in air exposure. These experiments were run in growth chambers (Precision Scientific Low Incubator model 815), with controlled temperature ($\pm 1^\circ\text{C}$) and dim fluorescent light. For experiments with humidity as a treatment (exps. 4–5), RH was increased in one incubator by adding pans of water.

Inferences about differences in survivorship between treatment groups were based on Chi Square

Table 2 Conditions and results of laboratory experiments on the effects of air exposure in Chinese mystery snails

Experiment	Start date	Environmental conditions			Survivorship (%) by endpoint time (days)		
		Temp. (°C)	RH (%)	SL (mm)	3	7	14
2	14 Jan 2010	24	49	7.8	–	30	5
3	27 Jan 2010	15	27	7.3	45	5	–
		21	25	7.3	45	20	–
		25	31	7.3	25	5	–
4	17 Feb 2010	20	34	7.0	30	0	0
		20	64	7.0	60	25	15
5	8 Apr 2010	20	71	6.4	40	–	–
				9.1	80	–	–
				12.2	95	–	–
		20	38	6.4	15	–	–
				9.1	80	–	–
				12.2	95	–	–

Abbreviations as in Table 1. The treatment factors of interest are temperature (experiment 3), humidity (experiment 4), and relative humidity and size (experiment 5). Different batches of 20 snails were used for each time endpoint

tests of independence or with Fisher Exact tests for two group comparisons, when expected cell frequencies were too low (<5.0) for χ^2 analysis.

Results

The three field experiments indicated that juvenile *C. chinensis* were highly resistant to air exposure (Table 1). Experiments 1 and 6 revealed that large juveniles (25 mm) can survive air exposure for at least 2 weeks, and experiment 7 extended this endpoint to 4 weeks, when 75% of the snails survived out of water. All these field experiments were conducted in northern Wisconsin, where conditions were moderate and humid (Table 1). Taken together, these results suggest that, under similar environmental conditions, large juveniles of Chinese mystery snails can survive at least 4 weeks out of water.

Smaller snails were more sensitive to air exposure than larger snails. In the second field experiment (#6) with three size classes the smallest size class had a 10% survival to 2 weeks, while the two larger size classes had survival of 95–100% (Table 1). Size was confirmed to be important in the laboratory, where the smallest juveniles were more sensitive to air exposure (lower survivorship) than the larger juveniles (Table 2: experiment 5). This pattern was statistically discernable at both high and low humidities ($\chi^2 = 15.923$, $P < 0.001$, $\chi^2 = 31.148$, $P < 0.001$, respectively).

The laboratory experiments also examined effects of temperature and humidity on resistance to air exposure (Table 2). In experiment 3, temperature had no discernable effect on survivorship after 3 days ($\chi^2_{2df} = 2.256$, $P = 0.324$) or after 7 days (Fisher exact test, $P = 0.263$), and no general trend with temperature is apparent (Table 2). In experiment 4, survivorship tended to be higher at the higher humidity treatment for all three time endpoints, but statistically discernable only after 7 days (Fisher exact test, $P = 0.036$) and marginally significant after 3 days ($\chi^2_{2df} = 3.636$, $P = 0.057$). In experiment 5, survivorship tended to follow the same trend for the smallest size class of snails, with the trend being marginally significant ($\chi^2_{2df} = 3.135$, $P = 0.077$). Interestingly, the two larger size classes had no measurable response to the different humidity treatments after 3 days (Table 2).

Discussion

I observed that Chinese mystery snails are highly resistant to air exposure, with the majority of individuals surviving 4 weeks exposure. Sensitivity to air exposure was dependent on size, with larger juveniles being considerably more resistant than smaller juveniles. In short-term experiments, small juveniles had reduced survival to air exposure at lower humidity, whereas no such effect was evident for larger juveniles. Larger juveniles also had no significant response to differences in temperature, although the small group sizes (20 individuals) resulted in large confidence intervals for survival estimates and hence small statistical power for discriminating differences. Nevertheless, the overall high resistance of *C. chinensis* to air exposure is robust to environmental conditions, within the range of this study (15–25°C, 34–64% RH).

The tolerance of Chinese mystery snails to air exposure tends to be higher than that of other aquatic snails (Table 3). Exceptional are the apple snails (e.g., *Pomacea paludosa*), which are common in subtropical and tropical wetlands and must endure long periods of drying in the mud (Darby et al., 2008). Other apple snails (*Pomacea* and *Pila*) are known to survive 3–25 months aestivation (Coles, 1968; Cowie, 2002).

Since Chinese mystery snails can survive for long periods of air exposure, these snails are likely to survive transport between lakes on overland vectors such as trailered boats. Although we do not yet have access to surveys for snails carried on boats, several indirect data sources are consistent with boats as vectors. First, the presence of a boat landing was a significant predictor of both *C. chinensis* (Solomon et al., 2009) and other aquatic invasive species in Wisconsin lakes (Johnson et al., 2008). Of course, we have to be careful with interpreting such survey data, as other lake attributes are correlated with boater access. Lakes with improved boat launches also tend to be more common lower in the landscape (Capelli & Magnuson, 1983), larger in area (Kratz et al., 2006), and higher in dissolved solids (Webster et al., 1996). A second source of indirect data on the association between Chinese mystery snails and boats is the distribution of this snail within lakes relative to position of boat launches. In an earlier study of 42 northern Wisconsin lakes with snails, Solomon et al.

Table 3 Tolerance to air exposure reported for freshwater snails

Species (Family)	Size	Location	Temp (°C)	RH (%)	LT ₅₀ (d)	Reference
Prosobranchia						
<i>Pomacea paludosa</i> (Ampullaridae)	L	Field	38 ^a	?	98	Darby et al. (2008)
<i>Pomacea paludosa</i> (Ampullaridae)	S	Field	38 ^a	?	21	Darby et al. (2008)
<i>Melanoides tuberculata</i> (Thiaridae)	L	Lab	25 (–)	80 (–)	5–20	Facon et al. (2004)
<i>Melanoides tuberculata</i> (Thiaridae)	S	Lab	25 (–)	80 (–)	<0.1–0.6	Facon et al. (2004)
<i>Melanoides tuberculata</i> (Thiaridae)	L	Lab	25 (24–26)	65 (60–70)	5.5	Dudgeon (1981)
<i>Thiara scabra</i> (Thiaridae)	L	Lab	25 (24–26)	65 (60–70)	2.5	Dudgeon (1981)
<i>Sinotaia quadrata</i> (Viviparidae)	L	Lab	25 (24–26)	65 (60–70)	12.5	Dudgeon (1981)
<i>Cipangopaludina chinensis</i> (Viviparidae)	M	Field	21 (8–30)	73 (37–100)	>28	This study
<i>Cipangopaludina chinensis</i> (Viviparidae)	S	Lab	20 (19–22)	38 (33–42)	>3	This study
Pulmonata						
<i>Lymnaea columella</i> (Lymnaeidae)	L	Lab	16 (15–17)	85 (80–90)	2.0	Harris & Charleston (1977)
<i>Lymnaea columella</i> (Lymnaeidae)	S	Lab	16 (15–17)	85 (80–90)	0.1	Harris & Charleston (1977)
<i>Lymnaea natalensis</i> ((Lymnaeidae)	L	Field	– (4–35) ^b	25 (–) ^b	<7	Cridland (1967)
<i>Physella integra</i> (Physidae)	?	Lab	20 (–)	58 (–)	0.3	Tucker et al. (1996)
<i>Biomphalaria pfefferi</i> (Planorbidae)	L	Field	– (3–35) ^b	– (14–24) ^b	7–14	Cridland (1967)
<i>Bulinus globosus</i> (Planorbidae)	L	Field	– (7–29) ^b	31 (–) ^b	<4	Cridland (1967)

Tolerance expressed as median time to lethality (LT₅₀). Size classes: *S* small, *M* medium, *L* large; for *Cipangopaludina chinensis*, *S* and *M* correspond to juveniles ca. 12 and 25 mm, respectively. Range in parentheses. Facon et al. (2004) used multiple clones of *Melanoides tuberculata*. Species ordered by family, within subclass

Temp temperature, RH relative humidity

^a Environmental conditions not given; temperature estimated from seasonal data in Darby et al. (2003)

^b Environment on the surface of dried mud

(2009) found *C. chinensis* to be widespread (21 lakes) and were more likely to occur at sites near launches than at sites more distant from launches. If the snails are moving slowly from their points of introduction as has been observed for invasive rusty crayfish (Wilson et al., 2004), then such a pattern is consistent with boaters as the source of colonizing snails. However, boat launches are also a likely place for aquarium dumping because of their ease of access, so transport by this alternate vector may also be occurring. A final link to recreational boats is direct surveys, which have revealed boats to carry live zebra mussels (Johnson & Carlton, 1996) and zooplankton (Havel & Stelzleni-Schwent, 2000). Thus, boater transport of aestivating snails seems quite plausible.

The process of boater transmission of invasive invertebrates may be particularly common with boats infested with macrophytes. Recent surveys reveal that, despite intensive efforts in public education, large numbers of boats arriving at Wisconsin lakes are infested with macrophytes. For instance, of

50,039 boats that were inspected in 2009, 15% of the boats were infested and 25% had been at another water body in the last 5 days (http://www.uwsp.edu/cnr/uwexlakes/cbcw/CBCWbehaviortrends_2009.pdf). Attachment to macrophytes has been recognized previously as a threat for transmission of zebra mussels (Johnson & Carlton, 1996). Chinese mystery snail juveniles are common among the roots of macrophytes (J. Havel, personal observation) and are present in rake samples of macrophytes (E. Vennie-Volrath, personal communication). The 4-week survival of larger juveniles to air exposure (Table 1) easily exceeds the 5-day interval for boats moving between lakes.

High resistance to air exposure can also be important for population persistence. Snails live in shallow water and sometimes get stranded on land by drought (Extence, 1981; Darby et al., 2008) and reservoir drawdowns (Jobin, 1970). Deliberate manipulation of water levels has been used as a tool for controlling snails that are intermediate hosts of

parasites (Cridland, 1967) or agricultural pests (Cowie, 2002). A high tolerance to air exposure would make this method impractical for some snail species. Population persistence is critically important in biological invasions. Improved survivorship reduces the risk of stochastic extinction events, which are more likely when populations are small or few in number (Shaffer, 1981), a situation that occurs early in an invasion.

My experiments revealed that small juveniles of *C. chinensis* were considerably more sensitive to air exposure than larger juveniles (Table 2). A similar pattern has been observed in other studies of air exposure tolerance in snails (Harris & Charleston, 1977; Dudgeon, 1981; Darby et al., 2008). This difference in susceptibility with size makes sense on the basis of allometry and physiology, as more water should be lost with greater aperture surface area to body volume for smaller snails. The particular cause of mortality (desiccation, starvation, anoxia) is not yet known. The implication for dispersal is that the smallest sizes, which are probably easiest to be carried on macrophytes, are at the greatest risk of dying during transport. Thus, it seems likely that there is an intermediate optimum for size of dispersing individuals.

Survivorship in the field experiments may have been enhanced by the cool mesic conditions of northern Wisconsin. Nevertheless, lab experiments suggest larger *C. chinensis* to have high survival even at relative humidities <40% (Table 2). Although we lack data for field exposures under more warmer and more-arid conditions, we would expect water losses to be higher and thus survivorship to be poorer. Consistent with this expectation is the distribution pattern of Chinese mystery snails in Texas, which was invaded 45 years ago and yet has shown little spread in the state (Karatayev et al., 2009).

The broad distribution of *C. chinensis* across the United States (USGS, 2010) and its high prevalence in Wisconsin (Solomon et al., 2009) and in other regions suggest that this exotic snail has a high capacity for overland dispersal. My results show that the mechanism for such dispersal may involve a high tolerance of air exposure by snails hitchhiking with recreational boats. The high population abundance of these large snails in some lakes suggests that the species has the potential to impact lake community and ecosystem functions. Understanding dispersal mechanisms is important for interrupting the spread

of invasive species. Changing human behavior, such as by encouraging removal of macrophytes, may reduce the spread of Chinese mystery snails as well as other invasive species of concern.

Acknowledgments This research was conducted at the University of Wisconsin Trout Lake Station, while I was supported by a faculty sabbatical leave from Missouri State University. I thank Meghan Lenhardt and Whitney Kelley for assistance with experiments and Pam Montz and the other TLS staff for making my stay at the station enjoyable and productive. Rob Dillon confirmed identity of the snails and Jennifer Filbert (Wisconsin Department of Natural Resources) provided the compiled list for Wisconsin lakes invaded by Chinese mystery snails. I am also grateful to John Magnuson, Jake Vander Zanden, Chris Solomon, and Chris Barnhart for comments on drafts of this paper, and the JVZ lab group for interesting discussions about invasive species in lakes. This article is dedicated to the memory of my mentor and friend, Stanley Ivan Dodson.

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